The evolution of pelvic aspiration in archosaurs

David R. Carrier and Colleen G. Farmer

Abstract.—Movements of the pelvic girdle have recently been found to contribute to inspiratory airflow in both crocodilians and birds. Although the mechanisms are quite different in birds and crocodilians, participation of the pelvic girdle in the production of inspiration is rare among vertebrates. This raises the possibility that the pelvic musculoskeletal system may have played a role in the ventilation of basal archosaurs. Judging from 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 abdominal cavity. From this basal mechanism, several archosaur lineages appear to have evolved specialized gastralia, pelvic kinesis, and/or pelvic mobility. Kinetic pubes appear to have evolved independently in at least two clades of Crocodylomorpha. This convergence suggests that a diaphragmatic muscle may be basal for Crocodylomorpha. The pelvis of pterosaurs was long, open ventrally, and had prepubic elements that resembled the pubic bones of Recent crocodilians. These characters suggest convergence on the pelvic aspiratory systems of both birds and crocodilians. The derived configuration of the pubis, ischium and gastralia of non-avian theropods appears to have enhanced the basal gastral breathing mechanism. Changes in structure of the pelvic musculoskeletal system that were present in both dromaeosaurs and basal birds may have set the stage for a gradual reduction in the importance of gastral breathing and for the evolution of the pelvic aspiration system of Recent birds. Lastly, the structure of the pelvis of some ornithischians appears to have been permissive of pubic and ischial kinesis. Large platelike prepubic processes evolved three times in Ornithischia. These plates are suggested to have been instrumental in an active expansion of the lateral abdominal wall to produce inspiratory flow. Thus, many of the unique features found in the pelvic girdles of various archosaur groups may be related to the function of lung ventilation rather than to locomotion.

David R. Carrier. Department of Biology, University of Utah, Salt Lake City, Utah 84112. E-mail: carrier@biology.utah.edu

Colleen G. Farmer. Department of Ecology and Evolutionary Biology, University of California, Irvine, California 92697. E-mail: cfarmer@uci.edu

Introduction

Basal archosaurs are generally believed to have pumped air in and out of their lungs through the active movements of their ribs. The axial muscles are thought to have rotated the ribs cranially and laterally, increasing thoracic volume to produce inspiration, and to have rotated the ribs caudally and medially, decreasing thoracic volume to produce expiration. Indeed, analysis of extant tetrapods suggests that this type of costal aspiration was present in the earliest amniotes and was likely to have been the primary ventilatory mechanism of basal amniotes (Liem 1985; Carrier 1989; Brainerd et al. 1993). To this basal mode of ventilation several groups have added mechanisms that serve an accessory role, such as gular pumping in some lizards (Owerkowicz et al. 1999) or mechanisms that have come to function as a primary pump, such as the di-

aphragm of mammals and the ''diaphragmatic'' and pectoral mechanisms of turtles (Gans and Hughes 1967; Gaunt and Gans 1969).

Among archosaurs, the lineage that gave rise to crocodilians also evolved a secondary ventilatory mechanism (Fig. 1) that uses a hepatic piston driven by a diaphragmatic muscle (Boelaert 1942; Naifeh et al. 1970; Gans and Clark 1976). In Recent crocodilians, diaphragmatic breathing appears to be the primary mechanism of aspiration (Gans and Clark 1976). Modifications of the basal ventilatory system also occurred in the lineage that gave rise to birds (Fig. 1). In birds, contraction of the intercostal muscles causes a ventral rotation of the sternum (Zimmer 1935). Most of the inspiratory change in volume of the body cavity results from this ventral expansion, rather than the lateral expansion observed in most amniotes. Thus, Recent crocodilians breathe
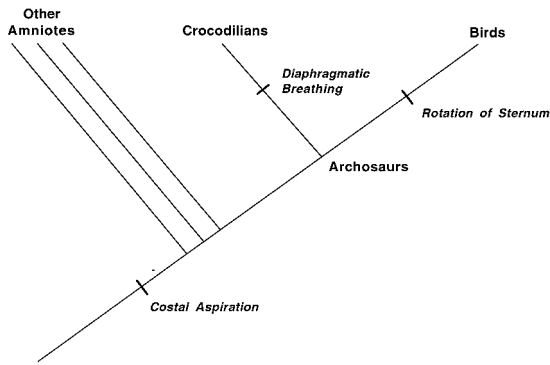
FIGURE 1.   Phylogeny of extant archosaurs showing the distribution of costal aspiration, diaphragmatic breathing, and rotation of the sternum for ventilation.

with costal and diaphragmatic aspiration, whereas birds use a modified form of costal aspiration in which the sternum rotates dorsoventrally.

Recent observations in alligators and birds have led us to suspect that there is another component to the breathing of archosaurs that has been overlooked previously. Some crocodilians (Farmer and Carrier 2000a) and some birds (Baumel et al. 1990) appear to use movements of the pelvic skeleton to assist in pumping air in and out of their lungs. We call this pelvic aspiration because it involves kinesis of pelvic elements, or movement of the entire pelvis, in a manner that changes the volume of the coelomic cavity and thereby assists in the production of ventilatory airflow. The mechanisms of pelvic aspiration in crocodilians and birds are quite different from each other. Nonetheless, although the abdominal muscles associated with the pelvic girdle are known to play an important role in expiration, it is unusual among vertebrates for the pelvic musculoskeletal system to play an active role in inspiration. Galloping mammals (Bramble and Carrier 1983; Young et al. 1992) and some marsupials (T. White personal communication 1988) are the only other examples we are aware of in which the pelvis contributes to inspiration. Consequently, the presence of pelvic aspiration in both birds and crocodilians raises the possibility that the pelvis may have played an important role in the ventilation of the common ancestor of these two groups. Because the lineages that gave rise to crocodilians and birds are believed to have diverged very early in the history of archosaurs (mid-Triassic), a pelvic role in ventilation may have been a basal character of the class.

Here we review what is known of pelvic aspiration in extant crocodilians and birds. We then attempt to reconstruct the primitive role of the pelvis in the breathing of archosaurs, and provide a speculative analysis of possible mechanisms of pelvic aspiration in selected extinct archosaurs. Our analysis suggests that the pelvic musculoskeletal system of basal archosaurs aided costal aspiration in the production of inspiration, but the basal archosaur pelvis was not kinetic and did not move to change the volume of the body cavity. Nevertheless, from its 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.

Pelvic Aspiration in Extant Archosaurs

Crocodilians.—In addition to using costal and diaphragmatic mechanisms of ventilation, crocodilians have recently been shown to use a pelvic mechanism that rotates the pubic bones dorsoventrally to change the volume of the abdominal cavity (Farmer and Carrier 2000a). 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. 2A). 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 (most caudal) gastralia. Activity of these muscles is associated with a ventral rotation of the pubic bones, a drop in intra-abdominal pressure, and inspiratory airflow. Ventral rotation of the pubic bones expands the posterior abdominal cavity, presumably to provide space for the caudal displacement of the viscera by the diaphragmatic muscle during inspiration. During expiration, contraction of the rectus ab-

A

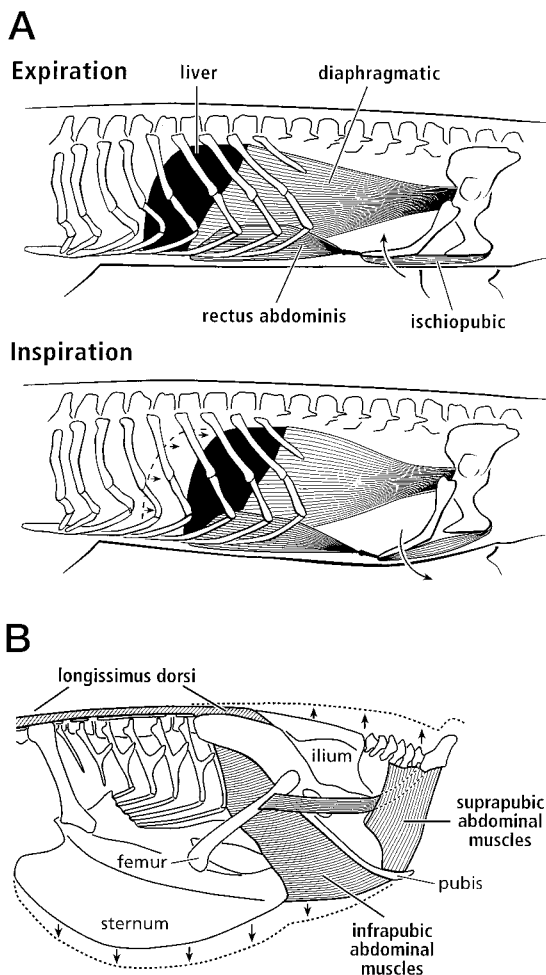**Expiration**

Inspiration

B

FIGURE 2. Illustrations of the mechanisms of ventilation in the American alligator and the pigeon. A, In alligators, expiration is produced by caudal rotation of the ribs and constriction of the abdominal cavity, which produce a cranial translation of the viscera. Constriction of the abdomen results from activity of the transversus abdominis muscle and the rectus abdominis muscle, the latter of which rotates the pubes dorsally. Inspiration is produced by cranial rotation of the ribs and caudal translation of the viscera. The viscera are pulled caudally by contraction of the diaphragmaticus muscle. The ischiopubic muscle increases the volume of the posterior abdomen by rotating the pubes ventrally. From Farmer and Carrier 2000a. B, During inspiration in pigeons the sternum rotates ventrally (ventrally pointing arrows) and activity of the longissimus dorsi muscle elevates the pelvic girdle on the dorsal vertebrae (dorsally pointing arrows). During expiration, activity of the suprapubic abdominal and infrapubic abdominal muscles depresses the pelvis and tail. Modified from Baumel et al. 1990.

dominis and transversalis muscles draws the pubic plates dorsally, decreasing abdominal volume. This apparently helps to shift the viscera cranially, decreasing thoracic volume. Thus, the highly derived pelvis of crocodilians, in which the pubic bones are separated from the acetabulum and form movable joints with the ischia, appears to play a role in lung ventilation. Furthermore, two pelvic muscles that originate on the ischia and insert on the cranial end of the pubes and the last two gastralia function in the production of inspiration.

Another factor that associates the pelvic musculoskeletal system of crocodilians with the function of inspiration is the diaphragmatic muscle. As explained above, this muscle originates on the pelvic girdle and posteriormost gastralia. Rather than receiving its innervation from a series of spinal nerves that correspond to its location in the body, as do hypaxial muscles such as the rectus abdominis and transversalis, the diaphragmaticus is innervated via its caudal end by branches of the twenty-second and twenty-third spinal nerves (Nishi 1938). These spinal nerves contribute to the lumbo-sacral plexus, and it is branches from the plexus that innervate the diaphragmatic muscle (Carrier unpublished observation). Both its origin and innervation suggest that the diaphragmaticus is derived from muscles associated with the pelvis, possibly the caudalmost segment of the rectus abdominis muscle or the ischiotruncus muscle. Thus, the diaphragmaticus is an inspiratory muscle that appears to be part of the pelvic musculoskeletal system.

Birds.—Baumel (1988) observed that the tail moves during vocalization of some birds (e.g., crows, warbling vireos, and lovebirds). These observations led Baumel et al. (1990) to study the role of the pelvic and tail musculature in the ventilation of pigeons. They found that in anesthetized pigeons, resting on their sternums, one of the epaxial muscles, the longissimus dorsi, was consistently active during inspiration. It elevated the pelvis at the notarial-synsacral joint and increased the volume of the thoracoabdominal cavity (Fig. 2B). Depression of the pelvis during expiration was attributed to the action of the infrapubic ab-

dominal muscles, which had previously been shown to be active during expiration (Kadano et al. 1963; Fedde et al. 1969). Baumel and his coworkers also found that three extrinsic tail muscles (the caudofemoralis, pubocaudalis externus, and pubocaudalis internus) and one suprapubic abdominal muscle (the transversus cloacae) were active during expiration. These muscles depress the tail and constrict the caudal abdominal wall, decreasing the volume of the thoracoabdominal cavity. Baumel and his collaborators speculated that in pigeons the ventilatory movements of the pelvis and tail may be important for ventilation when a bird is resting on its chest and possibly during flight.

