DINOSAUR GASTRALIA; ORIGIN, MORPHOLOGY, AND FUNCTION

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ABSTRACT—Gastralia are dermal ossifications situated in the ventral abdominal wall. Gastralia may be plesiomorphic for tetrapods, but are only retained in extant Crocodylia and *Sphenodon*, and possibly as part of the chelonian plastron. In contrast to previously published reports, a similar structural configuration of the gastralia is shared throughout prosauropods and (non-ornithurine) theropods. Within the Prosauropoda and Theropoda, the gastralial system consists of approximately 8 to 21 metameric rows. Each row consists of four bones: two lateral and two medial rods. Gastralia of the cranialmost or caudalmost rows may coalesce, forming a median chevron-shaped gastralium. The lateral gastralia articulate in parallel with the medial gastralia in an elongated groove. The medial gastralia imbricate with contralateral gastralia along the ventral midline, creating a series of cranially directed chevrons. Thus all the gastralia are connected to one another, and operate as a single functional unit. The bones recently identified as sauropod gastralia show no morphological similarities with the gastralia of prosauropods and theropods and are probably sternal elements. No gastralia have been recovered in the Ornithischia.

In contrast to the reduction of the gastralia in other amniote groups, theropod gastralia show elaborate modification. The anatomy of the gastralial system indicates a more active function than abdominal support or protection. The gastralia may have affected the shape and volume of the trunk in theropods, and may have functioned as an accessory component of the aspiration pump, increasing tidal volume. Moreover, if the caudal region of the lungs in some theropods had differentiated to form abdominal air-sacs, the gastralia might have ventilated them. Gastralial aspiration may have been linked to the generation of small pressure differences between potential cranial and caudal lung diverticula, which may have been important for the evolution of the unidirectional airflow lung of birds.

INTRODUCTION

Gastralia, dermal ossifications situated in the ventral abdominal region, are inadequately understood, probably in part because of their limited occurrence in modern vertebrates. Gastralia are only present in extant crocodylians and the tuatara (*Sphenodon*), although they may constitute part of the chelonian plastron (De Vos, 1938a; Gilbert et al., 2001). In addition, gastralia are "floating" bones, without a solid connection to the rest of the skeleton, and are rarely preserved in association with fossil skeletons. Furthermore, gastralia are frequently confused with other skeletal elements situated in the ventral abdominal area of vertebrates.

The ontogenetic difference between gastralia and endoskeletal bones found in the abdominal region of certain lizards or frogs was not immediately recognized (De Vos, 1938a). The first to acknowledge that the gastralia were of dermal origin appears to be Knox (1869). Detailed studies of the development and homologies of gastralia were made by Voeltzkow and Döderlein (1901) and Howes and Swinnerton (1901). However, literature that explicitly or implicitly assigns an endochondral origin to gastralia is not uncommon even today. Several inaccurate descriptions of gastralial morphology have contributed to an apparent proliferation of gastralial structures in the literature (e.g., von Huene, 1908; Osborn, 1916; Gilmore, 1920, 1924; Camp, 1936). Many different terms have been used to describe the gastralia, many of which have been coined without recognizing that they are dermal bones.

Gastralia may be plesiomorphic for tetrapods (e.g., Baur, 1889, 1897; Steinmann and Döderlein, 1891; Gegenbaur, 1898; Fürbringer, 1900; Voeltzkow and Döderlein, 1901; Peyer, 1931; Romer, 1956), and are possibly derived from the bony squamation on the ventral surface of the trunk of sarcopterygian fishes. In Paleozoic temnospondyls such as *Greererpeton* and *Trimerorhachis*, the ventral dermal ossifications generally retain a scale-like appearance. Typically they are subrectangular in

shape and arranged in cranially pointing chevron-shaped rows, forming a continuous covering between the pectoral and pelvic girdle. In basal amniotes such as *Protorothyris* and *Cephalerpeton*, the "abdominal ribs" have become more slender and rod-like (Voeltzkow and Döderlein, 1901; Romer, 1956; pers. obs.). However, whether all ventral dermal ossifications represent a single homologous series cannot be conclusively determined at this point.

Eudes-Deslongchamps (1838) first described dinosaur gastralia in the theropod *Poekilopleuron bucklandii*. Eudes-Deslongchamps did not recognize that the gastralia were dermal bones, but he did equate them with the abdominal ossifications found in crocodylians. In 1906, Osborn described gastralia in *Tyrannosaurus rex*, a publication sometimes referred to as the first description of dinosaur gastralia. After Osborn's rediscovery of gastralia, they were soon recognized in several other theropod and prosauropod taxa. Some of the early descriptions of gastralia are detailed and accurate (e.g., von Huene, 1915; Lambe, 1917), but the number and variety of morphological descriptions quickly grew (e.g., Osborn, 1916; Gilmore, 1920, 1924; Parks, 1928a, 1928b; Sternberg, 1933; Camp, 1936). In more recent decades, gastralia have generally received little attention in the osteological descriptions of dinosaurs, and, when mentioned, they are often not described in detail and are rarely illustrated.

In extant Aves, gastralia are no longer present. However, several basal birds, such as *Archaeopteryx*, *Confuciusornis*, and *Changchengornis* have well developed gastralia. References in this paper to theropod gastralial morphology or function should thus be taken as applying to non-ornithurine theropods, unless specified otherwise.

Recently, gastralia were described for a sauropod, *Apatosaurus yahnapin* (Filla and Redman, 1994). Although the evidence presented for the identification as gastralia consisted mainly of the location of the elements with respect to the rest of the skeleton, the existence of sauropod gastralia became generally ac-

cepted (e.g., McIntosh, 1997; McIntosh et al., 1997; Makovicky, 1997; Sereno et al., 1999). Marsh (1896) identified similar structures as sternal ribs.

Thulborn (1984) postulated that some chevron-shaped bones previously identified as gastralia were in fact furculae. Furculae have now been identified in many different theropod taxa (e.g., Barsbold, 1983; Chure and Madsen, 1996; Makovicky and Currie, 1998). However, several of Thulborn's furculae are in fact gastralia. The distinctive attributes of gastralia and furculae are discussed in this article.

Traditionally, the function of the gastralia has been described as protection and support of the viscera (e.g., Romer, 1956; Holtz and Brett-Surman, 1997). Perry (1983) suggested that the gastralia might have functioned as a passive component of the respiratory apparatus, preventing encroachment of the viscera into the lung space upon inspiration by stiffening the belly wall.

The purpose of this paper is twofold: first, to present a detailed morphology of dinosaur gastralia, and second, to examine the function of the gastralia in dinosaurs in light of the new morphological data. Some of the descriptions of gastralial morphology in earlier works are re-examined.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York, NY; **BMNH**, Natural History Museum, London, U.K.; **CMNH**, Carnegie Museum of Natural History, Pittsburgh, PA; **CLM**, Cleveland Museum of Natural History, Cleveland, OH; **DINO**, Dinosaur National Monument, Jensen, UT; **FMNH**, Field Museum, Chicago, IL; **GMV**, National Geological Museum of China, Beijing, China; **GPIT**, Geologisch-Paläontologisch Institut, Universität Tübingen, Germany; **IGM**, Geological Institute, Academy of Sciences, Ulan Batar, People's Republic of Mongolia; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, People's Republic of China; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, MA; **MNA**, Museum of Northern Arizona, Flagstaff, AZ; **MOR**, Museum of the Rockies, Bozeman, MT; **NMC**, Canadian Museum of Nature, Ottawa, Canada; **PIN**, Palaeontological Institute of the Russian Academy of Sciences, Moscow, USSR; **ROM**, Royal Ontario Museum, Toronto, Canada; **RTMP**, Royal Tyrrell Museum of Palaeontology, Drumheller, Canada; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart, Germany; **TM**, Tate Museum, Casper, WY; **TEY**, Teyler Museum, Haarlem, The Netherlands; **UA**, University of Alberta, Edmonton, Canada; **UCMP**, University of California, Museum of Palaeontology, Berkeley, CA; **UCMZ**, University of Calgary, Museum of Zoology, Calgary, Canada; **UMNH**, Utah Museum of Natural History, Salt Lake City, UT; **USNM**, United States National Museum, Washington D.C.; **YPM**, Yale Peabody Museum, New Haven, CT.

DEFINITION AND NOMENCLATURE

De Vos (1938a) noted that the nomenclature relating to the skeletal elements situated in the abdominal musculature of vertebrates was in a state of confusion. Today, many misconceptions regarding the abdominal skeleton persist.

Skeletal structures in the ventral abdominal wall of vertebrates have often been homologized on the basis of their anatomical position and without consideration of their developmental history (e.g., Cuvier, 1800; Eudes-Deslongchamps, 1838; Owen, 1866; Beddard, 1904, 1906; Camp, 1923; Noble, 1931; Kent, 1969; Walker, 1987; Kardong, 1998). However, a clear distinction has to be made between bones of dermal (or exoskeletal) origin and bones of endoskeletal origin (De Vos, 1938a; Patterson, 1977). These bones are of different developmental origin and are therefore not homologous (Patterson, 1977).

Dermal bones develop intramembranously without a cartilaginous precursor. Voeltzkow and Döderlein (1901), and Howes and Swinnerton (1901), independently showed that the "abdominal ribs" in both *Crocodylus* and *Sphenodon* form intramembranously within the dermis without a cartilaginous precursor. Voeltzkow and Döderlein (1901) showed that the incorporation of the "abdominal ribs" into the upper layers of the abdominal musculature in *Crocodylus* is secondary, occurring later in development. No partitioning of the M. rectus abdominis is present in the muscle body below the "abdominal ribs." The "abdominal ribs" are therefore not ossifications of the inscriptiones tendinae, as was suggested by Stannius (1846), Rathke (1866), Günther (1867), Gadow (1882), and Wiedersheim (1883).

The series of cartilages present in the ventral abdominal body wall of certain saurians (Etheridge, 1965; Romer, 1956; De Vos, 1938a; Camp, 1923; Beddard, 1904, 1906) and anurans (De Vos, 1938a, b; Noble, 1931) are not homologous with the dermal "abdominal ribs" of crocodylians and *Sphenodon*. Any cartilaginous elements must by definition be of endoskeletal origin (although endoskeletal elements need not pass through a cartilaginous state before ossification, and secondary cartilage may be formed on dermal bone [Patterson, 1977]).

The term "abdominal rib" has unfortunately been applied to a wide variety of skeletal structures and should be avoided. "Abdominal rib" has been used to describe various different parts of endoskeletal ribs (e.g., Owen, 1856, 1863; Remane, 1936), and the cartilaginous skeletal structures found in the ventral abdominal region of certain saurians and anurans (e.g., Boulenger, 1885–1887; Camp, 1923; Noble, 1931). The terms plastron (Boulenger, 1889) and parasternum (parasternalia) (Gegenbaur, 1898) have been used to indicate the ventral dermal "abdominal ribs" of crocodylians or *Sphenodon*, but should be avoided because they have also been used to indicate various other non-homologous anatomical structures. In the older literature, the term "abdominal cuirass" has often been used to indicate the whole system of ventral dermal ossifications.

Baur (1897) coined the term "gastralia" to describe the "abdominal ribs" of *Sphenodon*. The term "gastralia" has not been applied to anatomical structures other than ventral dermal "abdominal ribs" (De Vos, 1938a; Claessens, 1996a; contra Etheridge, 1965), and is in common use. In this study the term "gastralia" (singular: gastralium) will be applied, sensu Baur (1897), De Vos (1938a), and Romer (1956), to describe the rod-like dermal bones situated in the abdominal musculature. The term "inscriptional rib" is proposed for cartilaginous structures observed in the myocommata of saurians or anurans, sensu Etheridge (1965) and De Vos (1938a, b).

The following terms will be used to describe the different components of the gastralial system. The individual metameric segments will be referred to as "rows." The individual gastralial components in the Dinosauria are referred to as "medial," "lateral," or "chevron-shaped" gastralia, based on morphology and anatomical position.

