

The ligamental scar in the costovertebral articulation of the tyrannosaurid dinosaurs

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Hirasawa, T. 2009. The ligamental scar in the costovertebral articulation of the tyrannosaurid dinosaurs. *Acta Palaeontologica Polonica* 54 (1): 49–59.

The costovertebral articulation is integral to constrain the thoracic kinematics and to infer the breathing mechanism in the respect with costal aspiration. However, the structure of the costovertebral articulation in non-avian theropods has not been studied in great detail before. This study highlights the Tyrannosauridae, which is represented by numerous complete specimens. Costovertebral articulations of ten tyrannosaurid specimens, including two nearly in-situ articulated fossils, were investigated and compared with those in extant Archosauria. For extant archosaurs, dissections were conducted to rationalize the soft tissue anatomy in tyrannosaurids. This study shows that the rib articulates ventrally or posteroventrally with the distal end of the corresponding vertebral transverse process in the tyrannosaurid ribcage. A ligament (ligamentum costotransversarium) can be reconstructed to connect the rib tuberculum to the transverse process in each articulation. The scar for lig. costotransversarium is recognizable in many theropod skeletons, and this rugosity can be used to identify the rotational axis for the rib. This result provides a cornerstone for exploring the evolution of the ribcage and breathing mechanisms across the theropod lineage leading to birds.

Key words: Dinosauria, Theropoda, Tyrannosauridae, ribcage, vertebra, rib, soft tissue anatomy.

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Introduction

Costal aspiration is generally an essential component of the respiratory pump in amniotes (Brainerd 1999), and the architecture of the ribcage is expected to reflect potential breathing mechanisms. Breathing mechanisms in non-avian theropod dinosaurs recently have been in the spotlight for the probable existence of an air-sac system like in birds (O'Connor and Claessens 2005). Theropods possess widely separated bicapitate rib heads, and have been speculated to have a single rotational axis for each rib (Claessens et al. 1998). Accordingly, studies on non-avian theropod ribcages may lead to the intriguing implications for the evolution of respiratory systems. A monophyletic group of non-avian theropods, the Tyrannosauridae (Theropoda: Tetanurae: Coelurosauria) is ideally suited for analysis of thoracic structure. Tyrannosaurids ranged over North America and Asia in the Late Cretaceous (Holtz 2004) and are represented by a relatively large number of complete specimens, unlike some other theropod clades.

It is essential for studying tyrannosaurid thoracic kinematics to determine if and how the costovertebral articulation defines a specific plane of rib movement. The articular facet on the transverse process is difficult to identify, probably due to attachments of the intervertebral muscles and costal levator muscles to the distal ends of transverse process, which may obscure the articular facet for the rib tuberculum.

Historically, Lambe (1917) firstly described the morphology of the rib head in the tyrannosaurid *Gorgosaurus libratus*,

and proposed that the articular facet on the rib tuberculum faces posteroventromedially in the living body (Lambe 1917: 36). Therefore, Lambe (1917: fig. 24) considered the rib tuberculum to be articulated laterally with the distal surface of the transverse process in *G. libratus*. On the other hand, in the osteological description of *Tyrannosaurus rex*, Brochu (2003: 87) identified that the articular facet on the rib tuberculum faced anterodorsomedially (Brochu 2003: fig. 76), implying a difference from Lambe's (1917) reconstruction. Brochu (2003: 86) also indicated that the articular facet for the rib tuberculum lies on the posteroventral surface of the distal end of the transverse process (Brochu 2003: figs. 55–56). Brochu (2003) did not reconstruct the detailed structure of the costovertebral articulation, but there was a discrepancy between the costal and vertebral articular positions. In the description of *Tarbosaurus bataar*, Maleev (1974) indicated that the facet for the rib tuberculum was located on the distal surface of the transverse process and articulated with the ribs by a laterally and slightly ventrally directed surface, in the anterior thoracic vertebrae. Maleev (1974) also pointed out that the articular facet for the tuberculum shifted its position anteriorly on the transverse process in the few most posterior presacral vertebrae. The identifications of Lambe (1917), Brochu (2003), and Maleev (1974) indicate the level of complexity present in the costovertebral articulations of tyrannosaurids, and the need for further investigation.