Some evidence indicates that birds use pelvic aspiration during flight. Cineradiographic studies of black-billed magpies (*Pica pica*) showed that in some individuals the synsacrum rotates ventrally on the vertebral column 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 wingbeat cycle or the result of active recruitment of the axial muscles remains to be determined. Nevertheless, the timing of activity of the longissimus dorsi, levator caudae, and depressor caudae muscles (Gatesy and Dial 1993) and the pattern of ventilatory airflow (Boggs 1997) are consistent with the possibility that the pelvis is actively elevated and depressed to facilitate ventilation during flight in pigeons.

Cuirassal Breathing in Basal Archosaurs

The Pelvic Girdle.—Although the mechanisms of pelvic aspiration in crocodilians and birds are very different from each other, it is nevertheless 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 pelvis may have played a role in the ventilation of the common ancestor of these two groups. To provide a basis for a discussion of a potential involvement of the pelvis in inspiration of basal archosaurs, we briefly review
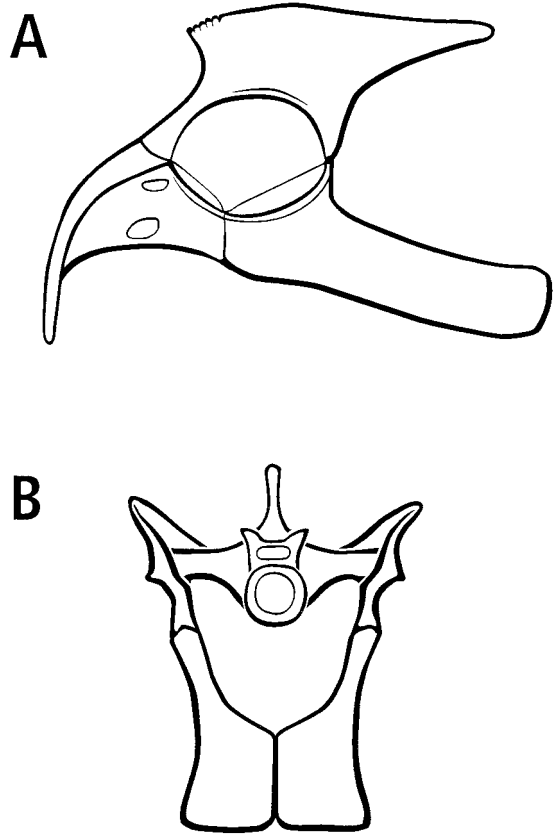

FIGURE 3. Structure of the pelvis of the basal archosaur *Euparkeria capensis*. A, Lateral view. All three bones meet in distinct sutures to form the acetabulum. B, Anterior view. The pubic bones are united ventrally to form an anteriorly facing apron. Modified from Ewer 1965.

the structure of the pelvic girdle of basal archosaurs.

Primitively, the three elements of the pelvis (ilium, ischium, and pubis) joined to form the acetabulum (Fig. 3). These bones were joined in broad, well-formed, joints. The ilium was relatively small and is thought to have been important as a site of attachment for axial muscles, but not particularly important as a site of attachment of limb muscles (Romer 1956). Below the acetabulum, the pubis and ischium formed a broad expanse of bone that faced ventrally and laterally and was a site for the attachment of limb muscles, most notably for the puboischiofemoralis externus muscle. Both the pubes and ischia met at the ventral midline to form a symphysis.

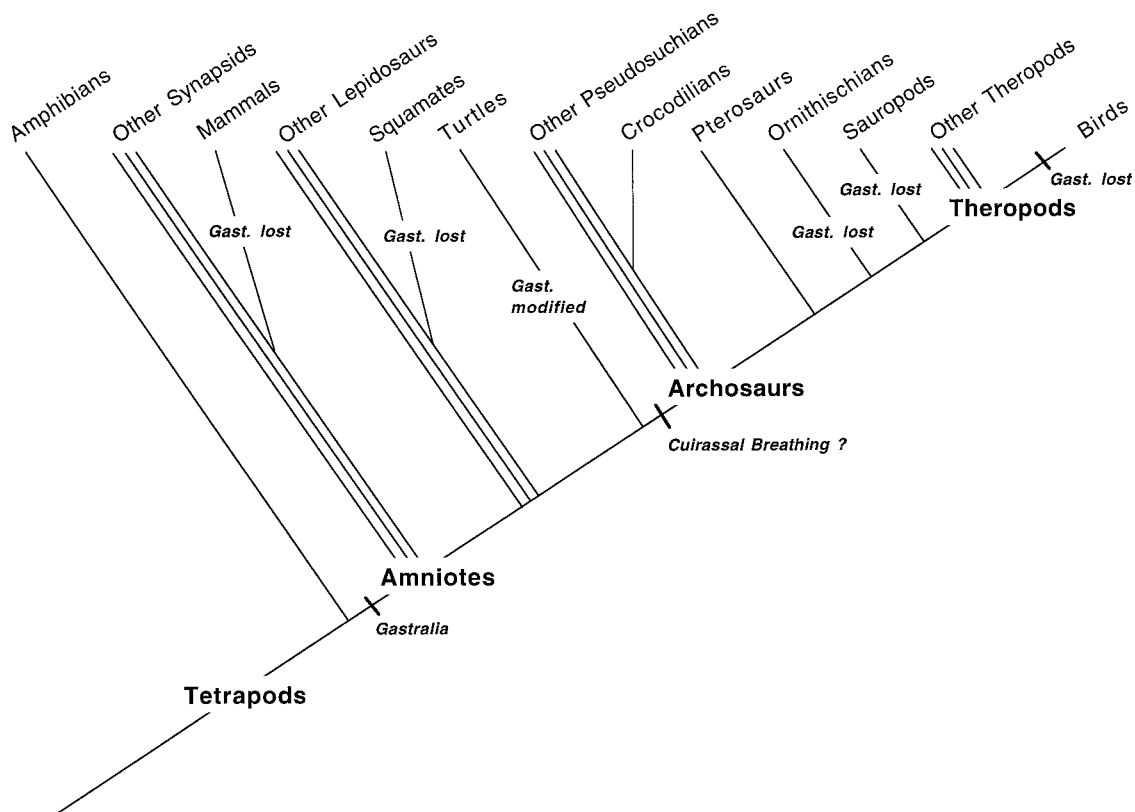The pelvic girdles of Recent crocodilians and birds are both highly derived. The pubis

FIGURE 4. Phylogeny of tetrapods showing the distribution of gastralia and our hypothesis (denoted by question mark) for the origin of cuirassal breathing in archosaurs. We suspect that the absence of gastralia in ornithischian and sauropod dinosaurs reflects the large gut mass of these animals rather than a loss of gastralia in the lineage that gave rise to dinosaurs. Phylogeny is compiled from Gauthier et al. 1988 and from Hedges and Poling 1999. Distribution of gastralia as described by Romer (1956) and Claessens (1997).

of Recent crocodilians is an elongated rod that is excluded from the acetabulum and extends forward from a movable joint with the ischium (Fig. 2A). In birds, the ilium is greatly expanded cranially and caudally, and both the pubis and ischium have rotated so that they project caudally and are aligned parallel to the caudal expansion of the ilium (Fig. 2B). Neither the pubes nor the ischia of birds meet ventrally. Given the highly derived pelvic girdles of crocodilians and birds, we cannot expect basal archosaurs to have had a ventilatory system that resembled the pelvic aspiration of either crocodilians or birds.

Cuirassal Breathing?—An ischiotruncus muscle that attached to the gastralia, similar to the arrangement in Recent crocodilians, could have functioned as a highly effective inspiratory pump in basal archosaurs. Gastralia are primitive for amniotes and appear to be ho-

mologous with the ventral body armor of basal Paleozoic tetrapods (Romer 1956) (Fig. 4). 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 lateral ends of the chevrons curve dorsally into the lateral hypaxial muscles. The function of gastralia has generally been associated with mechanical protection of the ventral body wall (Romer 1956), but several authors have suggested that gastralia may participate in lung ventilation (Lambe 1917; Perry 1983; Claessens 1996, 1997). Claessens (1996) proposed a ventilatory mechanism in theropods that involves the hypaxial muscles of the belly wall. We suspect that Claessens is cor-
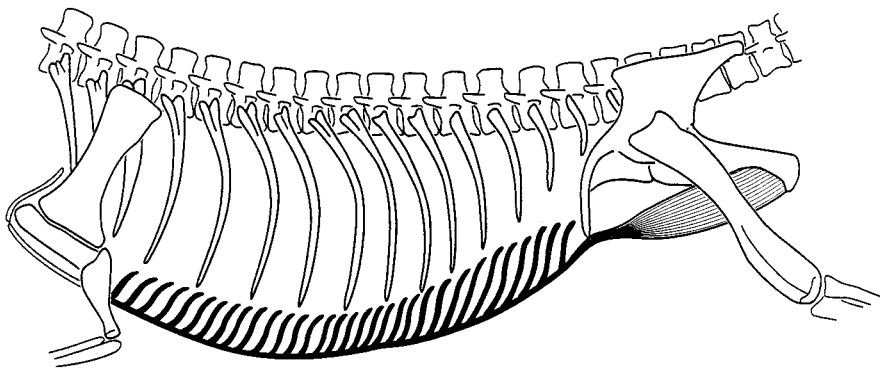
Expiration
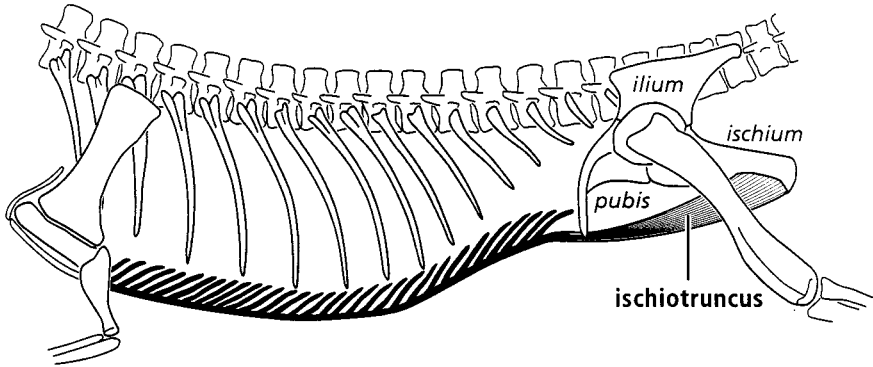
Inspiration

FIGURE 5.   Illustration of proposed cuirassal breathing mechanism in the archosauromorph *Euarkeria capensis.* During expiration, contraction of the rectus abdominis muscle pulled the medial portion of the gastralia anteriorly, causing an elevation of the ventral body wall. 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. Modified from Ewer 1965.

rect, but we also hypothesize that gastralia could have contributed to ventilation through the action of a parasagittally located ischio-truncus muscles that had the motor pattern observed in Recent alligators.

An ischiotruncus muscle that pulled the me-dial aspect of the gastralia caudally would function to swing the apex of the chevrons ventrally and thereby increase the volume of the abdominal cavity (Fig 5). Such a mecha-nism would be analogous to expansion of the buccal and gular cavities of fishes and many tetrapods by the hyobranchial (i.e., sternohy-oideus) muscles acting on the hyoid arches. If the lateral ends of the gastralia were anchored against caudal translation by hypaxial mus-cles, such as the external oblique muscle, a caudally directed force on the apex of the

chevrons would cause a caudoventral rotation. For this mechanism to work, the point of ro-tation (i.e., fulcrum) of the gastralia would have been located dorsally to the distal end of the pubes. This would have allowed the pubes to function as a guide that directed the mus-cular force so that a moment was applied to the fulcrum of the gastralia.