MORPHOLOGY

Prosauropod and theropod gastralia (Appendix 1) are slender, rod-like bones positioned in metameric rows in the ventral abdominal wall, between the pubis and sternum (Fig. 1A). The number of rows of gastralia varies considerably, ranging from approximately 8 in smaller species up to approximately 21 in the larger species. Each row consists of four individual bones: a lateral and a medial gastralium on each side of the midline (Fig. 1B). The lateral gastralia articulate in parallel with the medial gastralia in an elongated groove. The medial gastralia imbricate with contralateral gastralia along the ventral midline, creating a distinctive zig-zag pattern of articulation. The cranialmost or caudalmost gastralial rows may coalesce, and form a single median chevron-shaped gastralium (Fig. 1B).
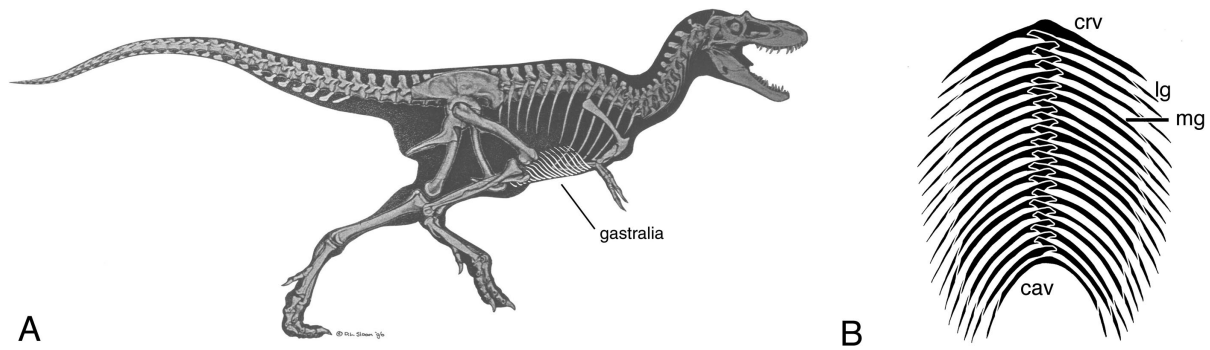
FIGURE 1. The position and general morphology of the gastralia in Theropoda: **A**, subadult *Albertosaurus libratus* RTMP 91.36.500, lateral view (reconstruction courtesy of Donna Sloan, Royal Tyrrell Museum); **B**, generalized tyrannosaurid gastralial system, ventral view. **Abbreviations**: **cav**, caudal chevron-shaped gastralium; **crv**, cranial chevron-shaped gastralium; **lg**, lateral gastralium; **mg**, medial gastralium.

Lateral Gastralia

Prosauropod and theropod lateral gastralia are slightly curved, rod-shaped bones, that taper at both extremities (Fig. 2A, B). Each lateral gastralium articulates in parallel with the medial gastralium along its craniolateral surface (Figs. 1B, 3A–C), via a groove on the caudomedial surface of the lateral gastralium (Fig. 2B). In prosauropods and small theropods such as coelophysids, troodontids, oviraptorids, and dromaeosaurids, the lateral gastralia are generally 1.5 to 2.5 times as long as their medial counterparts, and have a relatively shorter articular surface with the medial gastralium. In large theropods, such as allosaurids or tyrannosaurids, the lateral gastralia are generally much smaller than the medial gastralia, both in length and diameter. In large theropods, especially tyrannosaurids (RTMP 91.36.500, NMC 2120, MOR 555), the lateral and medial gastralia occasionally fuse.

Medial Gastralia

Prosauropod and theropod medial gastralia are convex, slender, rod-like bones, which articulate with one lateral gastralium, and two contralateral medial gastralia (Figs. 1B, 3A–C). The medial gastralium tapers laterally. A longitudinal groove for articulation with the lateral gastralium is positioned on the craniolateral surface (Fig. 4A, C, F, H, J). Medially, the medial gastralium bears two facets for articulation with two different contralateral medial gastralia: one articular facet on the dorsal,

and one articular facet on the ventral side of the gastralium (Fig. 4A–F). The dorsal facet is usually round to oval and slightly elevated. Occasionally additional rugosities are present on the dorsal surface. The ventral facets are positioned slightly less medial than the dorsal facets. In large theropods, such as allosaurids and tyrannosaurids, the ventral facets are situated on a caudal wing-like expansion of the diaphysis (Fig. 4A, B, E, F). The ventral facets are generally less well-defined in shape than the dorsal facets, and are generally larger than the dorsal facets (Fig. 4B, E).

In tyrannosaurids and allosaurids, the medial gastralia are generally at least twice as long and thick as the lateral gastralia. However, in prosauropods and small theropods (e.g., *Sellosaurus* [GPIT 18 392], *Ammosaurus* [MNA G2 7233], *Plateosaurus* [AMNH 21559], *Sinornithoides* [IVPP V9612], *Oviraptor* [IGM 100/1002], and dromaeosaurid [IGM 100/985]), the medial gastralia are generally shorter than the lateral gastralia by a factor of 1.5 to 2.5. The total length of the medial gastralia also has a considerable range within dinosaurs, from approximately 10 mm in *Sinornithoides* (IVVP V9612) to over 100 cm in *Tyrannosaurus rex* (FMNH PR2081).

In small theropods, the wing-like expansion of the medioventral articular facet is not as pronounced as in larger theropods, and may be absent. A slight caudad expansion can often be distinguished in ornithomimids (RTMP 95.110.1; RTMP 90.26.1), oviraptorids (IGM 100/1002), or dromaeosaurids (IGM 100/985), but appears relatively less pronounced than in allosaurids or tyrannosaurids. The dorsal and ventral articular facets of the medial gastralium may also be much less pronounced in smaller theropods, such as troodontids or ornithomimids (NMC 12340; UCMZ 1980.1). Often the dorsal articular facet is most clearly distinguishable, although it may be reduced to a terminal medial rugosity of the gastralium, rather than a distinct round to oval elevated articular facet. The ventral articular facet may often be reduced to a very slightly flattened or expanded rugosity, which does not stand out clearly from the texture of the surrounding diaphysis (Fig. 4G–J). In taxa with relatively short medial gastralia, such as the prosauropod *Plateosaurus* (AMNH 21559) or dromaeosaurids (IGM 100/985), the lateral articular facet is a low-angled craniolateral surface rather than a long groove.

Medial gastralia that are positioned closer to the pubis generally exhibit a more acute angle of curvature immediately lateral to the medioventral facet than gastralia that are positioned more cranially. The texture and elevation observed on many mediodorsal gastralial articular facets, notably in tyrannosaurids, appears similar to that of fossil synovial joint surfaces, and it is possible that the medial articular facets might have had a secondary cartilaginous covering.
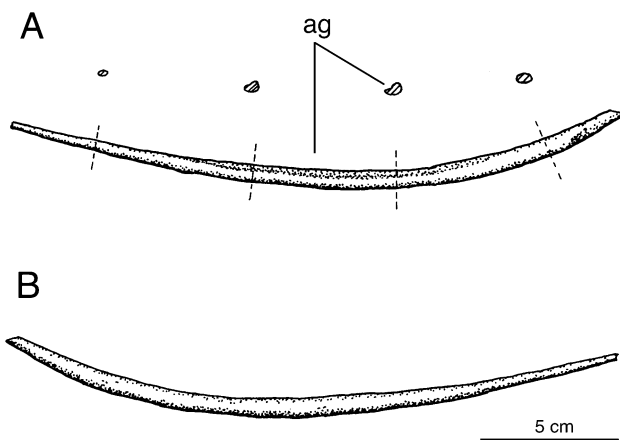

FIGURE 2. Lateral gastralium. Subadult *Albertosaurus libratus* RTMP 91.36.500: **A**, dorsal; **B**, ventral view. **Abbreviation**: **ag**, articular groove.
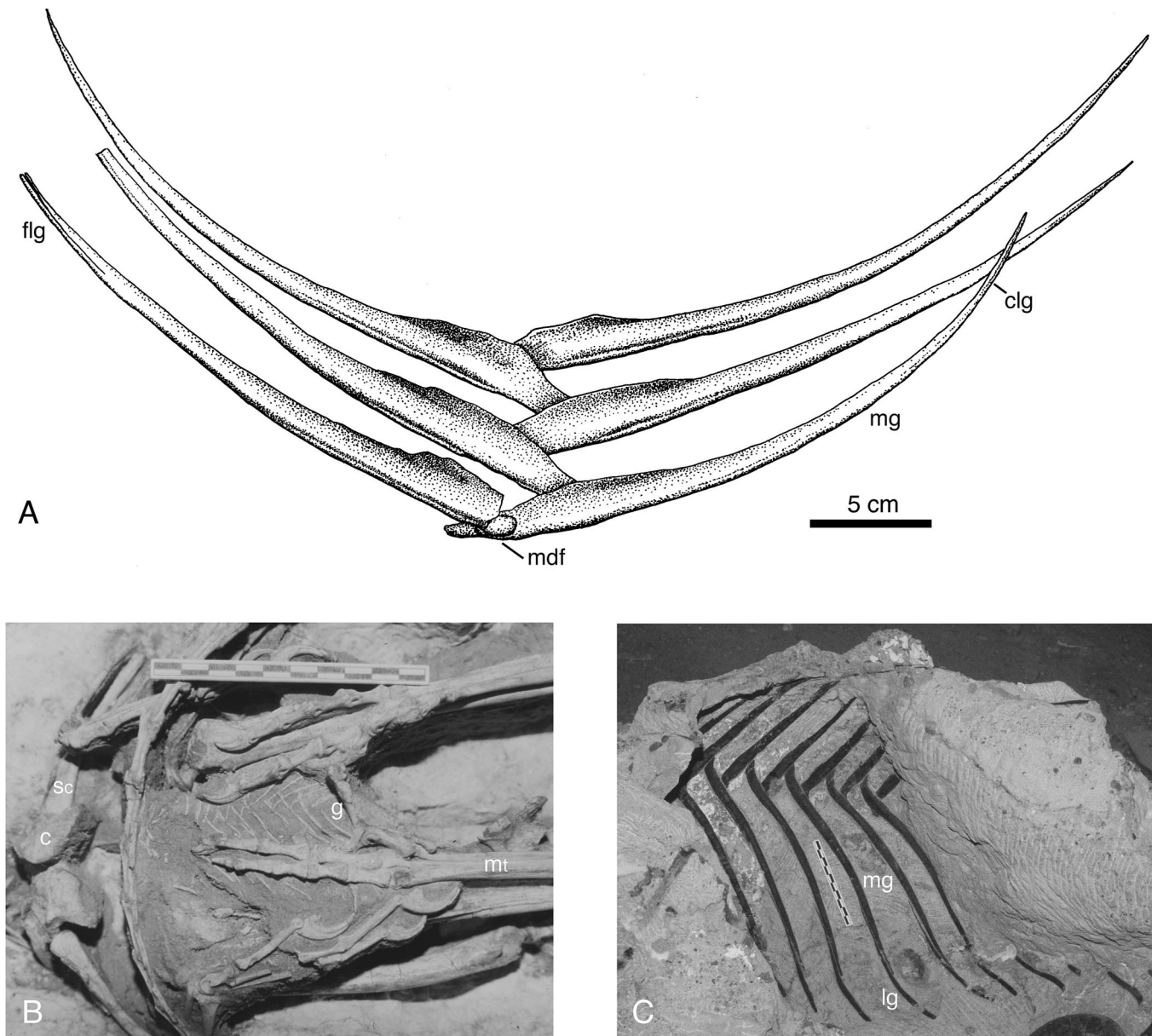
FIGURE 3.   In situ imbricating articulation of the gastralia in **A**, subadult *Albertosaurus libratus* RTMP 91.36.500, dorsal view; **B**, *Sinornithoides youngi* IVPP V9612, ventral view; **C**, *Allosaurus* DINO 11541, dorsal view. **Abbreviations**: as in Figure 1, and **c**, coracoid; **clg**, craniolateral groove; **g**, gastralia; **mdf**, mediodorsal facet; **mt**, metatarsal; **sc**, scapula. Scale in B and C is 10 cm.