This mechanism, which we call cuirassal breathing, provides a plausible functional ex-planation for the architecture that character-izes gastralia in many taxa: rhynchosaurs (Romer 1956); basal archosauriformes such as *Euparkeria* (Romer 1956; Ewer 1965), and pseu-dosuchians (Colbert and Mook 1951; Crush 1984; Sereno 1991); pterosaurs (Wellnhofer 1978); and prosauropod and theropod dino-saurs (Lambe 1917; Claessens 1997). Thus,
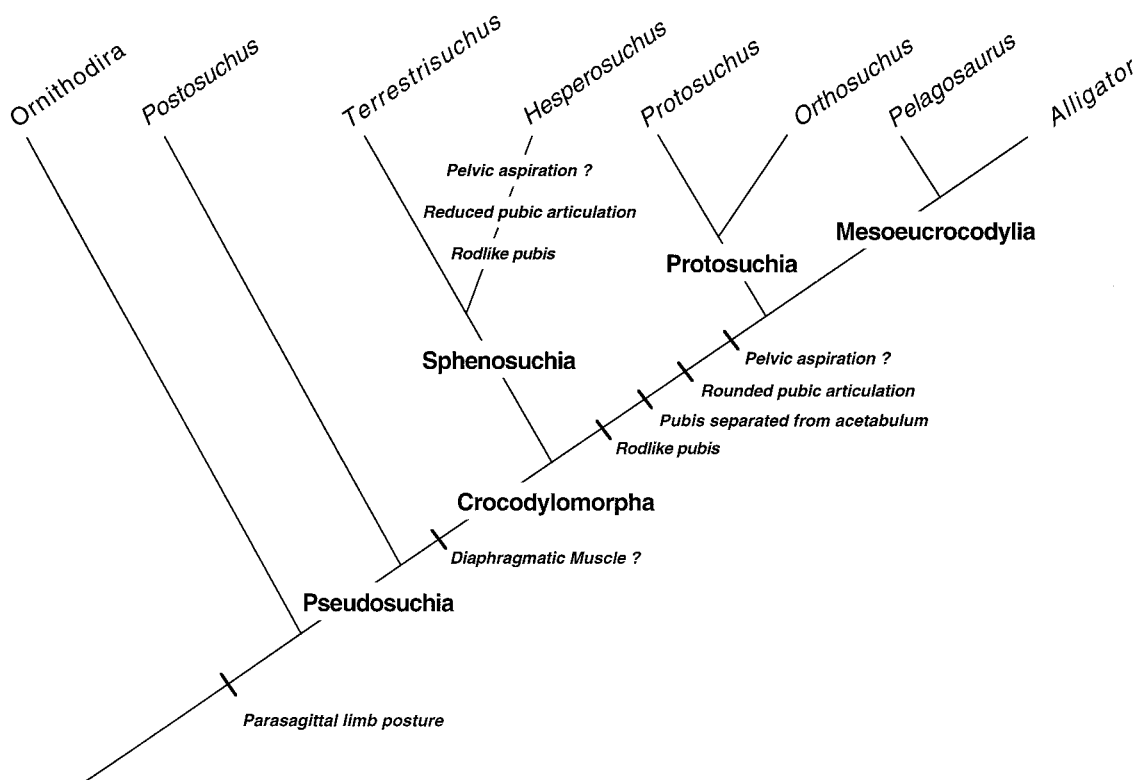
FIGURE 6. Phylogeny of Crocodylomorpha showing the distribution of characters associated with parasagittal limb posture and kinetic pubes, and our hypotheses (denoted by question marks) for the origins of a diaphragmaticus muscle and pelvic aspiration. Phylogenetic scheme follows that of Sereno and Wild (1992) and Wu et al. (1994). Distribution of characters is described and referenced in text.

judging from the inspiratory role of the pelvic musculoskeletal system in crocodilians, the function of the ischiotruncus muscle in crocodilians, and the presence of well-developed gastralia in basal archosauriforms such as *Euparkeria,* we suggest that basal archosaurs used cuirassal breathing (Fig. 4).

Crocodylomorpha

Three groups are recognized within the Crocodylomorpha: Sphenosuchia, Protosuchia, and Mesoeucrocodylia (Fig. 6) (Sereno and Wild 1992; Wu et al. 1994). The Poposauria, such as *Postosuchus* (Chatterjee 1985), are generally considered to be the sister group of the Crocodylomorpha (Wu et al. 1994). Basal Crocodylomorpha and their sister group, the Poposauria, were characterized by limbs that were long relative to those of Recent crocodilians (Cobert and Mook 1951; Crush 1984; Chatterjee 1985) and by parasagittal limb posture, as indicated by the following characters:

posteriorly directed glenoids (Chatterjee 1985; Benton and Clark 1988), posteriorly directed calcanei (Parrish 1987), bilaterally symmetrical feet (Chatterjee 1985; Benton and Clark 1988; Parrish 1991), supra-acetabular crests (Chatterjee 1985; Benton and Clark 1988), and fenestrated acetabula (Chatterjee 1985; Parrish 1991). In this analysis, we ask which members of Crocodylomorpha possessed a system of pubic kinesis similar to that of Recent crocodilians. We focus on members of Crocodylomorpha in which pelvic material is relatively well known: *Terrestrisuchus* and *Hesperosuchus* within the Sphenosuchia, *Protosuchus* and *Orthosuchus* within Protosuchia, and *Alligator* within Mesoeucrocodylia (discussed above).

Terrestrisuchus gracilis.—The pelvis of *Terrestrisuchus* was fairly typical of basal Pseudosuchia (Fig. 7). The ilium had a low profile and a laterally compressed anterior process (Crush 1984). The acetabulum was fenestrated and the bone that formed the medial wall of
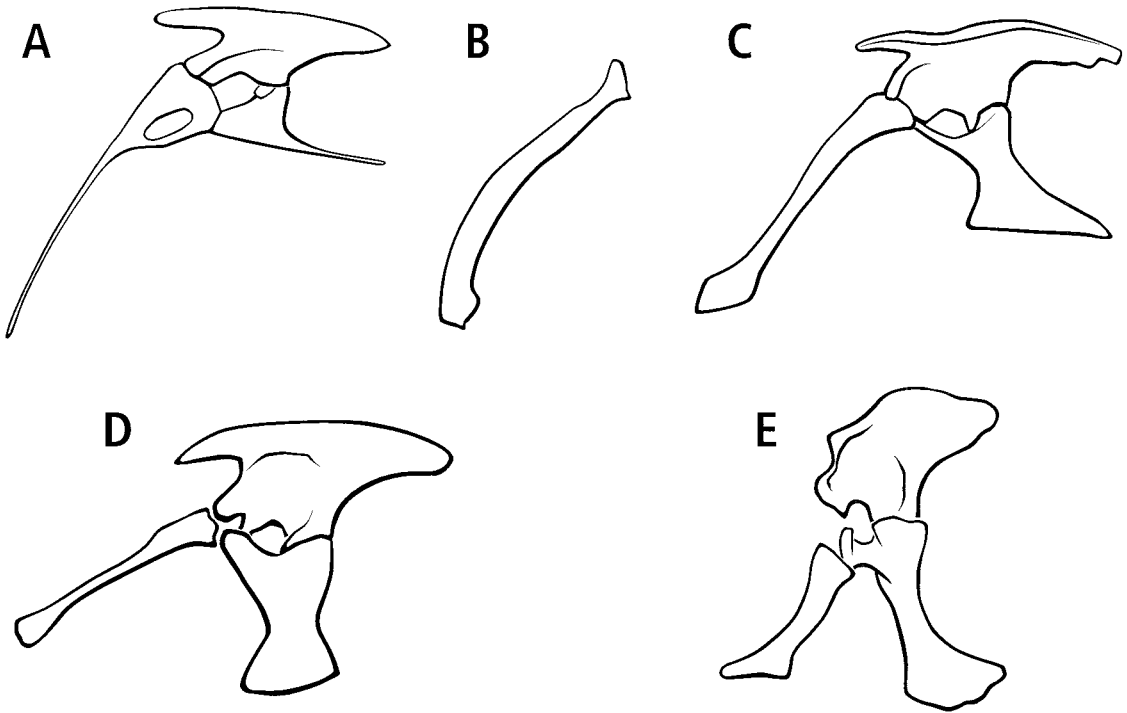
FIGURE 7.   Lateral views of the pelvic girdles of selected Crocodylomorpha. A, *Terrestrisuchus gracilis* (Crush 1984). B, *Hesperosuchus* (Parrish 1991). C, *Protosuchus richardsoni* (Colbert and Mook 1951). D, *Orthosuchus stormbergi* (Nash 1968). E, *Alligator* (Romer 1956).

the acetabulum was thin. The ilium was thickened where it articulated with the pubis and ischium. The pubis formed the anterior margin of the acetabulum; the anterior rami of the pubes joined medially and extended for a considerable distance anteroventrally to form a long, but typical, pubic apron. The ischial rami were shorter and projected caudally in the horizontal plane beneath the caudal expansion of the ilium. The gastralia were single ossifications that were broad, flattened, and V-shaped, and their lateral projections curved slightly dorsally (Crush 1984). Crush (1984) did not report the number of gastralia, but his reconstruction of *Terrestrisuchus* shows five elements adjacent to the distal end of the pubes.

Crush's reconstruction indicates that the pubes of *Terrestrisuchus* formed solid articulations with the ilia and ischia. This suggests that the pubic bones of *Terrestrisuchus* were not free to rotate as in Recent crocodilians. The elongate pubic apron and the V-shaped gastralia with dorsally curved distal ends lead us to suspect that *Terrestrisuchus* used a cuirassal breathing mechanism similar to what we suggest was present in basal archosaurs.

Hesperosuchus.—The pelvis of *Hesperosuchus* is represented by parts of both pubes from specimen UCMP 129740 (Parrish 1991). The right pubis is nearly complete, and the distal end of the left pubis is also preserved. The pubis of *Hesperosuchus* was nearly as long as its femur and was slightly recurved both ventrally and laterally (Fig. 7). The distal end was enlarged and had a dorsoventrally aligned groove that faced the ischium. The proximal articulation with the ilium and/or ischium, although not rounded, was much reduced in relative size from that seen in *Postosuchus* or *Terrestrisuchus.* The medial symphyseal regions of both pubes are missing, but there is some indication that *Hesperosuchus* had a thin pubic apron. Nevertheless, the pubes are much more rodlike in shape than those of *Terrestrisuchus.*

The most striking feature of the pubic bones of *Hesperosuchus* is the relatively small size of the proximal articulation with the pelvis. The

articular surface is similar both in size and shape to that of *Alligator* (Fig. 7) (see Romer 1923c). This small proximal end could not have contributed to the acetabulum in any significant way. Parrish (1991) suggests that the dorsoventrally aligned groove on the distal rugosity of the pubis served as the attachment site of a puboischiadic ligament. Alternatively, this groove may have been the attachment site of an ischiopubic muscle. Thus, pubic kinesis in *Hesperosuchus* seems very likely, given the shape and the small size of the pelvic articulation of the pubis. In fact, it is difficult to imagine how mobility of the pubes would have been avoided.

Protosuchus richardsoni.—The pelvis of *Protosuchus* differed from the basal configuration (i.e., that of *Postosuchus* and *Terrestrisuchus*) in at least three aspects that are relevant to our discussion of pelvic aspiration (Fig. 7). First, the acetabulum was formed primarily by the ilium and the ischium (Colbert and Mook 1951). The rounded proximal end of the pubis articulated with both the ilium and ischium, such that it formed only a small portion of the anterior margin of the acetabulum. Second, the pubis was elongated and had a rodlike shaft that curved medially. Distally the two pubes met along the midline in a flat expansion. Thus, the pubic apron that characterized basal archosaurs was not present. Third, the ischium was similar to that of Recent crocodilians, forming a ventrally directed expansion beneath the acetabulum. Thus, the pelvis of *Protosuchus* was similar to the pelvis of Recent crocodilians in most respects (Colbert and Mook 1951). *Protosuchus* also had gastralia that appear to have been concentrated near the distal end of the pubis (Colbert and Mook 1951).

Similarities between the pelvis and gastralia of *Protosuchus* and those of Recent crocodilians lead us to suggest that *Protosuchus* possessed the crocodilian mechanism of pubic kinesis. Although it is true that the pubis did articulate with both ilium and ischium and formed a small part of the acetabulum, there was nothing about the structure of these bones that would have precluded dorsoventral rotation of the pubes at the acetabula. The rodlike shape and distal expansion of the pubis,

as well as the concentration of gastralia near the pubes, resemble the configuration of Recent crocodilians and are consistent with the crocodilian mechanism in which the ischiopubic and ischiotruncus muscles shorten to rotate the pubes ventrally and caudally.

Orthosuchus stormbergi.—The pelvis of *Orthosuchus stormbergi* was remarkably similar in structure and appearance to that of Recent crocodilians (Nash 1968) (Fig. 7). The ischia were situated directly below the acetabula and were oriented vertically. The pubes were fully separated from the acetabula and had small rounded articular surfaces that made contact with rounded processes on the ilia and ischia. There was no fusion along the length of the pubes to form a pubic plate, although they may have met distally. All aspects of this pelvis lead us to propose that *Orthosuchus* possessed the mechanism of pubic kinesis observed in Recent crocodilians.

Evolution and Significance of Pubic Kinesis.— This analysis of pelvic anatomy suggests that pubic kinesis evolved independently at least twice in clades of Crocodylomorpha (Fig. 6). Assuming basal archosaurs used cuirassal aspiration to assist breathing, as suggested above, relatively small changes of pelvic structure would have been required to evolve the system of pubic kinesis present in Recent alligators. The pubic-pelvic joint had to change in a way that allowed pubic mobility, and the attachment site of the ischiotruncus muscle had to switch from the gastralia to the cranial end of the pubis. These two changes would have produced a system in which active rotation of the pubes would have expanded the abdominal cavity and could have assisted inspiration.

If the ancestors of Crocodylomorpha already had a system of cuirassal aspiration, why would they have switched to a system of pubic kinesis to accomplish the same function? We suspect that the main advantage of pubic kinesis is that it facilitates diaphragmatic breathing. Because the diaphragmaticus of Recent crocodilians envelops the abdominal viscera, it tends to pressurize the abdominal contents when it contracts. This could pose problems for effective venous return to the heart from the hindlimbs and tail (Farmer
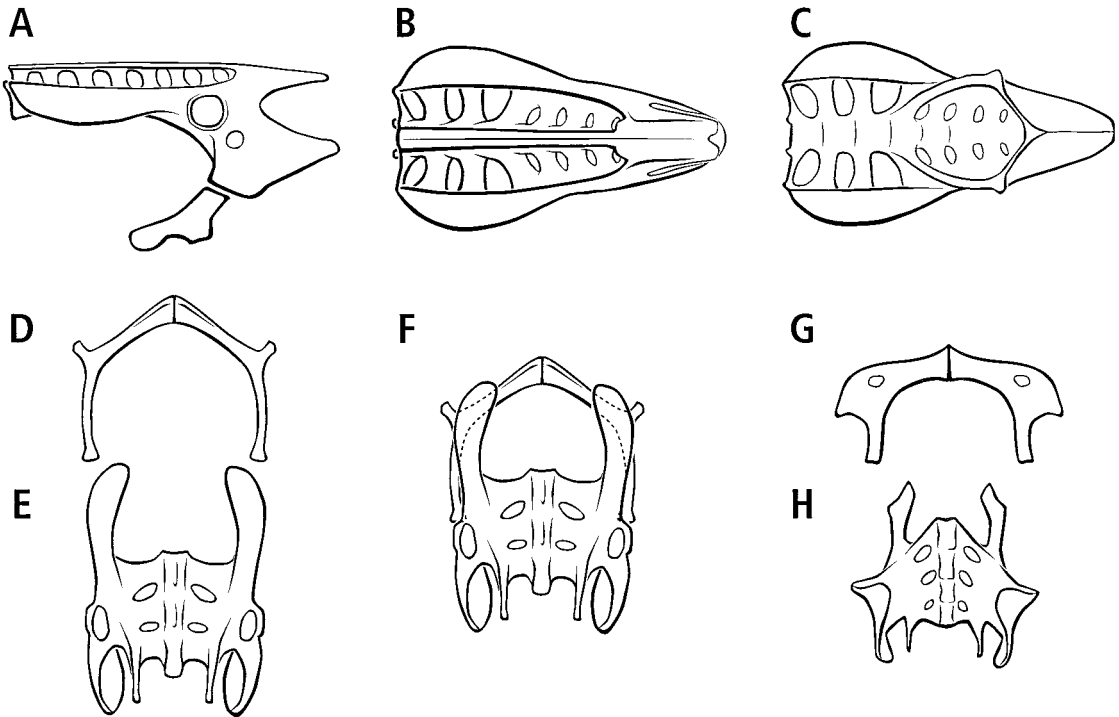
FIGURE 8. Pelvic girdle of selected pterosaurs. Lateral view (A), dorsal view (B), and ventral view (C) of *Pteranodon*. From Eaton 1910. Dorsal view of prepubis (D) and pelvis (E) of *Rhamphorhynchus musensteri.* After Wellnhofer 1978. Dorsal view of articulated pelvis and prepubis of *Rhamphorhynchus musensteri* (F). Ventral view of prepubis (G) and pelvis (H) of *Campylognathoides liasicus.* After Wellnhofer 1978.

and Carrier 2000a). In alligators, pressurization of the abdomen during inspiration is minimized by the active ventral rotation of the pubes (Fig. 2A). In contrast, ventral rotation of the gastralia would not reduce visceral pressure during diaphragmatic contraction because the gastralia are outside the volume enclosed by the diaphragmaticus. (Motion of the gastralia would displace the viscera ventrally but cannot influence the visceral pressure generated by contraction of a diaphragmaticus that envelops the viscera.) Thus, we suspect that the repeated evolution of pubic kinesis in Crocodylomorpha is associated with diaphragmatic breathing. This suggests that diaphragmatic breathing evolved very early in the Pseudosuchia and may be basal for Crocodylomorpha (Fig. 6).

If diaphragmatic muscles were present in basal crocodylomorphs, it is likely that this muscle represents an adaptation to increase metabolism during activity rather than an adaptation to control buoyancy in the relatively recent amphibious Mesoeucrocodylia. As stated above, early crocodylomorphs were fully terrestrial animals with parasagittal limb posture; some had very long, gracile limbs. In modern alligators, the diaphragmatic muscle helps to make simultaneous ventilation and locomotion possible (Farmer and Carrier 2000a,b). Thus, the presence of diaphragmatic muscles in basal crocodylomorphs would be consistent with the suggestion that this group of archosaurs was specialized to sustained vigorous activity early in its evolutionary history and that the limited aerobic capacity of modern crocodilians represents a secondary specialization to their modern lifestyle of aquatic sit-and-wait predators (Walker 1970; Carrier 1987).

Pterosaurs

The pelvis of pterosaurs had several characters that were convergent with birds and others that were convergent with crocodilians (Fig. 8). As in birds the three pelvic bones were solidly fused into a single unit, and an increased number of dorsal vertebrae were in-

corporated into the sacrum (three to five in *Rhamphorhynchus* and as many as ten in *Pteranodon*) (Wellnhofer 1978, 1991). 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 eight 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. Such specialization for dorsoventral mobility of the synsacrum appears to have been present in basal pterodactyloids (Jensen and Padian 1989). The notarium and synsacrum-like pelvic girdle appear to be convergent with birds and are generally associated with the need for trunk stabilization during flapping flight (Eaton 1910; Wellnhofer 1978).

Loosely articulated with the anteroventral margins of the pubic bones were prepubic elements that extended forward and curved medially to join at the ventral midline (Fig. 8; Wellnhofer 1978, 1991). In *Rhamphorhynchus,* the prepubic elements formed a broad U-shaped structure with lateral processes at the anterior margin. Among the Pterodactyloidea, the distal ends of the prepubes were expanded horizontally to form a flat platelike structure. These prepubic elements strongly resemble the organization of the pubic bones in crocodilians and suggest that pterosaurs were able to actively expand their posterior abdominal cavity.

Gastralia were present in pterosaurs (Wellnhofer 1978, 1991) but appear to have been somewhat reduced compared with basal archosaurs. *Rhamphorhynchus* had six anteriorly pointing, V-shaped elements in the ventral belly wall between the sternum and the pelvis. The gastralia were composed of a single curved medial element and a lateral element on each side. The medial element had an anteriorly directed process on the midline.

The convergent features of the pelvic girdles of pterosaurs, birds, and crocodilians provide grounds for speculation on the mechanism of lung ventilation in this group of archosaurs. The ventrally open, synsacrum-like pelvis and dorsoventral mobility at the notarial-synsacral joint suggest that pterosaurs, such as *Pteranodon,* used a pelvic aspiration pump similar to what has been described in pigeons, in which the epaxial muscles rotate the pelvis on the notarium to cause inspiration. Furthermore, the structure of the prepubic plates of pterosaurs is consistent with a crocodilian-like mechanism of posterior abdominal expansion. Observations in American alligators suggest that the kinetic pubes of crocodilians facilitate aspiration with a hepatic piston driven by a diaphragmatic muscle that originates on the pelvic girdle (Farmer and Carrier 2000a). Thus, the prepubic plates raise the possibility that pterosaurs breathed with a crocodilian-like diaphragmatic system. The craniolateral processes on the prepubic plates of the genus *Rhamphorhynchus* (Fig. 8) may have served as a site of origin for a diaphragmatic muscle. Alternatively, a birdlike mechanism for dorsoventral rotation of the pelvis and a crocodilian-like mechanism for abdominal expansion may indicate that pterosaurs possessed abdominal air sacs or diverticula of the lungs.

Dinosauria

The principal mechanism of ventilation in dinosaurs was almost certainly costal aspiration. Nevertheless, there are reasons to suspect that the pelvic musculoskeletal system may have played an important role in the ventilation of these animals. Compared with basal archosaurs, both ornithischian and saurischian dinosaurs had (1) a large preacetabular process on the ilium, (2) a reduction and dorsal relocation of the attachment sites of muscles that were basally associated with the pubis and ischium, and (3) exceptionally long and isolated pubes and ischia. It is generally agreed that the first two of these characters were a consequence of the shift from a sprawling limb posture to one in which the limbs were held more or less vertically in the parasagittal plane (Romer 1923a,b, 1927; Charig 1972; Walker 1977). A question that has not yet

been adequately addressed, however, is why the pubes and ischia of this group of archosaurs became so long, and, in some cases, loosely attached to the ilia. In the sections below, we suggest that many of the modifications observed in the pelvis of dinosaurs may be related to lung ventilation.

Pelvic Aspiration in Ornithischians?

Gastralia were lost in the lineage that gave rise to ornithischians (Claessens 1997) (Fig. 4). Thus, cuirassal breathing, which appears to have been important in many archosaurs, was not possible in these dinosaurs. The large herbivorous gut may have made cuirassal breathing uneconomical because of the energy required to lift the viscera with each expiration. The same circumstance may explain the loss of gastralia in sauropods. Nevertheless, the lack of gastralia leaves three possibilities for lung ventilation in ornithischians: (1) they relied solely on costal aspiration, (2) they used both costal and diaphragmatic breathing, and (3) in addition to costal aspiration, they used some unique form of pelvic aspiration. The first possibility seems unlikely for many groups of ornithischians. If one accepts the hypothesis that the ancestors of ornithischians used cuirassal breathing, it seems reasonable to expect that active ornithischians augmented costal ventilation in some way. Although we cannot exclude the possibility that ornithischians had a diaphragmatic muscle, we cannot provide any direct evidence of it. What is clear is that Ornithischia had pelvic organization that was completely distinct from that in any other group of tetrapod.

The ilium was elongated both cranially and caudally and appears to have played a greater role in the attachment of hindlimb protractors and retractors than was the case primitively (Romer 1927; Charig 1972; Fastovsky and Weishampel 1996). It was attached to the axial skeleton by an increased number of sacral vertebrae, at least 5 and as many as 11 in some ceratopsians (Fastovsky and Weishampel 1996). Ossified tendons ran along the neural spines and these ossifications appear to have been centered over the pelvic girdle, rendering the axial skeleton relatively immobile in this region (Romer 1927; Fastovsky and Weisham-

pel 1996). In bipedal forms, the neural spines were very long and exceptionally broad in the sagittal plane, which also limited dorsoflexion of the spine. In these aspects, the ilium and sacral vertebrae give the impression of great strength and limited iliosacral mobility.

In contrast, the pubis and ischium were relatively delicate bones that were loosely articulated to each other and to the ilium (Romer 1956). Instead of the distinct, well-defined joint surfaces that were present in basal archosaurs, the ilium had broad hemispherical knobs that served as articulation sites for the other two bones (Romer 1956). Both pubis and ischium are thought to have made little or no contribution to support of the femur at the hip joint (Charig 1972). This ''looseness'' leads to some ambiguity in how the three bones were articulated in life; in our experience museum mounts reflect this ambiguity in that the right and left sides of the same specimen are often reconstructed in different fashions.