Chevron-Shaped Gastralia

Two types of chevron-shaped gastralia occur: a cranial, obtusely angled gastralium (Fig. 5A–D, I) and a caudal acutely angled gastralium (Fig. 5G, H, J, K). The angle between the arms of obtuse gastralia is generally about 120–130 degrees; the angle between the arms of acute gastralia usually has a range of about 70–90 degrees.

The arms of both the obtuse and the acute chevron-shaped gastralia taper laterally (Fig. 5A–K). However, in obtuse chevron-shaped gastralia, the arms are often more blade-like, and the lateral gastralia are usually fused on (Fig. 5A–D). The apices of obtuse chevron-shaped gastralia often show a straight, cranio-caudal line of fusion (RTMP 91.36.500; NMC 2196) (Fig. 5A, D). A cranial or caudal notch may be present on the apex of an obtuse chevron-shaped gastralium (NMC 2196, IGM 107/3) (Fig. 5C, D), or absent (NMC 12340) (Fig. 5I). Often

the apex of an obtuse chevron-shaped gastralium is expanded cranially (e.g., NMC 2196; CMNH 9380; FMNH PR2081) (Fig. 5C, D).

Single large blade-like medial gastralia were recovered from tyrannosaurids NMC 2120, NMC 8506 and UA 10, and the allosaurid DINO 11541. These bones are part of an unfused anterior obtuse chevron-shaped gastralium (Fig. 5E, F). The blade-like gastralia exhibit a straight articular surface at their medial end, and lack the mediodorsal articular facets otherwise found on medial gastralia. A distinct medioventral articular facet is present on the right arm only (NMC 2120, NMC 8506, UA 10) (Fig. 5F). Because the arms of the cranialmost row of subadult tyrannosaurid specimen RTMP 91.36.500 are fused, whereas in the adult *Daspletosaurus torosus* specimen NMC 8506 both arms of the cranial chevron remain unfused, it is unlikely that lack of fusion can be ascribed solely to ontogenetic factors.
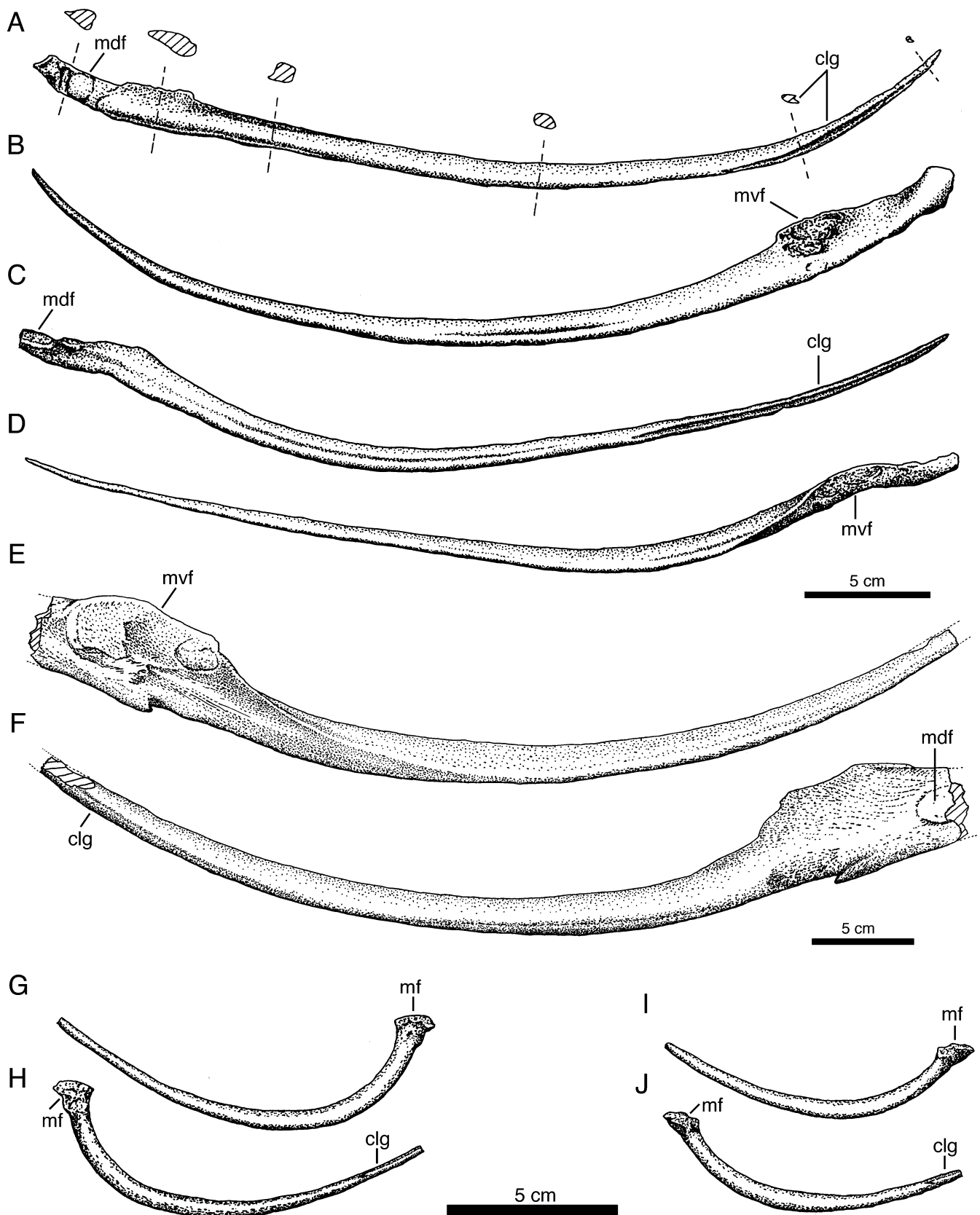
FIGURE 4.   Medial gastralia: **A–D**, left gastralium subadult *Albertosaurus libratus* RTMP 91.36.500, **A**, dorsal; **B**, ventral; **C**, cranial; **D**, caudal view; **E–F**, Right gastralium tyrannosaurid RTMP 67.22.1, **E**, ventral; **F**, dorsal view; **G–J**, *Troodon formosus*, NMC 12340, medial gastralia. **Abbreviations**: as in Figure 3, and **mf**, medial facet; **mvf**, medioventral facet.
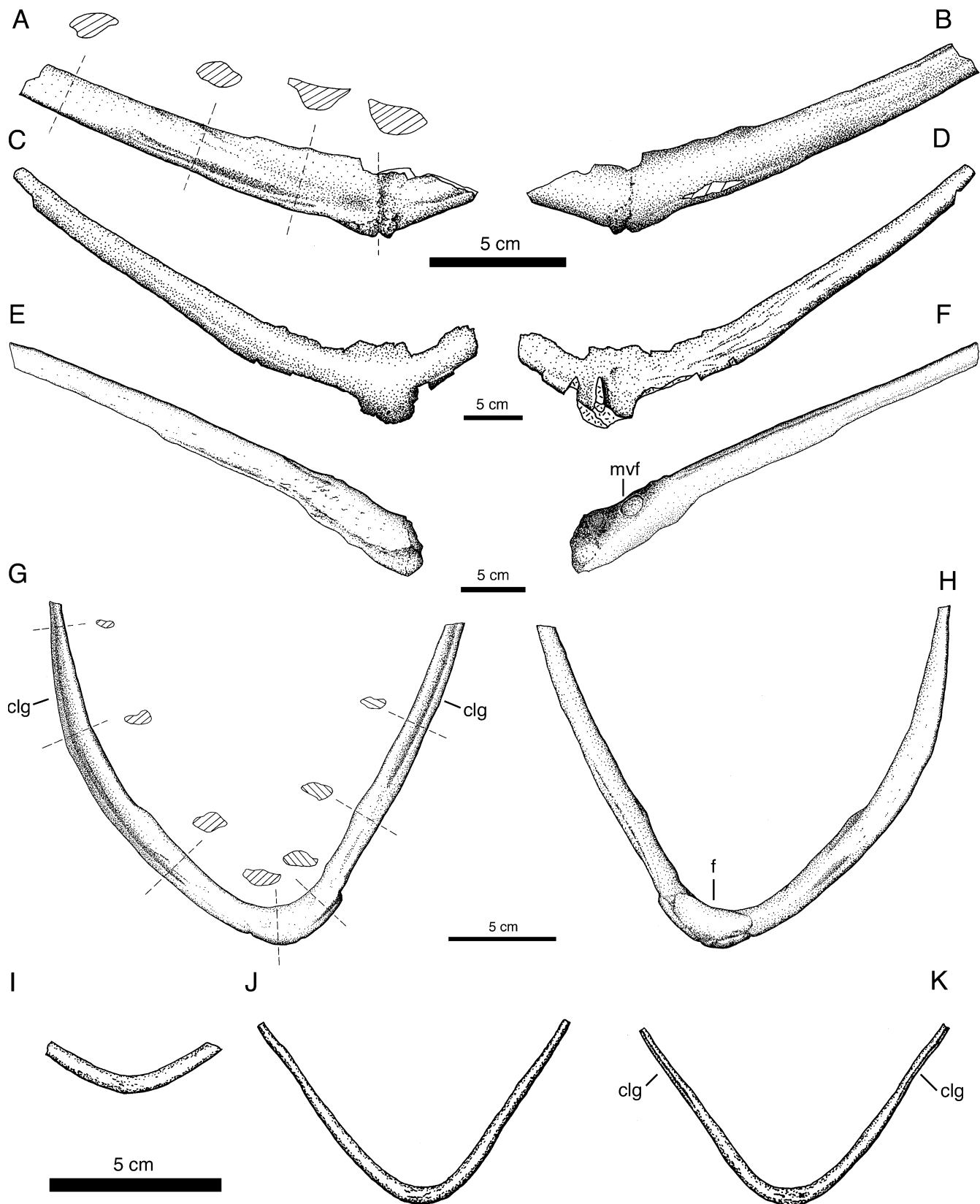
FIGURE 5.   Chevron-shaped gastralia: **A**, **B**, cranial chevron subadult *Albertosaurus libratus* RTMP 91.36.500, **A**, dorsal; **B**, ventral view; **C**, **D**, cranial chevron *Daspletosaurus torosus* NMC 2196, **C**, ventral; **D**, dorsal view; **E**, **F**, *Albertosaurus libratus* UA 10 right arm of cranial chevron, **E**, ventral; **F**, dorsal view; **G**, **H**, caudal chevron *Daspletosaurus torosus* NMC 11315, **G**, ventral; **H**, dorsal view; **I**, cranial chevron *Troodon formosus*, NMC 12340; **J**, **K**, caudal chevron *Troodon formosus*, NMC 12340, **J**, dorsal; **K**, ventral view. **Abbreviations**: as in Figure 3, 4, and **f**, fused facets.
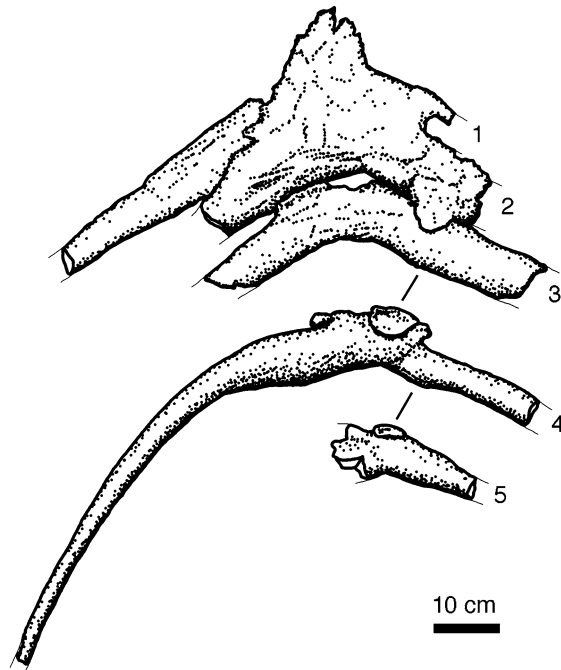
FIGURE 6. Cranial chevron-shaped gastralia in *Tyrannosaurus rex* FMNH PR 2081, dorsal view. Individual diaphyses marked one through five. Caudad chevrons (diaphyses 4 and 5) are separated from the preceding chevrons to show the single right mediodorsal articular facets that articulate with the right medioventral facet of the preceding chevron. Lines indicate the position of the facets.