The absolute magnitude of locomotor forces applied to joints increases as body size increases and locomotor performance improves. Consequently, reductions in the relative size and precision of pelvic girdle articulations are characters that one would not expect to find in very large, active tetrapods. Similarly, a significant reduction in the contributions by the pubis and ischium to the support of the femur at the hip joint is unexpected. These characters suggest that the pubis and ischium of ornithischians played a reduced role in the generation of locomotor forces. Nonetheless, instead of disappearing, the pubis and ischium of ornithischians acquired elaboration. At least three groups of ornithischians independently developed a broad and paddle-shaped anterior prepubic process on the pubis (Fig. 9). The prepubis was small in primitive ornithischians such as Lesothosaurus (Weishampel and Witmer 1990a). It was also small in basal Ornithopoda (Weishampel and Witmer 1990b) and in basal Ceratopsia (Dodson and Currie 1990; Sereno 1990). Thus, a large platelike prepubis evolved independently in ceratopsians, stegosaurs, and ornithopods. In many ornithopods, the ischia were as long as, or longer than, the femora and were directed almost horizontally beneath the tail. In contrast, in
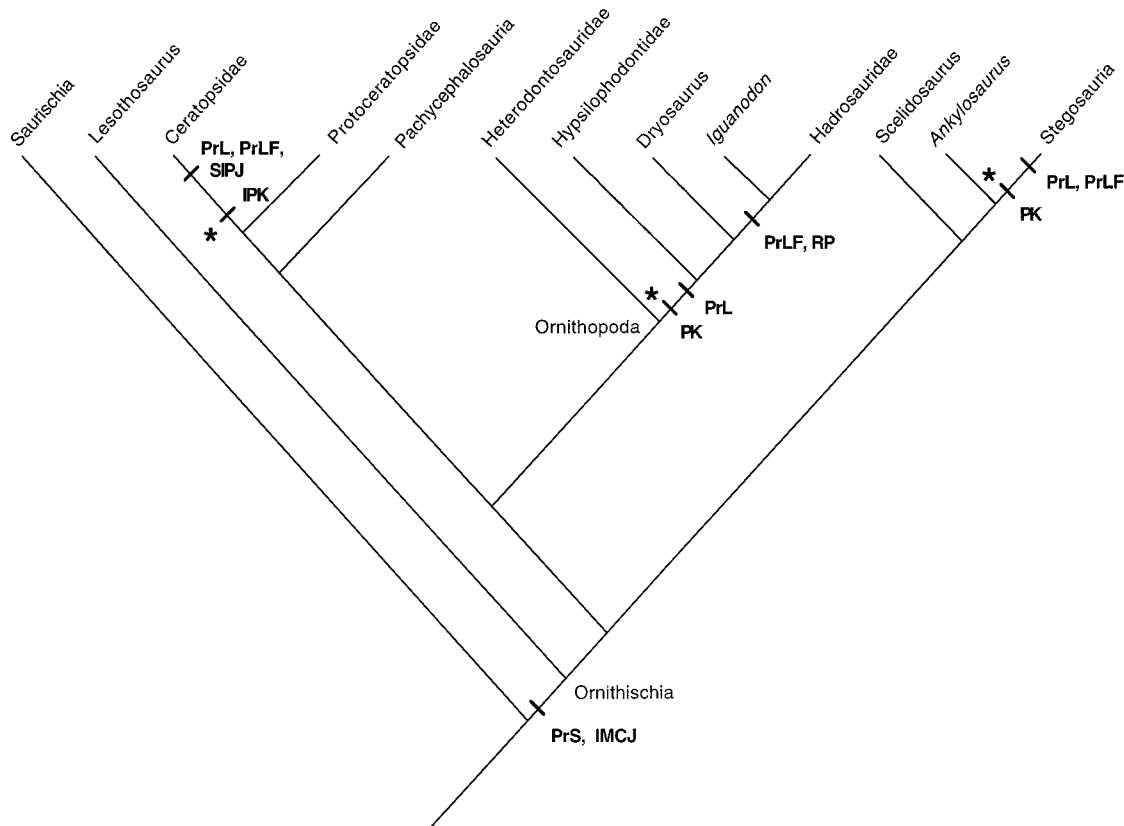
FIGURE 9. Phylogeny of Ornithischia showing the distribution of characters associated with elaborated pubes and ischia, and our hypotheses (denoted by question marks) for the origins of pubic and ischial kinesis. Phylogeny follows that of Sereno (1986) and Dodson and Currie (1990). IPK = hypothesized ischial and pubic kinesis; PrL = prepubic process long; PrLF = prepubic process laterally flattened; SIPJ = sliding ischiopubic joint; PK = hypothesized pubic kinesis; RP = reduced pubis. Character distribution is described and referenced in text.

Ceratopsidae ceratopsians the ischia were oriented more vertically and had a dramatic cranially directed curve (i.e., decurved) (Dodson and Currie 1990), and they appear to have enclosed and supported the posterior abdominal contents. As suggested above, the reduction in pelvic joints and the limited involvement of the ischium and pubis in the hip joint imply that these elaborations of the pubes and ischia were not associated with locomotion. If not locomotor function, what role did the unique features of ornithischian pubes and ischia play?

We suspect that the pubis and ischium of some ornithischians may have been specialized for lung ventilation. Although the ideas that follow are highly speculative and will likely be difficult to test, we believe they warrant mention for three reasons. First, many of the unique and strange aspects of the pelvic girdles of ornithischians do not yet have compelling functional interpretations. Second, as argued above, many of the derived aspects of the ornithischian pubes and ischia may not be related to locomotor function. Third, there is ample reason to believe that the pelvic musculoskeletal system of the ancestors of ornithischians functioned in cuirassal breathing.

Neoceratopsians.—In neoceratopsians, such as *Triceratops,* the anterior process of the pubis formed a vertically oriented plate that extended forward under the preacetabular process of the ilium, and the shaft of the ischium formed a gently curved, vertically oriented arc beneath the postacetabular process (Fig. 10A) (Marsh 1891; Dodson 1996). The iliopubic and ilioischial joints were formed by rounded bosses on each of the articulating bones rather
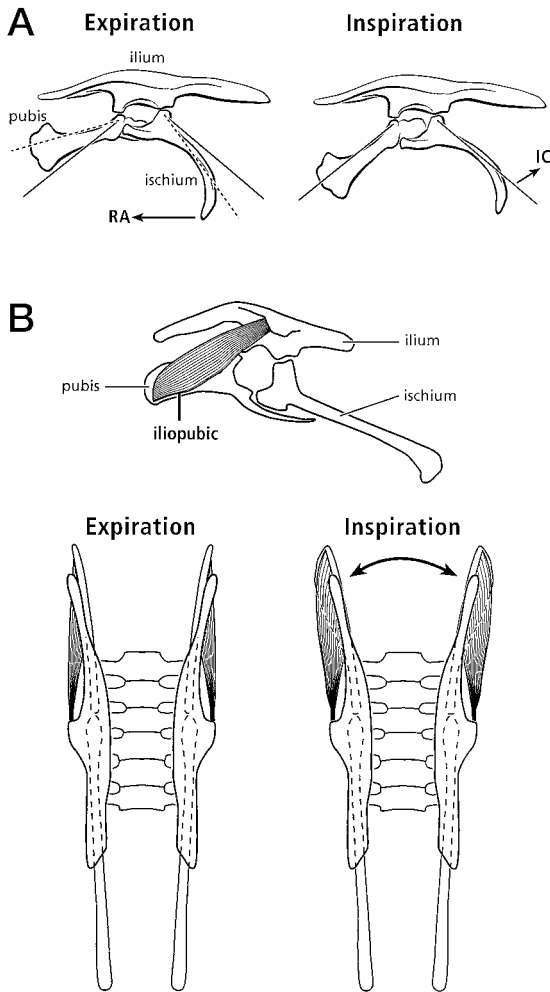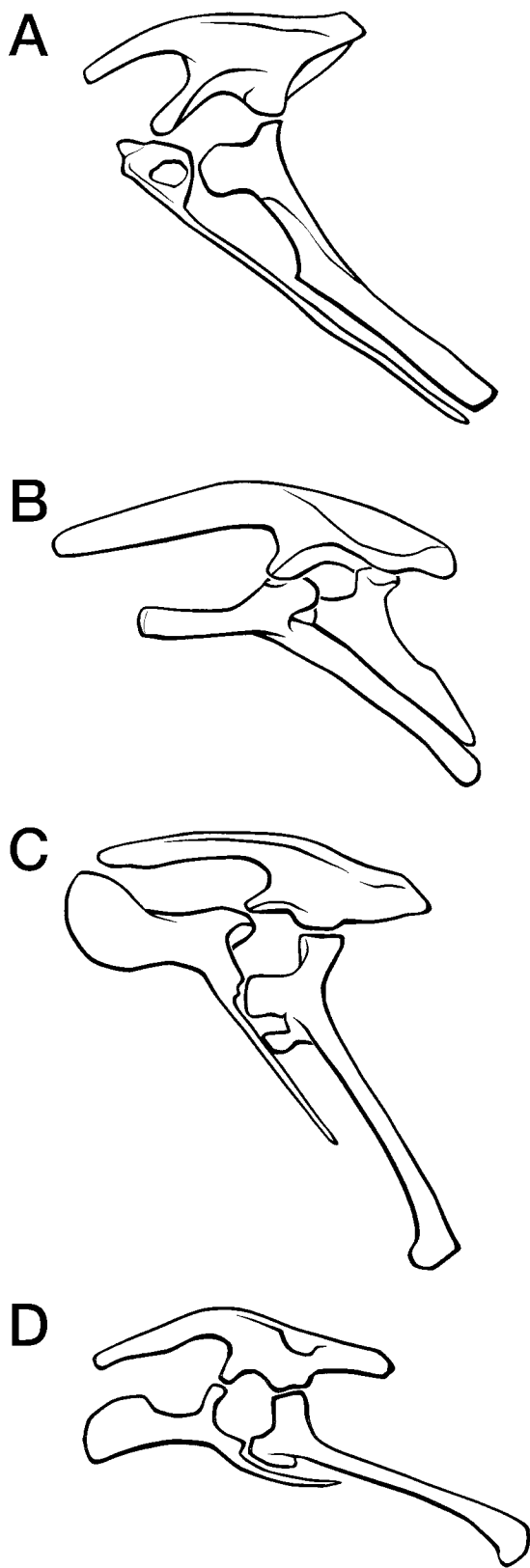
FIGURE 10. Illustration of the proposed mechanisms of pubic and ischial kinesis in derived ornithischian dinosaurs. A, The pelvis of *Triceratops prorsus.* We suggest that during inspiration, contraction of an ischiocaudalis muscle caused a caudal rotation of the ischium at the ilioischial joint. Translational motion at the ischiopubic joint would have resulted in a ventral rotation of the prepubis at the iliopubic joint. We hypothesize that during expiration, contraction of the rectus abdominis muscle produced a cranial rotation of the ischium, which pushed on the pubis and caused a dorsal rotation of the prepubis. B, Pelvis of the hadrosaur *Corythosaurus casuarius,* illustrating the proposed mechanism of pubic kinesis in Ornithopoda and Stegosauria. The lateral view shows the hypothesized configuration an iliopubic muscle. The dorsal views show the lateral rotation of the prepubic plate on the iliopubic and ischiopubic joints resulting from contraction of the iliopubic muscle.

than by distinctly fitted sutures. The puboischial joint was formed by an arm of the ischium that extended forward beneath the acetabulum to abut a broad articular surface on the pubis. We suggest that all three pelvic joints were kinetic and that motion at the iliopubic and ilioischial joints was primarily rotational in the parasagittal plane, whereas motion at the puboischial joint was translational in the parasagittal plane (Fig. 10A).

If this were true, contraction of the rectus abdominis muscle would have caused a cranial rotation of the ischium, which in turn would have levered the prepubic blade of the pubis dorsally. The rectus abdominis muscle is recognized as an expiratory muscle in mammals (De Troyer and Loring 1986), birds (Fedde et al. 1969; Fedde 1976), and crocodilians (Farmer and Carrier 2000a). If shortening of this muscle functioned to rotate the ischium of ceratopsians anteriorly it would have reduced the volume of the pleuroabdominal cavity by pushing the abdominal viscera cranially into the thorax. At the same time, the requisite dorsal rotation of the prepube would have allowed a medial collapse of the lateral abdominal body wall. Caudal rotation of the ischium, by the ischiocaudalis muscle or an ischioilium muscle, would have produced a ventral rotation of the prepube that would likely have caused a lateral expansion of the abdominal body wall. Thus, both caudal rotation of the ischium and ventral rotation of the prepube could have increased the volume of the body cavity. In *Triceratops prorsus,* the gear ratio of this mechanism was approximately 2, such that one degree of rotation of the ischium would have produced two degrees of rotation of the prepube (Fig. 10A).

Ornithopoda and Stegosauria.—In basal ornithischians such as *Lesothosaurus*, the pubis and ischium were equal in length and lay parallel, in close approximation (Fig. 11) (Weishampel and Witmer 1990a). Furthermore, the structure of the pelvic joints was such that the ischiopubic interosseous margin (i.e., margin between the two bones) was roughly colinear with the iliopubic and ilioischial joints. This architecture made possible a long-axis rotation of the pubis along its long contact with the ischium (Fig. 11). It is unlikely that a long-axis rotation of the pubis in basal ornithischians would have served any function. However, both ornithopods and stegosaurs independently evolved large, laterally flattened pre-

pubic processes (Galton 1990; Norman and Weishampel 1990; Weishampel and Horner 1990) (Figs. 9, 11). In both groups, the prepubic process was directed cranially under the preacetabular process of the ilium, such that the prepube was set at an acute angle to the long-axis of the pubis proper. If the pubis were to rotate along its long-axis, the prepubis would swing laterally and expand the volume of the abdomen (Fig. 10B).

In this scenario, the prepubic plates of ornithopods and stegosaurs functioned as rotating flaps that produced a lateral expansion of the belly wall. Two muscles that potentially could have produced the lateral rotation of the prepubes are ischiopubic and ischiotruncus muscles, which are associated with inspiration in extant crocodilians (Farmer and Carrier 2000a). This, however, would have required that the pubic attachment of the ischiopubic muscle migrate from the distal end of the pubic bone to the cranial end of the prepubic process. An intermediate function during such a migration is hard to imagine. Similarly, an ischiotruncus muscle would likely have been lost from the lineage with the loss of gastralia. An alternative is a new muscle that originated on the supra-acetabular crest of the ilium and inserted on the cranial margin of the prepubic process (Fig. 10B).

In summary, we are suggesting that a mechanism of pubic and ischial kinesis evolved in advanced ceratopsians, and that the ornithopod and stegosaur lineages independently evolved mechanisms of lateral rotation of their prepubic plates (Fig. 10). In all three cases, the proposed pelvic kinesis would have functioned to assist costal ventilation in pumping air in and out of the lungs. If this scenario were true, the three examples of convergent or parallel evolution within ornithischians

←

FIGURE 11. Lateral view of the pelvic girdles of selected ornithischian dinosaurs. A, The basal ornithischian *Lesothosaurus diagnosticus* (Thulborn 1972; Santa Luca 1984; Weishampel and Witmer 1990a). B, *Stegosaurus* (Gilmore 1914; Ostrom and McIntosh 1966; Galton 1990). C, The iguanadon *Ouranosaurus nigeriensis* (Taquet, 1976; Norman and Weishampel 1990). D, The hadrosaur *Corythosaurus casuarius* (Brown 1916; Weishampel and Horner 1990).

would suggest strong selection for pelvic aspiration. We can imagine two plesiomorphic conditions in which the evolution of pelvic aspiration would be strongly favored. If basal ornithischians had a diaphragmatic muscle similar to that of extant crocodilians, a pelvic mechanism to expand the posterior abdomen would have helped to eliminate restrictions on venous return, as has been suggested to be the case in crocodilians. Alternatively, if basal ornithischians had air sacs or lung diverticula that extended into the lumbar region, the proposed mechanism could have provided a more effective means of ventilating these lung diverticula than the more cranially located thoracic ribs.

Non-avian Theropods

The anatomy of non-avian theropods is consistent with the mechanism of cuirassal breathing that we propose for basal archosaurs. Non-avian theropods were characterized by well-developed gastralia in the belly wall between the pubes and sternum (Claessens 1997). The pubis was elongate and had cranial and caudal expansions at the distal end called a boot or foot. The ventral margin of the boot was often convex in shape, covered by cartilage, and aligned with the distal end of the long ischium (Fig. 12A). 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 as a guide that oriented the force of the ischiotruncus muscle on 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. 12B). 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). Small fossae on the ventral side of the proximal ends of the gastralia may have been the site of attachment of the ischiotruncus
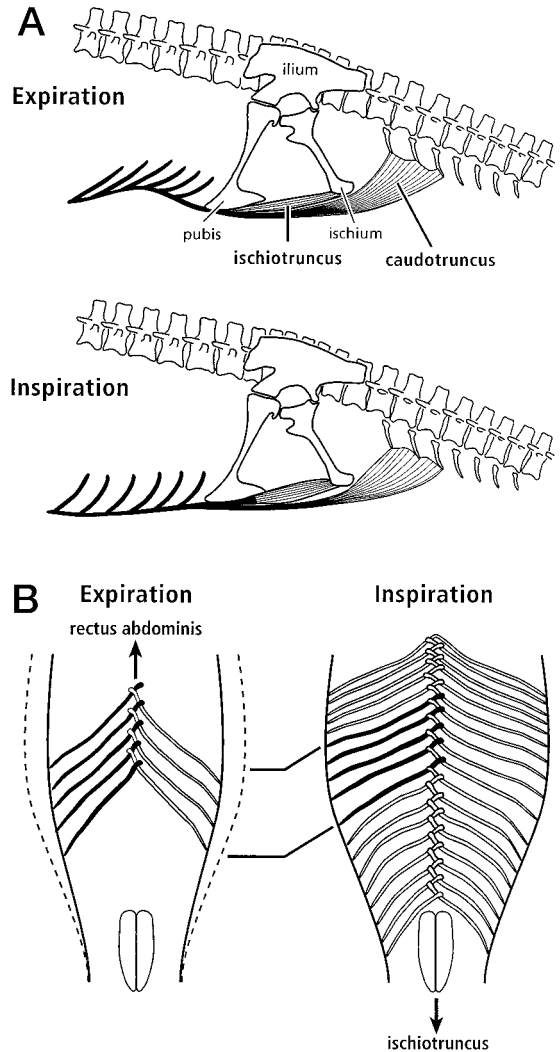

FIGURE 12. Illustration of the proposed mechanism of cuirassal breathing in the theropod *Allosaurus* sp. A, During expiration, contraction of the rectus abdominis muscle pulls the medial portion of the gastralia anteriorly, causing an elevation and lateral compression of the ventral body wall. During inspiration, contraction of the ischiotruncus and caudotruncus muscles pulls the medial portion of the gastralia posteriorly, forcing the body wall to expand ventrally and laterally. B, Ventral view of the gastralia of *Allosaurus* sp. showing the lever mechanism that is proposed to cause lateral expansion of the abdominal cavity. We suggest that the ischiopubic muscle inserted on the expanded facets of the medial ends of the gastralia. Contraction of this muscle would have pulled the medial ends posteriorly, producing cranial rotation of the lateral ends of the gastralia and expanding the body wall laterally. Contraction of the rectus abdominis muscle would have pulled the medial ends of the gastralia anteriorly, forcing the lateral ends of the gastralia to swing posteriorly and reducing the volume of the body cavity.

muscle. If the medial ends of the gastralia were drawn caudally by the ischiotruncus muscle, the lever system of the gastralia would have produced a lateral expansion of the belly (Fig. 12B). Furthermore, the latticelike articulations of theropod gastralia would have reduced the ventral expansion of cuirassal breathing we have proposed for basal archosaurs (L. Claessens personal communication 1999). Instead, cuirassal breathing in non-avian theropods was likely to have been a combination of mediolateral and dorsoventral expansion and contraction of the belly.

We have attempted to model the relative volume change that would have occurred as a result of this lever system in *Allosaurus.* In specimen No. 11541 from Dinosaur National Monument, the ratio of the out-lever to the in-lever of the cuirassal system was approximately 9 to 1 (Fig. 12B). We assumed a starting angle of 75° between the gastralia on the two sides of the body at the beginning of inspiration. (This angle varies from approximately 75° next to the pubis to 105° next to the sternum in specimen No. 11541.) We also assumed that the ischiotruncus muscle could shorten to produce a 10% decrease in the distance between adjacent gastralia, and that shortening of the ischiotruncus muscle would draw the gastralia caudally. When we modeled the system in this way, shortening of the ischiotruncus muscle caused a lateral rotation of the gastralia to a new angle of approximately 105°, and this increased the volume of the abdominal cavity by 14%.

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 provide proper alignment for an ischiotruncus muscle to effect increases in abdominal volume by drawing the medial aspect of the gastralia caudally; through the special lever system of theropod gastralia, this would have produced a lateral and ventral expansion of the belly. In this scheme, the ischium functioned as the site of origin of the ischiotruncus muscle, and the expanded foot of the pubis acted as a guide to direct the force of the muscle.

Another mechanism to assist costal aspiration has recently been proposed by Ruben et al. (1999). They suggest that theropod dinosaurs used a hepatic piston driven by a diaphragmatic muscle to produce ventilation. Although non-avian theropods may have possessed a diaphragmatic muscle, our analysis provides no support for this possibility. Instead, the specialized gastralia and pelvic girdle of basal theropods and the presence of pneumatic openings in all presacral vertebrae of oviraptors and dromaeosaurs (Britt et al. 1998) lead us to suspect that theropods used cuirassal breathing to ventilate abdominal diverticula of the lung.

Aves

The mechanism of pelvic aspiration in Recent birds (Baumel et al. 1990) is very different from what has been observed in Recent alligators (Farmer and Carrier 2000a), and very different from the cuirassal breathing mechanism that we are suggesting was present in non-avian theropods. A fair criticism of our scenario is that the pelvic aspiration system of birds may in no way be homologous to that of crocodilians. Nevertheless, changes in structure of the pelvic musculoskeletal system that are plesiomorphic for Aves and its sister group, the Dromaeosauridae, may have set the stage for a gradual reduction in the importance of cuirassal breathing and the evolution of the pelvic aspiration system of Recent birds.