The arms of acute, chevron-shaped gastralia do not exhibit a blade-like morphology like that of obtuse chevron-shaped gastralia. Craniolateral grooves for articulation with lateral gastralia are usually present on both sides (NMC 12340, NMC 11315, ROM 807), and fusion with the lateral gastralia seems to be much less common than in obtuse chevron-shaped gastralia (Fig. 5G, H, J, K). The sutures in the apices of acute gastralia are usually similar to the overlapping medial extremities of individual medial gastralia (NMC 12340, NMC 11315), and are not a straight cranio-caudal line as observed in obtuse chevron-shaped gastralia. Articular facets are obscured by the fusion of the medial arms in the apex of acute chevron-shaped gastralia (Fig. 5G, H).

Chevron-shaped gastralia occur in the cranialmost and caudalmost positions of the theropod and prosauropod gastralial apparatus. The obtuse chevrons are found in the cranial position; the acute chevrons are positioned near the pubis. Earlier reports illustrating chevron-shaped gastralia throughout the gastralial apparatus are not based on (in situ) fossil evidence (e.g., Eudes-Deslongchamps, 1838; von Huene, 1908, 1915; Gilmore, 1920; Camp, 1936; Madsen, 1976). Chevron-shaped gastralia are not found in all theropod specimens, and the occurrence of these bones even appears to vary within species.

In *Tyrannosaurus rex* FMNH PR2081 the first five cranial rows of gastralia are fused in the ventral midline, to form four chevrons (Fig. 6). The first chevron has a large plate-like apex with two diaphyses extending laterally in each direction (Fig. 6). The apices of the fourth and fifth chevron-shaped gastralia show sutures similar to overlapping fused medial gastralia, and have distinct mediodorsal articular facets. These facets are derived from the medial end of the left gastralial arm, and are situated slightly to the right of the ventral midline (Fig. 6). Each dorsal facet articulates with the medioventral facet of the preceding right arm. It seems likely that the relatively elaborate

caudad extent of ventral midline fusion in FMNH PR2081 is pathologic, possibly a factor of old age.

Lambe (1917) identified a distorted bony plate of *Albertosaurus libratus* NMC 2120 as remains of the sternum, and in a reconstruction identified two elongated processes as representing the attachment point of sternal ribs. When compared to the cranial fused plate of gastralia in both Osborn's (1906) *Tyrannosaurus rex* AMNH 973 (now CMNH 9380) and FMNH PR2081, the resemblance between the sternum of *Albertosaurus libratus* NMC 2120 and the fused cranial double gastralial rows of CMNH 9380 and FMNH PR2081 is apparent. Brochu (2003) has suggested that the "sternum" of *Albertosaurus libratus* NMC 2120 might in fact comprise the apex of two additional fused cranial chevron-shaped gastralial rows. In extant crocodylians and *Sphenodon* the gastralia exhibit a relatively large amount of plasticity in development, which may explain the relatively large amount of fusion and other minor variations observed in the gastralial apparatus. Gastralial pathologies are treated in more detail later in this paper. Because the sternum described by Lambe (1917) for *Albertosaurus libratus* is the only theropod sternum known outside of Maniraptora, this re-identification has potentially important consequences for phylogenetic systematics (Brochu, 2003).

Furculae

Amid the recent interest in theropod furculae (Thulborn, 1984; Barsbold, 1983; Bryant and Russell, 1993; Chure and Madsen, 1996; Norell et al., 1997; Makovicky and Currie, 1998) has been debate about the correct identification of chevron-shaped bones associated with the ventral trunk skeleton of theropods. Both theropod furculae and chevron-shaped gastralia have been recovered in situ; a furcula has been recovered in situ with *Allosaurus* (DINO 11541), described by Chure and Madsen (1996), and an in situ preserved chevron-shaped gastralium is present in the gastralial apparatus of *Tarbosaurus* (IGM 107/3). Furculae have now been documented in allosaurids (Chure and Madsen, 1996), oviraptorids (Barsbold, 1983), dromaeosaurids (Norell et al., 1997), and tyrannosaurids (Makovicky and Currie, 1998), and tentatively identified in *Coelophysis* (pers. obs., 1998; Downs, 2000).

Dinosaur gastralia and furculae can easily be distinguished based on morphological characteristics. The rami of theropod furculae do not taper like chevron-shaped gastralia (Fig. 7A–D). The lateral extremities of theropod furculae often bear spatulate articular facets for articulation with the scapulocoracoid (Fig. 7C, D), instead of grooves for articulation with lateral gastralia (Fig. 5G, H, J, K). The spatulate articular facets are often slightly flattened in the sagittal plane. The rami of the furcula generally exhibit a sigmoid curvature. The angle between the rami of the furcula in allosaurids and tyrannosaurids ranges from 125° to 135°; in oviraptorids the angle is approximately 80°. The structure of the apex of the furcula can vary widely, as in chevron-shaped obtuse gastralia. A hypocleideum may be present or absent, but the distinct midline or asymmetrical sutures observed in many cranial or caudal fused chevron-shaped gastralia, respectively, are not present in the apices of theropod furculae. In larger theropods such as allosaurids and tyrannosaurids, the furcula is only about a third of the size of a cranial chevron-shaped gastralium.

The argument that the angles of the chevron-shaped elements recovered with *Allosaurus fragilis* are too obtuse to represent furculae (Bryant and Russell, 1993) is no longer valid considering the new morphological evidence. However, the chevron-shaped bones of *Albertosaurus libratus* (NMC 2120) and *Troodon formosus* (NMC 12340; Fig. 5J, K), identified by Thulborn (1984) as possible furculae, are in fact chevron-shaped gastralia, because they exhibit lateral tapering, have grooves for artic-
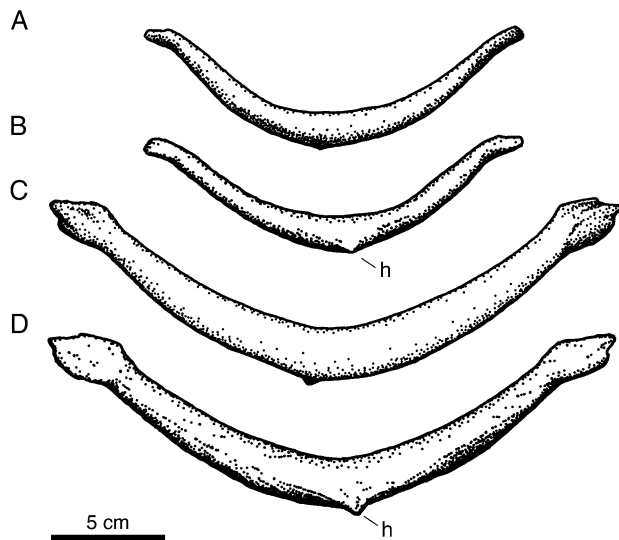
FIGURE 7.   Tyrannosaurid furculae: **A**, **B**, *Daspletosaurus torosus* NMC 8506, **A**, ventral; **B**, dorsal view; **C**, **D**, *Daspletosaurus torosus* NMC 11315, **C**, ventral; **D**, dorsal view. **Abbreviation**: **h**, hypocleideum.

FIGURE 8.   Cladogram depicting the presence of gastralia, and imbricating mid-ventral articulation versus articulation in individual gastralial rows in the Archosauromorpha. The plesiomorphic condition, imbricating or separate rows, is unknown. The loss of gastralia in the Ornithischia is considered to be autapomorphic for the group.

ulation with lateral gastralia, and, in the case of *Albertosaurus libratus* NMC 2120, also have a medioventral articular facet.

Articulation

Traditionally, dinosaur gastralia were described as separate, non-imbricating metameric rows, similar to the arrangement in extant crocodylians and *Sphenodon* (e.g., Eudes-Deslongchamps, 1838; Osborn, 1906; Lambe, 1917; Gilmore, 1920; Romer, 1956; Maleev, 1974; Russell and Dong, 1993). Barsbold (1983) briefly noted that the rows of gastralia in *Tarbosaurus* and other ''carnosaurs'' imbricated along the ventral midline. Recently, Claessens (1996a, b, 1997) noted that the gastralia imbricated along the ventral midline in all theropods and prosauropods, and Norell and Makovicky (1997) described a dromaeosaurid specimen with imbricating gastralia.

The imbricating ventral midline articulation of the gastralia can be observed in situ in multiple non-avian theropod specimens (Fig. 3A–C), including the basal theropod *Coelophysis* (CMNH 31798), *Allosaurus* (DINO 11541), tyrannosaurids *Albertosaurus* (RTMP 91.36.500; RTMP 86.64.1) and *Tarbosaurus* (IGM 107/3), troodontid *Sinornithoides* (IVPP V9612), and dromaeosaurid (IGM 100/985). The imbricating articulation pattern is also observed in fossil birds that retain gastralia, such as the Berlin *Archaeopteryx* and the confuciusornithids *Confuciusornis* (GMV 2152) and *Changchengornis* (GMV 2129).

Although most dinosaur gastralia are not preserved in situ, the ventral midline articulation pattern can easily be deduced from the structure of individual medial gastralia. Because each medial gastralium has both a mediodorsal and a medioventral articular facet, each individual gastralial row would have one facet of each type that would not be in articulation, unless imbricated along the ventral midline. If the medial gastralia articulated in individual rows, only a single ventral facet on the medial gastralium of one side of the body, and a corresponding dorsal facet on the contralateral medial gastralium would suffice.

No prosauropod specimens were noted during this survey in which an in situ arrangement of imbricating ventral midline articulation could be positively identified. However, based on the presence of dorsal and ventral articulations on individual
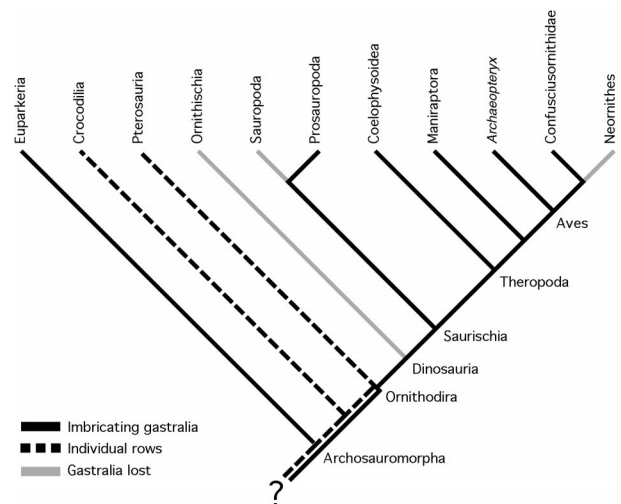
medial gastralia, the existence of an imbricating system could be deduced in *Plateosaurus* (AMNH 21559) and other disassociated prosauropod gastralial material.