The pelvis of dromaeosaurs differed from that of other non-avian theropods in ways that would have influenced cuirassal breathing. In dromaeosaurs, the pubes were directed caudally rather than cranially (i.e., retroverted) and the ischia were much shorter than the pubes (Norell and Makovicky 1997) (Figs. 13A, 14). This anatomical arrangement is not compatible with an ischiotruncus muscle. Dromaeosaurs, however, did retain both a well-developed foot on the pubis and gastralia that were typical of non-avian theropods. These characters lead us to believe that dromaeosaurs used cuirassal breathing. However, for cuirassal breathing to work in this group, a caudotruncus muscle extending from the base of the tail to insert on the gastralia would have been required (Fig. 13A). (A caudotruncus
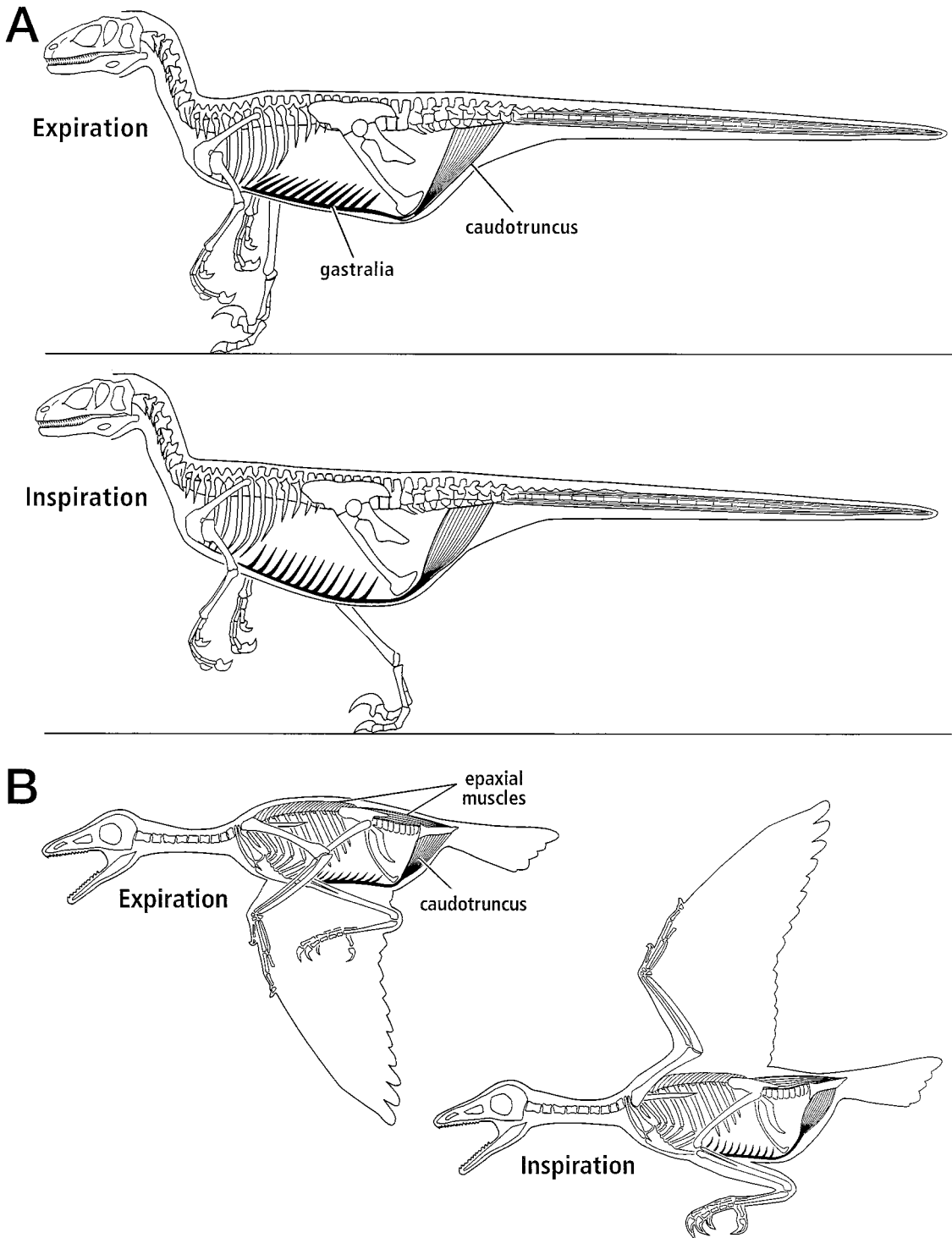
FIGURE 13.   Illustration of the proposed cuirassal breathing mechanism in the theropod *Deinonychus antirrhopus* and the early bird *Sinornis santensis.* A, The orientation and size of the pubes indicate that an ischiotruncus muscle was not present in maniraptorid theropods. For cuirassal breathing to work, a caudotruncus muscle would have to have been present. Modified from Ostrom 1969 and Norell and Makovicky 1997. B, In early birds, inspiratory activity of

muscle is present in Recent crocodilians but does not appear to be involved in ventilation (Farmer and Carrier 2000a)). If the tail did become the primary anchor for the muscles that expanded the belly during inspiration, activity of the epaxial muscles would have been required at the same time to stabilize the tail against the force exerted on the gastralia. Thus, the early shift in Maniraptora to retroverted pubes and relatively short ischia may have set the stage for the association of epaxial muscle activity with inspiration in Recent birds by requiring the tail to be stabilized against the ventrally directed pull of the caudotruncus muscle.

Among basal birds (Fig. 14), gastralia have been observed in *Archaeopteryx* (Ostrom 1976; Wellnhofer 1992), in confuciusornithids (Hou et al. 1996; Ji et al. 1999), and in one enantiornithid, *Sinornis* (Sereno and Chenggang 1992). Gastralia have not been observed in any hesperornithiforms or in Neornithes. Pubic boots were present in both *Archaeopteryx* (Ostrom 1976) and *Sinornis* (Sereno and Chenggang 1992), but are absent in confuciusornithids (Hou et al. 1996), most enantiornithids (L. Chiappe personal communication), and all known ornithurids (Padian and Chiappe 1998). Confuciusornithes, Enantiornithes, and Ornithurae shared a shortened tail with a pygostyle (Hou et al. 1996), and a well-formed synsacrum with seven or more vertebrae (Padian and Chiappe 1998; Ji et al. 1999). Ornithurae are characterized by the absence of pubic and ischial symphyses and the presence of a long sternum that reached the abdominal region (Padian and Chiappe 1998).

The Late Jurassic and Early Cretaceous confuciusornithids and the enantiornithid *Sinornis* possessed well-formed gastralia but had tails that were almost modern in size and structure. The structure of the pelvis in these birds suggests that an ischiotruncus muscle was not present and that a caudotruncus muscle would have originated on the pygostyle of the tail (Fig. 13B). For cuirassal breathing to work in these birds, as suggested above for dromaeosaurs, activity of the epaxial muscles would have been required during inspiration to stabilize the tail against the ventral pull of the caudotruncus muscle. Thus, confuciusornithids and *Sinornis* may represent an intermediate stage in the transition from cuirassal breathing of non-avian theropods to the pelvic aspiration of Recent birds.

The absence of gastralia and pubic symphyses in Ornithurae make it clear that basal Hesperonithiformes and Neornithes did not supplement their costal ventilation with cuirassal breathing. Although we believe that a pubic boot is not essential for cuirassal breathing, particularly in small animals, it is hard to imagine the proposed mechanism of cuirassal breathing working in animals that lacked pubic and ischial symphyses. In this context, it is significant that there are no known species that possessed gastralia but lacked pubic and ischial symphyses. The evolution of the ventrally open pelvis of Ornithurae appears to be associated with the loss of cuirassal breathing.

The absence of gastralia and pubic symphyses in Ornithurae and the presence of a well-developed synsacrum lead us to suggest that the system of pelvic aspiration observed in pigeons was present in the common ancestor of Hesperoniformes and Neornithes (Fig. 14). The presence of pneumatic openings in all presacral vertebrae of oviraptors and dromaeosaurs (Britt et al. 1998) suggests that abdominal diverticula of the lung were a primitive feature of the respiratory system of Maniraptora. In dromaeosaurs and basal birds, abdominal lung diverticula would likely have been ventilated by abdominal expansion due to a cuirassal mechanism. In Ornithurae, the caudal expansion of the sternum and ventral opening of the pelvis made cuirassal breathing unworkable. In these birds, abdominal

←

the caudotruncus muscle would have required simultaneous activity of the epaxial muscles to stabilize the tail against ventral rotation. Modified from Sereno and Chenggang 1992. Note that if the caudotruncus muscle originated on the chevrons and pygostyle, as illustrated, the digestive tract would have had to pass through the belly of the muscle to reach the vent. Alternatively, the caudotruncus muscle could have taken its origin from the superficial myosepta of the tail, as it does in the American alligator (Farmer and Carrier 2000a).
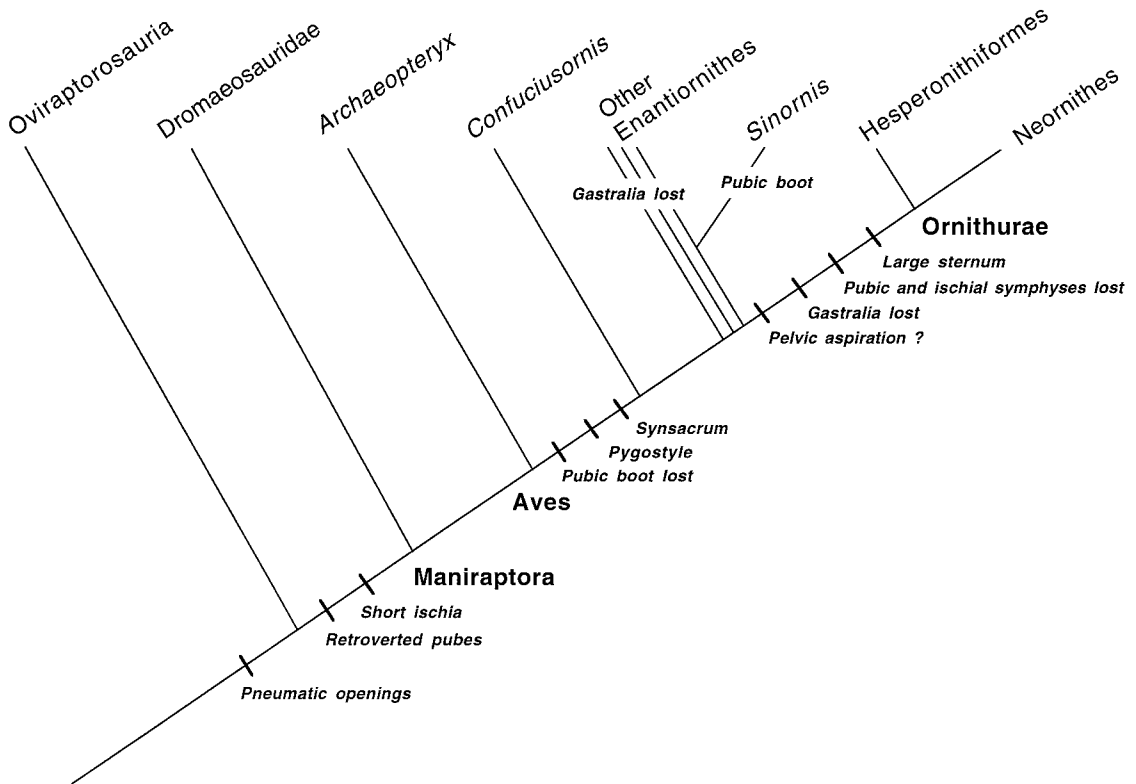
FIGURE 14. Phylogeny of Aves showing the distribution of characters associated with the loss of cuirassal breathing in Ornithurae and our hypothesis (denoted by question mark) for the origin of pelvic aspiration in Ornithurae. Phylogeny compiled from Padian and Chiappe 1998, Forster et al. 1998, and Ji et al. 1999. Pneumatic openings indicates clade in which pneumatic openings were present in all presacral vertebrae. Synsacrum indicates clade in which a synsacrum composed of seven or more vertebrae was present. Pygostyle indicates clade with a pygostyle on tail. Character distribution is described and referenced in text.

lung diverticula may have been ventilated by action of the epaxial muscles to dorsally rotate the synsacrum on the dorsal vertebrae, as has been observed in pigeons.

Conclusions

1. The pelvic musculoskeletal system appears to contribute to inspiratory airflow in both crocodilians and birds. Although the mechanisms in birds and crocodilians differ considerably, participation of the pelvic girdle in the production of inspiration is rare among vertebrates. This raises the possibility that the pelvic musculoskeletal system may have played a role in the ventilation of basal archosaurs.

2. The mechanism of pelvic aspiration in crocodilians and the structure of gastralia in basal archosaurs 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 abdominal cavity. From this basal mechanism (i.e., cuirassal breathing), several archosaur lineages appear to have evolved specialized gastralia, pelvic kinesis, and/or pelvic mobility.

3. Kinetic pubes appear to have evolved independently in at least two clades of Crocodylomorpha. Observations in alligators suggest that kinetic pubes facilitate diaphragmatic breathing. Thus, the convergent evolution of kinetic pubes suggests that diaphragmatic muscles were present in the basal crocodylomorphs and were associated with selection for increased metabolism during activity rather than for buoyancy control.

4. The pelvis of pterosaurs was long, open ventrally, and had prepubic elements that

resembled the pubic bones of Recent crocodilians. These characters suggest convergence on the pelvic aspiratory systems of both birds and crocodilians. The prepubic elements are consistent with the possibility that pterosaurs ventilated their lungs with a crocodilian-like hepatic piston driven by diaphragmatic muscles that originated on the pelvic girdle.

5. The structure of the pelvis of some ornithischians appears to have been permissive of pubic and ischial kinesis. Large platelike prepubic processes evolved three times in Ornithischia. These plates may have been instrumental in an active expansion of the lateral abdominal wall to produce inspiratory flow.

6. The derived configuration of the pubis, ischium, and gastralia of non-avian theropods appears to have enhanced the basal cuirassal breathing mechanism. Changes in structure of the pelvic musculoskeletal system that were present in both dromaeosaurs and basal birds may have set the stage for a gradual reduction in the importance of cuirassal breathing and for the evolution of the pelvic aspiration system of Recent birds.