The imbricated articulation pattern of the gastralia is present in basal taxa, such as coelophysids and prosauropods, and in derived groups such as maniraptorans and basal birds. The imbricating articulation pattern is present in the smallest forms, such as the troodontids, and in larger dinosaurs, such as the tyrannosaurids. It appears reasonable to assume that this articulation pattern is primitive for, and is present throughout, the Dinosauria. Whether the imbricating ventral midline articulation pattern of the gastralia is derived for dinosaurs, or whether it is the primitive condition for dinosaurs or a larger group, is unclear (Fig. 8). Ewer (1965) described a ventral midline articulation pattern of the gastralia in *Euparkeria* that is reminiscent of the imbricating pattern observed in dinosaurs, and the arrangement of the ventral body armor in early tetrapods such as *Greererpeton* (CLM 11090) already appears to have the same basic imbricating structure (Fig. 9A, B). However, several other tetrapod groups, such as some genera of the Pterosauria and Plesiosauria, possessed a gastralial system composed of separate rows positioned between the pubis and sternal region, similar to the only extant groups to retain gastralia, the Crocodylia and *Sphenodon*. The evolution of the different articulation pat-
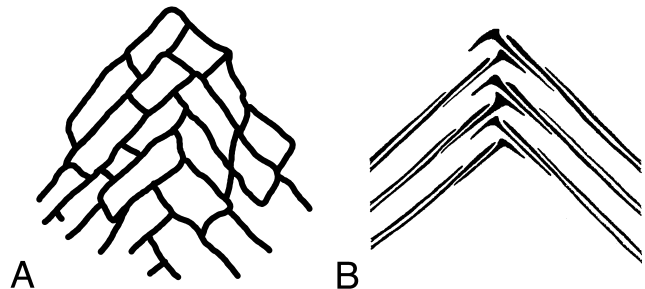

FIGURE 9.   Imbricating mid ventral articulation of the gastralia in: **A**, the Carboniferous colosteid *Greererpeton burkemorani* CMNH 11090 (redrawn from Romer, 1972); and **B**, the basal archosauromorph *Euparkeria* (redrawn from Ewer, 1965).

terns of the gastralia in tetrapods needs more study before it can be resolved.

Number of Bones per Gastralial Row

Each gastralial row consists of four bones, two lateral and two medial rods. Midline fusion of the medial gastralia may reduce the total number of bones per row to three, or even one, if the lateral gastralia are also fused, but these reduced numbers are only observed in the cranialmost or caudalmost gastralial rows.

A large variation in the number of bones per gastralial row in the Dinosauria is recorded in the literature (e.g., Eudes-Deslongchamps, 1838; Osborn, 1906, 1916; von Huene, 1908, 1915; Gilmore, 1920; Sternberg, 1933; Camp, 1936; Madsen, 1976; Nicholls and Russell, 1981; Currie and Zhao, 1993). However, examination reveals that the identification of additional bones per row (e.g., Osborn, 1916; Gilmore, 1920) is usually based on broken or pathologic material, and the identification of fewer elements is based on the assumption of midline fusion of the medial gastralia throughout the gastralial apparatus (e.g., von Huene, 1908, 1915; Camp, 1933). Rapid reduction within the Dinosauria in the number of bones per gastralial row and in the total number of gastralial rows, as suggested by Osborn (1916), Gilmore (1920), and Sternberg (1933), does not occur.

Number of Rows, Pathologies, and Variability

The variation in the number of rows between different theropod groups seems to be related to size. Smaller theropods generally have the fewest rows of gastralia, whereas larger theropods appear to have the most. There is no correlation between the number of vertebral segments and the number of gastralial rows. However, there is minor variation in the number of preserved rows within groups such as the Ornithomimidae or Tyrannosauridae, for which many specimens with completely preserved gastralial systems are known. In for instance *Ornithomimus* RTMP 95.110.1, 16 gastralial rows are present, in *Struthiomimus* UCMZ 1980.1, 15 gastralial rows are present, in *Struthiomimus* RTMP 90.26.1, 14 gastralial rows are present, and in *Struthiomimus* AMNH 5339 as few as 13 rows may be preserved. It does not appear likely that taphonomic processes account for the range of preserved gastralial rows, considering that most of the skeletons in question are relatively undisturbed. Also, there is no bimodal distribution of variation in the number of preserved gastralial rows, so sexual dimorphism is unlikely. Sternberg (1933) noted a difference in the number of rows preserved in *Ornithomimus edmontonicus* (NMC 8632), recording 14 gastralial rows on the left side and 15 rows on the right side.

In the development of the gastralia in *Crocodylus niloticus* (*madagascariensis*), Voeltzkow and Döderlein (1901) observed an initial formation of ten rows, of which only eight are carried to full development. The cranialmost two rows are completely reduced before hatching. Some variation occurs in the number of gastralial rows observed within the Crocodylia. The total number of rows is generally eight, but more or fewer rows are frequently observed (Eudes-Deslongchamps, 1838; Chiasson, 1962; pers. obs.). In addition to the observed variation in the number of gastralial rows within Crocodylia, individual rows sometimes consist of only two medial or two lateral gastralia, or have a third additional intermediate component (Eudes-Deslongchamps, 1838; Voeltzkow and Döderlein, 1901; pers. obs.). The abnormal rows usually appear to be confined to either the cranialmost or caudalmost positions in the gastralial apparatus. Only fusion of lateral to medial elements seems to be more widespread throughout the gastralial apparatus. However, the latter type of synostosis can occur later in ontogeny and is not necessarily embryological in origin. Fusion of the apices of

consecutive rows of gastralia in *Sphenodon*, in conjunction with other occasional asymmetries has also been reported (Howes and Swinnerton, 1901; Gilmore, 1920; Daiber, 1920). The apical fusion of consecutive rows much resembles that observed in the cranial chevrons of *Tyrannosaurus* (CMNH 9380, FMNH PR2081).

The apparent developmental plasticity of the gastralia has considerable implications for the importance of minor variations in the number of rows or the morphology of individual rows within or between groups. The use of minor variations in the composition of the gastralial system in phylogenetic analysis is likely to introduce false patterns, and is insufficient grounds for separating species. The occasional occurrence of aberrant fusions and alterations to rows, such as the pronged gastralium in dromaeosaurid IGM 100/985 noted by Norell and Makovicky (1997) and the additional incomplete caudal row in ornithomimid RTMP 95.110.1, is likely to have only limited significance.

Healed fractures are not uncommon in dinosaur gastralia. The frequent occurrence of healed fractures and pseudo-arthroses in *Allosaurus* specimens from the Cleveland-Lloyd Quarry probably prompted Gilmore (1920) to describe a gastralial apparatus with seven to nine bones per row for this genus (Claessens, 1996a; Chure, 2000). In other groups healed gastralia are not infrequently observed (e.g., Sander, 1992; Kälin, 1937; pers. obs.). The occurrence of pseudo-arthrosis might point to a relatively high level of mobility of the gastralia, preventing proper healing.

SAUROPOD "GASTRALIA" OR STERNAL RIBS

Until recently, gastralia were thought not to be present within the Sauropoda. However, after Filla and Redman (1994) described what they identified as a nearly complete set of gastralia in a new species of *Apatosaurus*, (*A. yahnapin*, TM 001), the occurrence of gastralia within the Sauropoda quickly became accepted in the literature (e.g., McIntosh, 1997; McIntosh et al., 1997; Makovicky, 1997; Sereno et al., 1999).

The "gastralia" of *A. yahnapin* (TM 001) were preserved in nine V-shaped rows in which the apices point cranially. There was no overlap of the single rod-like bones of each body half in the ventral midline. The rod-like bones range widely in length; the caudalmost "gastralium" is approximately five times smaller than the cranial "gastralia." The bones are rod-like or flattened strips. The shape of the cross-sections varies considerably. Rugosities and knobby outgrowths are present over the entire bone surface (Fig. 10A, B).

With the type specimen of *Apatosaurus excelsus* (YPM 1980) several bone fragments were recovered near the sternal plates that were identified as sternal ribs (Marsh, 1896) (Fig. 10C, D). These bones exhibit the same rugosities and outgrowths observed on the *A. yahnapin* (TM 001) "gastralia," and the rod-like elements are without a doubt similar structures. However, one of the bony elements of *A. excelsus* (YPM 1980) is flat and three-pronged (Fig. 10D).

When Filla and Redman (1994) described the elements recovered with *A. yahnapin* (TM 001) as gastralia, they drew upon a body of literature that allowed a wide range of morphological structures to be designated as gastralia. However, the current survey of gastralial morphology indicates a remarkable consistency in the composition of the gastralial apparatus in dinosaurs, in contrast to information available in the literature.

The bones identified as sauropod gastralia lack several of the characteristics observed in a wide range of taxa including basal archosauromorphs such as *Euparkeria*, extant crocodylians, prosauropods, theropods, and *Sphenodon*. The gastralia of these groups all consist of lateral and medial components, taper at either the lateral or both ends, and possess grooves for articu-
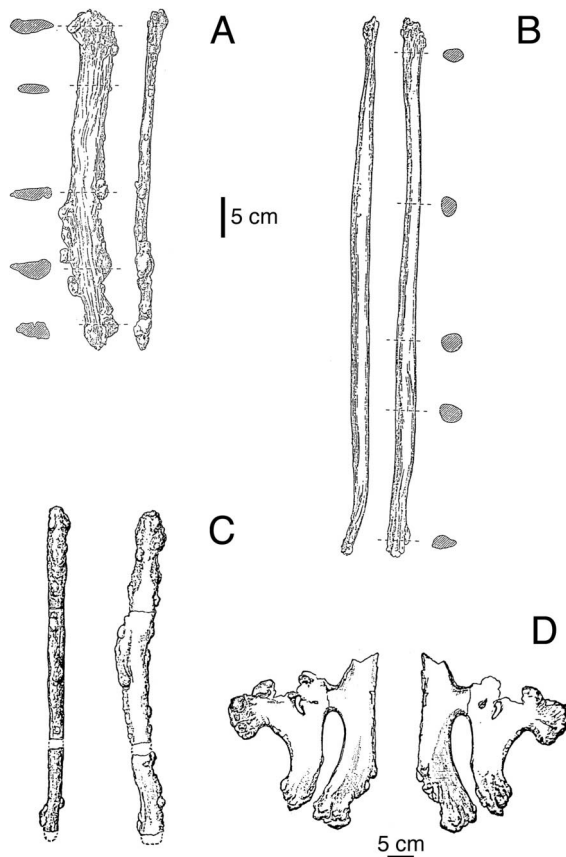
FIGURE 10. Sauropod sternal ribs: **A**, **B**, *Apatosaurus yahnapin* TM 001, **A**, eighth sternal rib; **B**, second sternal rib (redrawn after Filla and Redman, 1994, with original material at hand); **C**, **D**, *Apatosaurus excelsus* YPM 1980 (redrawn after Marsh, 1896, with original material at hand).

conform exactly with the number of sternal ribs originally drawn by Marsh in his reconstruction of *A. excelsus* (YPM 1980). The significant decrease in length of the ''gastralia'' caudad would conform with the expected caudad decrease in length of the cartilaginous extensions of the true ribs. The sternal ribs of tetrapods generally do not taper as archosaur gastralia do, and generally articulate at their distal extremities with other costal or sternal structures via end-to-end contacts rather than elongate grooves or articular facets on the diaphysis. Also, the rarity of ''gastralia'' in the relatively extensive sauropod fossil record would be more plausible considering the limited ossification or fossilization of cartilaginous structures such as sternal ribs.

All of the arguments for identification as sternal ribs are opposed only by the fact that the bones were recovered in cranially pointing, V-shaped rows close to the pubic bones. However, collapse of the thorax could have moved the sternal ribs in the same position as that in which the supposed gastralia were recovered. In fact, the distal extremities of the thoracic ribs (where the proximal sternal ribs articulate) were preserved adjacent to the proximal extremities of the supposed gastralia.

Other rod-like bones associated with sauropod skeletons have been re-identified as ''gastralia,'' including an elongate bone of *Camarasaurus supremus*, which Osborn and Mook (1921) identified as a sternal rib. Similar bones, possibly of *Camarasaurus*, are present in the wall at Dinosaur National Monument. Although the extent of the rugosities on the *Camarasaurus* material appears to be limited to the extremities, all morphological attributes point to sternal ribs rather than gastralia. Sereno et al. (1999) reported the discovery of gastralia in *Jobaria*, but did not discuss gastralial morphology.

Histological study of the *Apatosaurus* bones may decisively rule out their identification as gastralia if the bones consist of calcified cartilage, because gastralia are dermal bones. However, if the sauropod sternal ribs were fully ossified they might be histologically indistinguishable from gastralia. Unfortunately, neither the *A. yahnapin* nor the *A. excelsus* material is available for such invasive study at present. It is the author's opinion, however, that currently there are no solid grounds to question the original identification of the sauropod bones as sternal ribs (Marsh, 1896; Osborn and Mook, 1921).

ORNITHISCHIAN ''GASTRALIA''

Gastralia have never been found in ornithischians. Owen (1863) noted the possible presence of ''abdominal ribs'' in *Scelidosaurus harrisonii*, but the term is intended to indicate a sternal rib rather than a gastralium. Gilmore (1924) described the ''gastralia'' of *Stegoceras validus* (UA 2), which at that time was incorrectly synonymized with the theropod genus *Troodon*. The bones described by Gilmore (1924) as gastralia are ossified tendons (Sues, 1977; Claessens, 1996a).

DISCUSSION

The Relationship Between Gastralia and Soft Tissue Anatomy

In *Sphenodon* and in extant crocodylians, the gastralia are attached to the pubis and sternum through midventral ligaments (Daiber, 1920; Voeltzkow and Döderlein, 1901; pers. obs.). The last row of gastralia in extant crocodylians attaches to the pubis medially through a broad ligamentous sheet, and laterally through a thick round ligament (Voeltzkow and Döderlein, 1901; pers. obs.) (Fig. 11B).

In prosauropods and theropods, the attachment of the gastralia to the pubic bones and sternum was probably similar to that of extant crocodylians. In *Ornithomimus* RTMP 95.110.1, a large tuberosity on the lateral surface of the pubis, immedi-

lation between medial and lateral gastralia. Although it is unclear whether the primitive pattern of gastralial midline articulation in dinosaurs was imbricating or in separate rows (Fig. 8), midline articulation of the elements would most likely have been present. By contrast, the elements described as sauropod gastralia do not show any of these morphological characteristics. There are no articular facets present on the bones like those observed on prosauropod or theropod gastralia. There is no overlap in the ventral midline. The bones do not taper laterally. Each gastralial row of *A. yahnapin* consists of two identical rod-like bones, rather than four bones per gastralial row as in other dinosaurs.

There are only nine individual rows in *A. yahnapin*, compared to a range of approximately 14–16 in prosauropods and 8–21 in theropods. In an animal with an abdomen as large as a sauropod, having only nine rows of ''gastralia'' would result in a relatively wide spacing. The five-fold range in relative size of the individual ''gastralia'' from cranial to caudal also is unprecedented within prosauropods or theropods, in which length differences between individual medial or lateral gastralia from a single individual generally do not exceed a 1 1/2-fold range.

If the bones identified by Filla and Redman (1994) were in fact sternal ribs rather than gastralia, as suggested by Marsh (1896), almost all the discrepancies would be resolved. The peculiar rugose texture and knobby outgrowths might be the result of the mineralization of cartilage. The tri-capitate element (Fig. 10D) of *A. excelsus* could be a part of the xiphisternal apparatus. The low number of nine rows of ''gastralia'' would
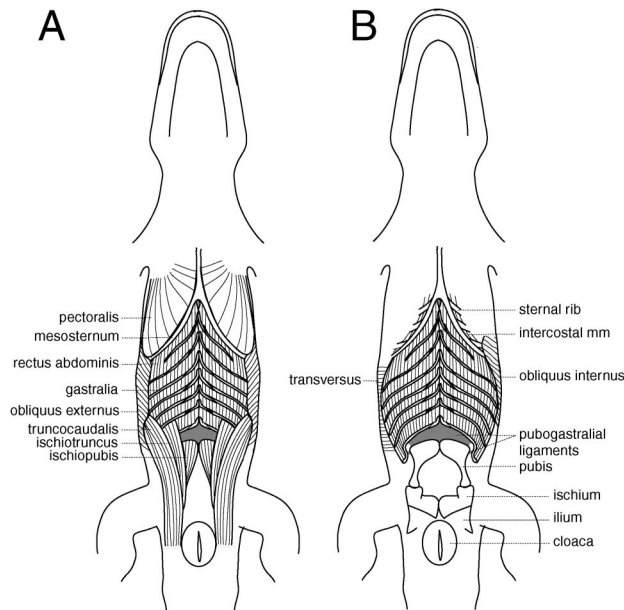
FIGURE 11. Topology of the ventral abdominal musculature and gastralia in *Alligator mississippiensis*: **A**, Superficial topology (aponeuroses of the lateral body wall musculature covering the rectus abdominis and gastralia and inserting on the linea alba not shown). The lateral extremities of the gastralia and rectus abdominis are covered in part by the truncocaudalis and ischiotruncus muscles, and the internal and external obliques, which insert partly on the lateral parts of the gastralia. **B**, Deeper dissection, pectoral muscles, the external obliques, internal oblique (left side only), and pelvic musculature removed.
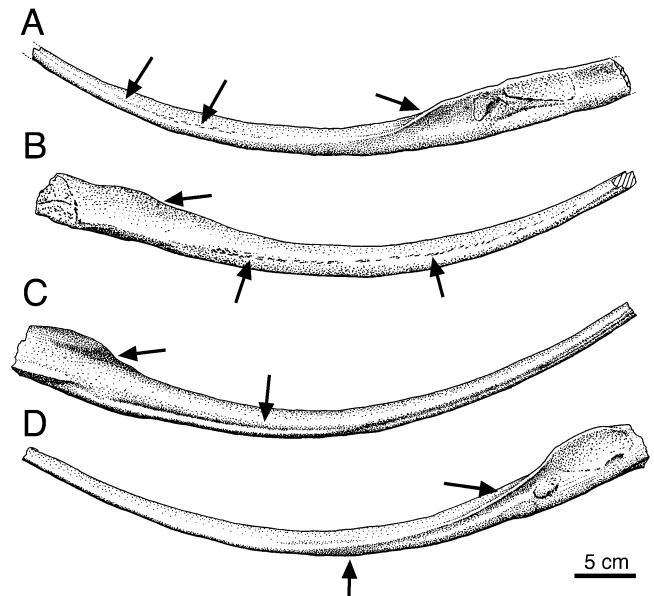

FIGURE 12. Muscle scars on tyrannosaurid gastralia: **A**, RTMP 94.12.722, ventral view; **B**, RTMP 94.12.722, dorsal view; **C**, RTMP 82.28.1, dorsal view; **D**, RTMP 82.28.1, ventral view.

ately adjacent to the lateral curve of the last row of gastralia, suggests a lateral connective ligament.

The gastralia in both *Sphenodon* and extant crocodylians are embedded in the superficial layers of the M. rectus abdominis. Slips of the M. rectus abdominis attach to each individual gastralium, and provide the majority of muscle fiber insertions on the gastralia (Byerly, 1925; Chiasson, 1962; pers. obs.). In crocodylians, the M. rectus abdominis extends from the caudal border of the sternum to the last two rows of gastralia, which are thicker than the preceding rows. Attachment of the M. rectus abdominis to the pubis is indirect, via the ligamentous sheet attaching the caudalmost gastralial row. A separate posterior portion of the M. rectus abdominis, the M. truncocaudalis, extends from the ventral surface of the M. ischio-caudalis to the lateral margins of the caudal rows of the gastralia and the fascia of the M. rectus abdominis and M. obliquus externus (Maurer, 1896; Romer, 1923; pers. obs.) (Fig. 11A, B).

I propose that the gastralia of prosauropods were embedded in the M. rectus abdominis in a manner similar to that observed in extant crocodylians and *Sphenodon*. On the medial gastralia of tyrannosaurids, distinct muscle or ligament scars can often be observed running longitudinally along the cranial and caudal borders of the diaphysis (Fig. 12A–D). The gastralia of smaller theropods also often exhibit muscle and ligament striae, but distinct regions of possible attachment are not easily identified (Fig. 4G–J). The caudalmost rows of gastralia in ornithomimids and prosauropods are thicker than the preceding rows, which may be an indication of a similar arrangement of insertion of the M. rectus abdominis (Russell, 1972; Claessens, 1996a). The absence of thickened caudal gastralia in large theropods might possibly be explained by the already large size of these structures. Mid-ventral fusion of the cranialmost or caudalmost medial gastralia into a single chevron may have facilitated the

ligamentous attachment to the sternum and pubis, respectively, of the mobile imbricating gastralial apparatus.

In extant crocodylians, several other muscle groups attach to the gastralia besides the M. rectus abdominis (Fig. 11A, B). Muscle fibers of the M. obliquus externus abdominis and the M. obliquus internus abdominis, which lie lateral and superficial to the M. rectus abdominis, insert on the lateral aspects of the gastralia (Romer, 1923; Chiasson, 1962; pers. obs.). The M. transversus abdominis lies deep to the M. rectus abdominis, and extends from the transverse fascia to the lateral gastralia. Occasionally, muscle fibers of the transversus also appear to insert on the lateral extremities of the gastralia. The M. ischiopubis and the M. ischiotruncus extend from the ischium to the cranial margin of the pubis and the two caudalmost rows of gastralia, respectively, and insert on the ventral (superficial) surface of the caudalmost gastralial rows and the M. rectus abdominis (Farmer and Carrier, 2000) (Fig. 11A, B).

Because theropods have a relatively narrow body profile compared with the body profile of extant crocodylians, it is possible that the area of attachment on the gastralia of the M. obliqui abdomini and the M. transversus abdominis was greater than in extant crocodylians.