Acknowledgments

Literature Cited

Baumel, J. J. 1988. Functional morphology of the tail apparatus of the pigeon (*Columba livia*). Advances in Anatomy, Embryology and Cell Biology 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*). The Journal of Experimental Biology 151:263–277.

Benton, M. J., and J. Clark. 1988. Archosaur phylogeny and the relationships of the Crocodylia. Pp. 289–332 in M. J. Benton, ed. The phylogeny and classification of the tetrapods, Vol. I. Clarendon, Oxford.

Boelaert, R. 1942. Sur la physiologie de la respiration de l'*Alligator mississippiensis.* Archives Internationales de Physiologie 52:57–72.

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

Boggs, D. F., F. A. Jenkins, and K. P. Dial. 1997. The effects of the wingbeat cycle on respiration in black-billed magpies (*Pica pica*). The Journal of Experimental Biology 200:1403–1412.

Brainerd, E. L., J. S. Ditelberg, and D. M. Bramble. 1993. Lung ventilation in salamanders and the evolution of vertebrate air-breathing mechanisms. Biological Journal of the Linnean Society 49:163–183.

Bramble, D. M., and D. R. Carrier. 1983. Running and breathing in mammals. Science 219:251–256.

Britt, B. B., P. Makovicky, J. Gauthier, and N. Bonde. 1998. Postcranial pneumatization in *Archaeopteryx.* Nature 395:374–376.

Brown, B. 1916. *Corythosaurus casuarius*: skeleton, musculature and epidermis. Bulletin of the American Museum of Natural History 35:709–716.

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

———. 1989. Ventilatory action of the hypaxial muscles of *Iguana iguana*: a function of slow muscle. Journal of Experimental Biology 143:435–457.

Charig, A. F. 1972. The evolution of the archosaur pelvis and hind-limb: an explanation in functional terms. Pp. 121–155 in K. A. Joysey and T. S. Kemp, eds. Studies in vertebrate evolution. Winchester, New York.

Chatterjee, S. 1985. *Postosuchus,* a new thecodontian reptile from the Triassic of Texas and the origin of tyrannosaurs. Philosophical Transactions of the Royal Society of London B 309: 395–460.

Claessens, L. 1996. Dinosaur gastralia and their function in respiration. Journal of Vertebrate Paleontology 16:28A.

———. 1997. Gastralia. Pp. 269–270 in P. J. Currie and K. Padian, eds. Encyclopedia of dinosaurs. Academic Press, San Diego.

Colbert, E. H., and C. C. Mook. 1951. The ancestral crocodilian *Protosuchus.* Bulletin of the American Museum of Natural History 97:146–182.

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

De Troyer, A., and S. H. Loring. 1986. Action of the respiratory muscles. Pp. 443–561 in P. T. Macklem and J. Mead, eds. Handbook of physiology: the respiratory system. American Physiological Society, Bethesda, Md.

Dodson, P. 1996. The horned dinosaurs. Princeton University Press, Princeton, N.J.

Dodson, P., and P. J. Currie. 1990. Neoceratopsia. Pp. 593–618 in Weishampel et al. 1990.

Eaton, C. F. 1910. Osteology of *Pteranodon.* Memoirs of the Connecticut Academy of Arts and Sciences 2:1–38.

Ewer, R. F. 1965. The anatomy of the thecodont reptile *Euparkeria capensis* Broom. Philosophical Transactions of the Royal Society of London B 248:379–435.

Farmer, C. G., and D. R. Carrier. 2000a. Pelvic aspiration in the American alligator (*Alligator mississippiensis*). Journal of Experimental Biology (in press).

———. 2000b. Ventilation and gas exchange in the American alligator (*Alligator mississippiensi*s) during treadmill-exercise. Journal of Experimental Biology (in press).

Fastovsky, D. E., and D. B. Weishampel. 1996. The evolution and extinction of the dinosaurs. Cambridge University Press, Cambridge.

Fedde, M. R. 1976. Respiration. Pp. 122–145 *in* P. D. Sturkie, ed. Avian physiology. Springer, New York.

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

Forster, C. A., S. D. Sampson, L. M. Chiappe, and D. W. Krause. 1998. The theropod ancestry of birds: new evidence from the Late Cretaceous of Madagascar. Science 279:1915–1919.

Galton, P. M. 1990. Stegosauria. Pp. 435–455 *in* Weishampel et al.1990.

Gans, C., and B. Clark. 1976. Studies on ventilation of *Caiman crocodilus* (Crocodilia: Reptilia). Respiration Physiology 26:285–301.

Gans, C., and G. M. Hughes. 1967. The mechanism of lung ventilation in the tortoise *Testudo graeca* Linne. Journal of Experimental Biology 47:1–20.

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

Gaunt, A. S., and C. Gans. 1969. Mechanics of respiration in the Snapping Turtle, *Chelydra serpentina* (Linne). Journal of Morphology 128:195–228.

Gauthier, J. A., A. G. Kluge, and T. Rowe. 1988. The early evolution of Amniota. Pp. 103–155 *in* M. J. Benton, ed. The phylogeny and classification of the tetrapods, Vol. 1. Clarendon, Oxford.

Gilmore, C. W. 1914. Osteology of the armored dinosaurs in the United States National Museum, with special reference to the genus *Stegosaurus.* Bulletin of the United States National Museum 89:1–136.

Hedges, S. B., and L. L. Poling. 1999. A molecular phylogeny of reptiles. Science 283:998–1000.

Hou, L., L. D. Martin, Z. Zhou, and A. Feduccia. 1996. Early adaptive radiation of birds: evidence from fossils from northeastern China. Science 274:1164–1167.

Jensen, J. A., and K. Padian. 1989. Small pterosaurs and dinosaurs from the Uncompahgre fauna (Brushy Basin Member, Morrison Formation:? Tithonian), Late Jurassic, Western Colorado. Journal of Paleontology 63:364–373.

Ji, Q., L. M. Chiappe, and S. Ji. 1999. A new late Mesozoic confuciusornithid bird from China. Journal of Vertebrate Paleontology 19:1–7.

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

Lambe, L. M. 1917. The Cretaceous carnivorous dinosaur *Gorgosaurus.* Geological Survey of Canada Memoir 100:1–84.

Liem, K. F. 1985. Ventilation. Pp. 185–209 *in* M. Hildebrand, D. M. Bramble, K. F. Liem, and D. B. Wake, eds. Functional vertebrate morphology. Harvard University Press Cambridge.

Marsh, O. C. 1891. The gigantic Ceratopsidae, or horned dinosaurs, of North America. American Journal of Sciences 41:167–178.

Nash, D. 1968. A crocodile from the Upper Triassic of Lesotho. Journal of Zoology 156:163–179.

Nishi, S. 1938. Muskeln des Rumpfes. Pp. 351–442 *in* L. Bolk, E. Goppert, E. Kallius, and W. Lubosch, eds. Handbuch der vergleichenden Anatomie der Wirbeltiere. Urban und Schwarzenberg, Berlin.

Norell, M. A., and P. J. Makovicky. 1997. Important features of the dromaeosaur skeleton: information from a new specimen. American Museum Novitates 3215:1–28.

Norman, D. B., and Weishample D. B. 1990. Iguanodontidae and related orhithopods. Pp. 510–533 *in* Weishampel et al. 1990.

Ostrom, J. H. 1969. Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. Peabody Museum of Natural History Bulletin 30:1–165.

———. 1976. *Archaeopteryx* and the origin of birds. Biological Journal of the Linnean Society 8:91–182.

Ostrom, J. H., and J. S. McIntosh. 1966. Marsh's dinosaurs. Yale University Press, New Haven, Conn.

Owerkowicz, 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 L. M. Chiappe. 1998. The origin and early evolution of birds. Biological Review 73:1–42.

Parrish, M. J. 1987. The origin of crocodilian locomotion. Paleobiology 13:396–414.

———. 1991. A new specimen of an early crocodylomorph (cf. *Sphenosuchus* sp.) from the Upper Triassic Chinle Formation of Petrified Forest National Park, Arizona. Journal of Vertebrate Paleontology 11:198–212.

Perry, S. F. 1983. Reptilian lungs, functional anatomy and evolution. Advances in Anatomy, Embryology, and Cell Biology 79:1–81.

Romer, A. S. 1923a. The ilium in dinosaurs and birds. Bulletin of the American Museum of Natural History 48:141–145.

———. 1923b. The pelvic musculature of saurischian dinosaurs. Bulletin of the American Museum of Natural History 48:605–617.

———. 1923c. Crocodilian pelvic muscles and their avian and reptilian homologues. Bulletin of the American Museum of Natural History 48:533–552.

———. 1927. The pelvic musculature of ornithischian dinosaurs. Acta Zoologica 8:225–275.

———. 1956. The osteology of the Reptilia. University of Chicago Press, Chicago.

Ruben, J. A., C. Del Sasso, N. R. Geist, W. J. Hillenius, T. D. Jones, and M. Signore. 1999. Pulmonary function and metabolic physiology of theropod dinosaurs. Science 283:514–516.

Santa Luca, A. P. 1984. Postcranial remains of Fabrosauridae (Reptilia: Ornithischia) from Stormberg of Southern Africa. Palaeontologia Africana 25:151–180.

Sereno, P. C. 1986. Phylogeny of the bird-hipped dinosaurs (Order Ornithischia). National Geographic Research 2:234–256.

———. 1990. Psittacosauridae. Pp. 579–592 *in* Weishampel et al. 1990.

———. 1991. Basal archosaurs: phylogenetic relationships and functional implications. Society of Vertebrate Paleontology Memoir 2. Journal of Vertebrate Paleontology 11:1–53.

Sereno, P. C., and R. Chenggang. 1992. Early evolution of avian flight and perching: new evidence from the Lower Cretaceous of China. Science 255:845–848.

Sereno, P. C., and R. Wild. 1992. *Procompsognathus*: theropod, ''thecodont'' or both? Journal of Vertebrate Paleontology 12:435–458.

Taquet, P. 1976. Géologie et paléontologie du gisement de Gadoufaoua (Aptien du Niger). Cahiers de Paléontologie, C.N.R.S., Paris.

Thulborn, R. A. 1972. The post-cranial skeleton of the Triassic ornithischian dinosaur *Fabrosaurus australis.* Palaeontology 15:29–60.

Walker, A. D. 1970. A revision of the Jurassic reptile *Hallopus victor* (Marsh), with remarks on the classification of crocodiles.

Philosophical Transactions of the Royal Society of London B 257:323–371.

———. 1977. Evolution of the pelvis in birds and dinosaurs. Pp. 319–357 *in* S. M. Andrews, R. S. Miles and A. D. Walker, eds. Problems in vertebrate evolution. Academic Press, New York.

Weishampel, D. B., and J. R. Horner. 1990. Hadrosauridae. Pp. 534–561 *in* Weishampel et al. 1990.

Weishampel, D. B., and L. M. Witmer. 1990a. *Lesothosaurus*, *Pisanosaurus*, and *Technosaurus*. Pp. 416–425 *in* Weishampel et al. 1990.

———. 1990b. Heterodontosauridae. Pp. 486–497 *in* Weishampel et al. 1990.

Weishampel, D. B., P. Dodson, and H. Osmolska, eds. 1990. The Dinosauria. University of California Press, Berkeley.

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

———. 1991. The illustrated encyclopedia of pterosaurs. Crescent Books, New York.

———. 1992. A new specimen of *Archaeopteryx* from the Solnhofen Limestone. Pp. 3–23 *in* K. E. Campbell ed. Papers in avian paleontology. Natural History Museum of Los Angeles, Los Angeles.

Wu, X. C., D. B. Brinkman, and J. C. Lu. 1994. A new species of *Shantungosuchus* from the Lower Cretaceous of Inner Mongolia (China), with comments on *S. chuhsienensis* Young, 1961 and phylogenetic position of the genus. Journal of Vertebrate Paleontology 14:210–229.

Young, I. S., R. McN. Alexander, A. J. Woakes, P. J. Butler, and L. Anderson. 1992. The synchronization of ventilation and locomotion in horses (*Equus*). Journal of Experimental Biology 166:19–31.

Zimmer, K. 1935. Beitrage zur Mechanik der Atmung bei den Vogeln in Stand und Flug. Zoologica 33:1–69.