Previously Suggested Functions of the Gastralia

Romer (1956) suggested that the ventral dermal ossifications in basal tetrapods protected the belly wall against abrasion and supported the viscera. If the ventral scutes and gastralia were homologous in basal tetrapods, the gastralia evolved a more rod-like morphology in most lineages. Many different tetrapod groups, such as dinosaurs, reduced the number of gastralial rows and the number of bones per row, which suggests a decreased importance in protecting the abdomen. Changes in the surface texture indicate that the gastralia probably migrated from a dermal position in basal tetrapods, to a deeper location in the exterior abdominal musculature in many more derived tetrapod groups, which suggests a decreased importance in reducing abrasion. It also seems less plausible that the gastralia were needed to support the viscera in more derived tetrapods such as theropods, because these structures are absent in ani-
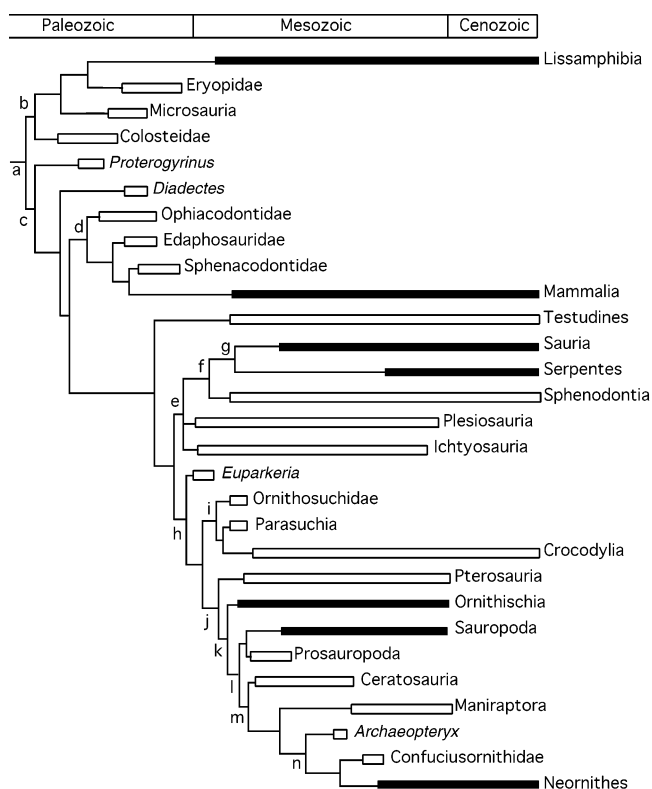
FIGURE 13. Tetrapod phylogeny showing various independent losses of gastralia. Different solutions to the problem of collapse of the belly wall during the inspiratory act have evolved in the various groups. Gastralia are the primitive solution, only retained in modern crocodylians and *Sphenodon*. In turtles the gastralia are probably incorporated in the plastron. Mammals evolved a muscularized intercoelomic diaphragm. In birds the trunk is generally rigidly encased by the ribs and sternum, and the belly wall is spanned between the caudal margins of the ribs and the expanded pelvis. In ornithischian dinosaurs a similar tension of the belly wall by the laterally oriented prepubic extension may have been present. The weight of the viscera on the belly wall likely prevented abdominal collapse in sauropods. Some lizards and frogs have evolved elaborate cartilaginous extensions of the true ribs, called inscriptional ribs, which may be analogous to the primitive solution of gastralia. Many other squamates and lissamphibians have highly compliant lungs, which may shield them from abdominal collapse. Homology between early tetrapod ventral scutes and gastralia is assumed, and the ventral osteoderms of caecilians and skinks are not plotted since they are considered skeletal neoformations, similar to the ventral osteoderms that overly the gastralia in some extant crocodylians. Phylogeny modified after Benton, 1997 and Carroll, 1988.

mals that have an equally large or larger abdomen to support such as ornithischians or sauropods.

Lambe (1917) and Paul (1988) noted that the apparent flexibility of the gastralial system in theropods allows minor changes in trunk volume during feeding, moving, or breathing. However, passive flexibility would suffice for these functions, and was probably already adequately present in the multi-row, multi-element gastralia of earlier tetrapods.

A central question is why so many groups of vertebrates appear to have lost gastralia (Perry, 1983; Claessens, 1996a, b) (Fig. 13). Perry (1983, 1989, 1992) suggested that the gastralia were passive respiratory structures that prevented "abdominal collapse." Abdominal collapse is an inward movement of the belly wall and viscera that may occur in aspiration breathing, and which reduces the space available for filling the lungs. Ob-

viously, stiffening of the belly wall with gastralia increases resistance against abdominal collapse.

All vertebrate groups that have lost gastralia seem to have evolved different mechanisms to prevent "abdominal collapse." Mammals, for instance, evolved a diaphragm that prevents visceral encroachment upon lung space during inspiration; birds have rigidly encased their lungs within the thorax; and sauropods were protected against abdominal collapse by gravitational loading of the abdominal wall by the large viscera (Fig. 13).

Preventing abdominal collapse by stiffening the belly wall with gastralia, however, is a passive function that was already adequately performed by the gastralia of basal tetrapods. The evolution of intricate mid-ventral articulations, and the reduction of the number of rows and bones per row, would be unnecessary, if not counterproductive, to such a passive function.

Gastralia as an Active Accessory Breathing Mechanism

The modifications of the gastralial apparatus of prosauropods and theropods indicate a change in function of these structures (Claessens, 1996a, b). The imbricating articulations observed in prosauropods and theropods unite the gastralial system into a single functional unit. No significant movement of individual gastralia can take place without affecting the position of other components. The mid-ventral articulations limit movement to a single plane (Fig. 14A–D). Effectively, retraction and protraction of the gastralial system narrows and widens the ventrolateral dimensions of the trunk (Fig. 14A–D). A plausible function for active retraction and protraction of the gastralial system is lung ventilation (Claessens, 1996a, b).

Contraction of the M. rectus abdominis, which probably provided the majority of muscle fiber insertion on the embedded gastralia, protracts the gastralial system, thus paradoxically decreasing the inter-gastralial distance and at the same time widening the ventral abdominal area (Fig. 14A–D). In extant crocodylians and birds, the M. rectus abdominis contracts during expiration and aids in decreasing the volume of the body cavity (Gans and Clark, 1976; Farmer and Carrier, 2000; Powell, 2000). In alligators inter-gastralial distance and gastralial width are slightly decreased during expiration (L. Claessens, unpubl. data). However, due to the imbricating articulation of theropod gastralia, contraction of the rectus can only lead to gastralial protraction, resulting in abdominal widening (Fig. 14A–D).

Contraction of the M. obliquus externus abdominis would also protract the gastralial system. Contraction of the M. transversus abdominis and M. obliquus internus abdominis retracts the gastralial system, narrowing the ventrolateral dimensions of the trunk.

Gastralial movement would result in a slight lengthening of the gastralial system at the ventral midline upon retraction, and a slight shortening of the gastralial system at the ventral midline upon protraction (Fig. 14A–D). However, because of the large lateral extent of the gastralia between the median points of articulation, gastralial movement would result in a large degree of lateral broadening of the belly wall, with minimal shortening (Fig. 14C, D). Slip of the dorsal articular facet in the "oversized" ventral facet, which is prominently present in for instance tyrannosaurids, could have reduced the changes in length of the imbricating joint system to a certain degree (Fig. 15A, B).

In ornithomimids preserved in situ, the ventral outline of the abdominal wall as indicated by the gastralia is usually concave. Although this may be a taphonomic artifact, midventral shortening of the gastralial system associated with protraction would result in ventral movement of the abdominal wall (Fig. 16A–C). The ventral movement of the body wall during protraction
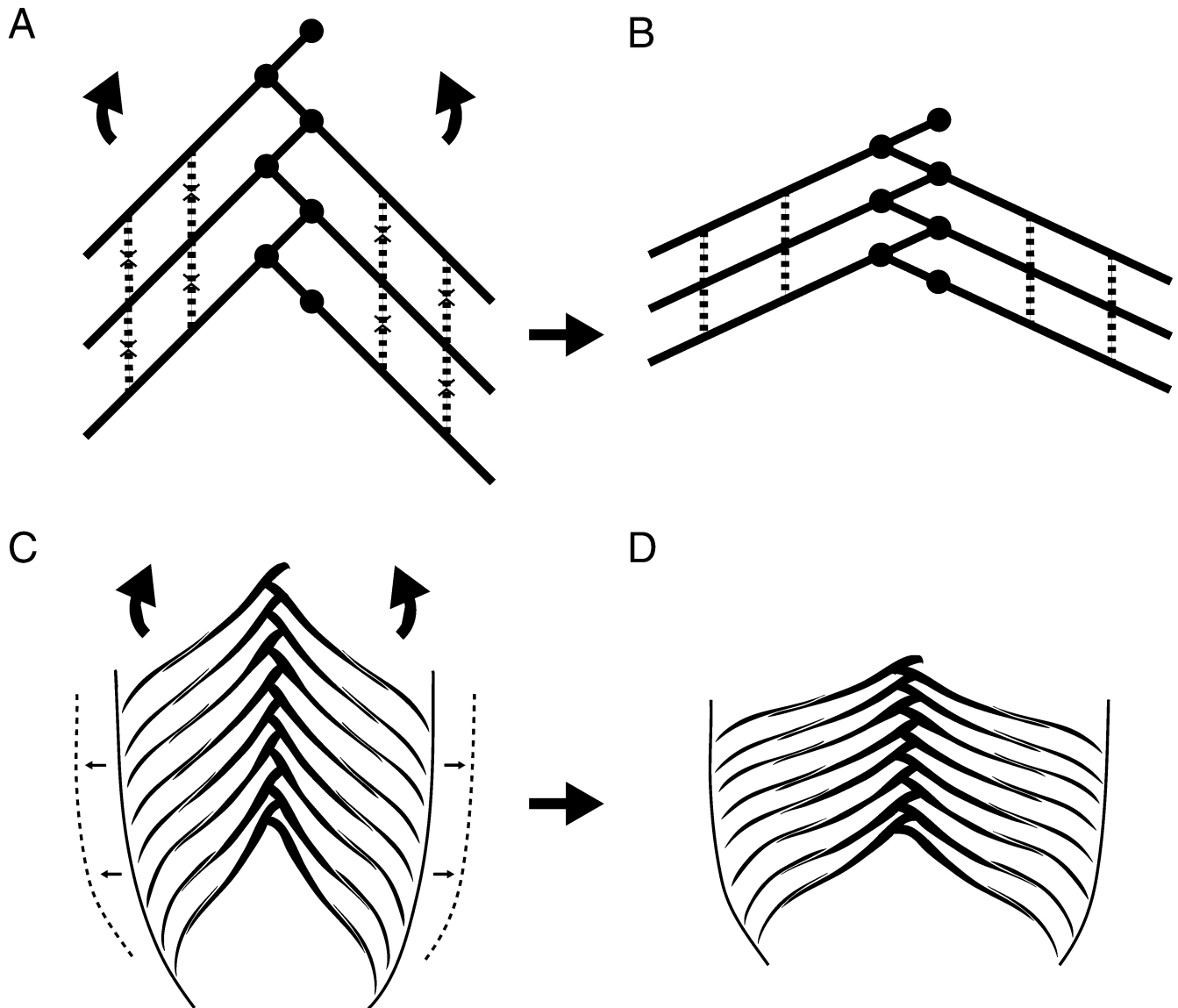
FIGURE 14. Gastralial retraction and protraction (dorsoventral view): **A**, **B**, Schematic representation of the imbricating joint system. Black circles represent the joints, which only allow rotational movement in a frontal plane. Shortening of the rectus abdominis muscle fibers (dotted lines), results in protraction of the gastralia (B), leading to an increase in lateral width of the gastralial system and a shortening of the total length of the system. **C**, **D**, eight gastralial rows, modeled after *Allosaurus*, showing the degree of widening of the lateral abdominal wall upon a rotation of 40 degrees (D). Retraction and protraction angles are within the range observed in obtuse and acute chevron-shaped gastralia. No adjustment for slip within the joints is made in this figure.

would result in an additional increase in trunk volume (Fig. 16C).

Carrier and Farmer (2000a, b) proposed that pelvic kinesis might have been a primitive mechanism in archosaurs that contributed to inspiration. Based on earlier work by Claessens (1996a, b), Carrier and Farmer (2000a, b) proposed that the M. ischiotruncus exerted a caudad pull on the gastralia and thus powered a gastralial aspiration pump, analogous to the pelvic rotation mechanism in extant crocodylians. Though prosauropod and theropod dinosaurs undoubtedly did not possess a level of pubic mobility similar to that of extant crocodylians, in which the pubic bones are separate from the acetabulum and attached to the ischia via movable joints, it is possible that an ischiotruncus muscle contributed to the muscular system by actively manipulating the shape and position of the gastralial system. However, rather than a retractive function for the M. rectus

abdominis as proposed by Carrier and Farmer (2000a, b), the M. rectus abdominis appears to function as a protractor of the gastralial system, and contraction of the M. ischiotruncus only leads to gastralial protraction if its insertion is close to the ventral midline. Carrier and Farmer (2000a) calculated that widening the gastralial system in *Allosaurus* DINO 11541 could increase the volume of the abdominal cavity by 14%.

Basal birds such as *Archaeopteryx* and *Confuciusornis* still retained gastralia, but the gastralia are lost in Neornithes. The caudad expansion of the sternum in Neornithes probably made the gastralia redundant, by preventing abdominal collapse and working as an active component of the aspiration pump. Although the extensive fusion of consecutive cranial gastralial rows observed in some tyrannosaurid specimens may be pathologic, possibly an artifact of old age, the fused gastralial chevrons may have functioned as an analogue of a large "sternal"
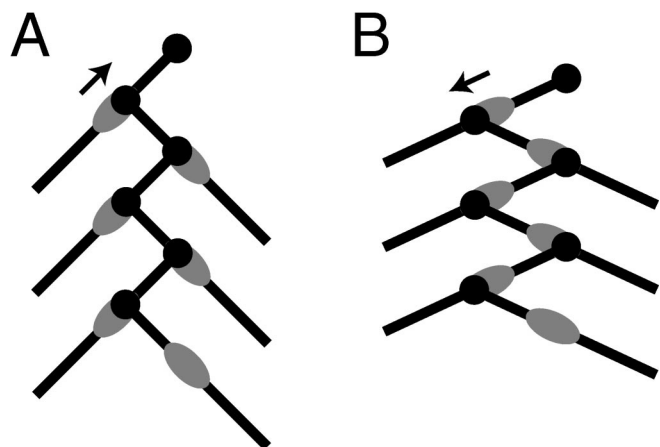
FIGURE 15. Slip in medial gastralial joints. Inward slip of the mediodorsal joints on gastralial retraction (**A**), combined with outward slip of the joints upon gastralial protraction (**B**), may accommodate for some of the lengthening and shortening of the whole gastralial system during protraction and retraction. In tyrannosaurids the long axis of the ventral facet can be twice as wide as the dorsal facet, and in theropod genera with poorly defined ventral facets, slip might occur along the gastralial diaphysis.

plate, rotated ventrodorsally by the movements of the partially underlying sternocostal apparatus.

Function of the Gastralial Aspiration Pump in the Dinosaur Respiratory System

Perry (1983, 1989) suggested that dinosaurs may have had multicameral, heterogeneously partitioned lungs. Pneumatic vertebrae in Saurischia indicate that the lungs were attached dorsally, and had limited mobility at and near their points of insertion (Perry, 1983; Britt, 1993, 1997). Not all large fossae and foramina in the skeleton are associated with diverticula of the lungs, however, and some caution needs to be exerted in the interpretation of pneumatic features (O'Connor, 1999). The extent of the distribution of individual lung diverticula throughout the body cavity probably also cannot be determined with

accuracy from skeletal pneumaticity, and lung diverticula may have been restricted to the actual skeletal elements that were invaded.

Dinosaurs probably relied on costal movement for lung ventilation (e.g., Perry, 1989; Hengst, 1997; Claessens et al., 1998). The surface area for muscle attachment on the proximal costal diaphysis is usually extensive, especially within the Saurischia. Costovertebral attachments in the trunk area are bicondylar, and have generally well-defined planes of movement.

The gastralia may have been an accessory component of the theropod aspiration pump, and may have increased tidal volume to a certain extent regardless of lung type ventilated. However, if diverticula of the theropod lung were so extensive that an abdominal air sac complex was present, the gastralia would have been ideally positioned to ventilate them. Although the precise dynamics of airflow in the avian lung are still not fully understood, there is some evidence that the abdominal air sacs and craniocaudal pressure differences between the various lung diverticula are an important aspect of airflow pathways in the avian lung (Butler et al., 1988; Kuethe, 1988; Boggs et al., 1997).

The protraction of the gastralia caused by the M. rectus abdominis in theropods might indicate a change in the function of this muscle from expiratory to inspiratory, or it might indicate a diachronous expansion and contraction of the thorax and the ventral abdominal area during breathing. The latter scenario might also be related to the generation of pressure differences in a lung with extensive diverticula. However, theropod respiratory airflow dynamics hypotheses based on the physiology of extant birds are admittedly speculative. From the current evidence it appears impossible to ascertain exactly when lung diverticula stretching throughout the whole body cavity or unidirectional airflow originated, and this may well have been long after the origin of birds.
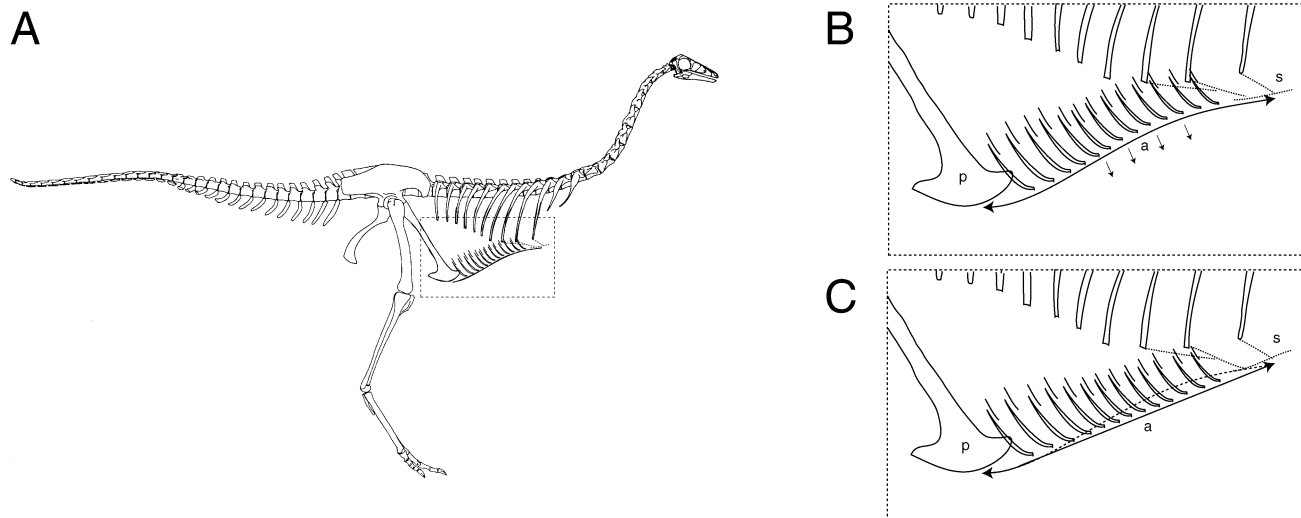
FIGURE 16. Potential dorsoventral volumetric changes in the trunk caused by gastralial protraction and retraction. If ornithomimids possessed a concave body wall (**A**), Protraction of the gastralial apparatus with associated shortening of the total length (a) of the gastralial apparatus may cause an additional increase in dorsoventral trunk volume through a ventral movement of the abdominal wall (**B**, **C**). **Abbreviations**: **a**, abdominal wall; **p**, pubis; **s**, sternum. Reconstruction of *Struthiomimus* (AMNH 5339) modified after Russell (1972). Pectoral girdle not shown.

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APPENDIX 1

Partial list of gastralia examined in this study. Generally excludes specimens consulted in the literature only (main references listed), and excludes most disassociated and uncatalogued specimens.

Taxon	Genus	Specimen number	Medial gastralia preserved	Lateral gastralia preserved	Chevron-shaped gastralia preserved	In situ imbri-cation	Furcula preserved	Comments
Prosauropoda	*Ammosaurus*	MNA G2 7233	yes	yes	—	—	—	
	Plateosaurus	AMNH 21559	yes	yes	—	—	—	
	Sellosaurus	GPIT 18392	yes	yes	—	—	—	Von Huene, 1915
Coelophysoidea	*Coelophysis*	CMNH acc 31798	yes	yes	—	yes	—	
	Coelophysis	AMNH 7224	yes	yes	—	?	—	
Allosauroidea	*Allosaurus*	MOR 693	yes	—	—	—	—	
	Allosaurus	UMNH 94	yes	—	—	—	—	
	Allosaurus	UMNH 282	yes	—	—	—	—	
	Allosaurus	UMNH 333	yes	—	—	—	—	
	Allosaurus	UMNH 340	yes	—	—	—	—	
	Allosaurus	DINO 11541	yes	yes	yes	—	yes	
	Allosaurus	USNM 4734	yes	yes	—	—	—	pathologic (pseudoarthrosis)
	Allosaurus	USNM 8367	yes	—	—	—	—	pathologic (pseudoarthrosis)
	Acrocanthosaurus	SMU 74646	—	—	yes	—	—	Harris, 1998 (caudal chevrons only)
	Sinraptor	IVPP 10600	yes	yes	—	—	—	
Ornithomimidae	*Dromiceiomimus*	ROM 840	yes	yes	—	—	—	Russell, 1972
	Ornithomimus	RTMP 95.110.1	yes	yes	—	—	—	
	Ornithomimus	ROM 851	yes	yes	—	—	—	Russell, 1972
	Ornithomimus	NMC 8632	yes	yes	—	—	—	Sternberg, 1933
	Struthiomimus	RTMP 90.26.1	yes	yes	—	—	—	
	Struthiomimus	AMNH 5339	yes	yes	—	—	—	
	Struthiomimus	UCMZ 1980.1	yes	yes	—	—	—	
Tyrannosauridae	*Albertosaurus*	RTMP 91.36.500	yes	yes	yes	yes	yes	
	Albertosaurus	RTMP 86.64.1	yes	yes	—	yes	yes	
	Albertosaurus	RTMP 81.10.1	yes	yes	—	—	—	
	Albertosaurus	UA 10	yes	—	—	—	—	
	Albertosaurus	NMC 2120	yes	yes	—	—	—	
	Albertosaurus	AMNH 5664	yes	yes	—	—	—	
	Albertosaurus	ROM 807	yes	yes	yes	—	—	Parks, 1928a
	Albertosaurus	NMC 2196	yes	yes	yes	—	—	
	Daspletosaurus	NMC 8506	yes	yes	—	—	yes	
	Daspletosaurus	NMC 11315	yes	yes	yes	—	yes	
	Daspletosaurus	MOR 590	yes	—	—	—	—	
	Tarbosaurus	PIN 552-1	yes	—	yes	—	—	Maleev, 1974
	Tarbosaurus	GI 107/3	yes	yes	yes	yes	—	
	Tyrannosaurus	AMNH 5881	yes	—	—	—	—	
	Tyrannosaurus	FMNH PR2081	yes	yes	yes	—	—	
	Tyrannosaurus	CMNH 9380	yes	yes	yes	—	—	Formerly AMNH 973, Osborn (1906)
	Tyrannosaurus	MOR 555	yes	yes	—	—	—	
	incert. sed.	RTMP 82.28.1	yes	—	—	—	—	
	incert. sed.	RTMP 94.12.722	yes	—	—	—	—	
	incert. sed.	RTMP 67.22.1	yes	—	—	—	—	
	incert. sed.	RTMP 82.16.374	yes	—	—	—	—	
Oviraptoridae	*Khaan*	GI 100/1002	yes	yes	—	—	—	
	Khaan	GI 100/1127	yes	yes	—	—	—	
	incert. sed.	GI 100/979	yes	yes	—	—	—	
Troodontidae	*Sinornithoides*	IVPP V9612	yes	yes	—	yes	—	
	Troodon	NMC 12340	yes	yes	yes	—	—	
Dromaeosauridae	*Deinonychus*	YPM 5247	yes	yes	—	—	—	
	Saurornitholestes	MOR 660	yes	—	—	—	—	
	Velociraptor	GI 100/25	yes	yes	—	—	—	
	incert. sed.	GI 100/985	yes	yes	—	yes	—	
Aves	*Archaeopteryx*	Berlin specimen	yes	yes	—	yes	—	Dames, 1884; De Beer, 1954
	Archaeopteryx	Teyler specimen	yes	yes	—	—	—	
	Confuciusornis	GMV 2152	yes	yes	—	yes	—	Chiappe et al., 1999
	Changchengornis	GMV 2129	yes	yes	—	yes	—	Chiappe et al., 1999
Theropoda incert. sed.	*Poekilopleuron*		yes	yes	yes	—	—	Eudes-Deslongchamps, 1838
	Segisaurus	UCMP 32101	yes	yes	—	—	—	
	Sinosauropteryx	GMV 2123	yes	yes	—	—	—	