Among many descriptive works on the other theropods, only a few papers provide detailed descriptions of costo-

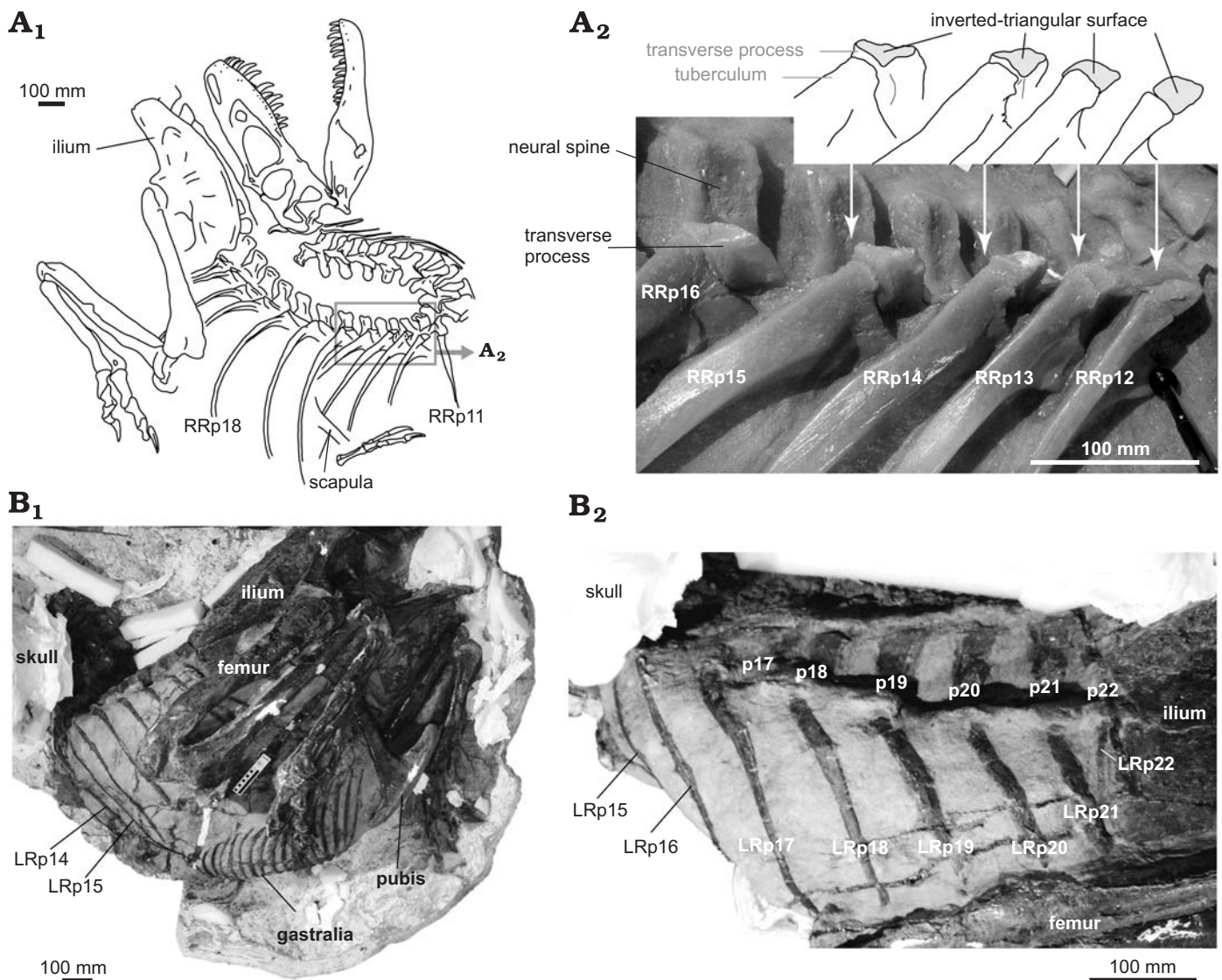


Fig. 1. Two articulated skeletons of tyrannosaurid dinosaur *Gorgosaurus libratus* Lambe, 1914 from the Campanian Dinosaur Park Formation of Dinosaur Provincial Park, Alberta, Canada. A. RTMP 2005.00.24 (the cast of incompletely prepared RTMP 91.36.500); A₁, line drawing, right lateral view; A₂, costovertebral articulations, right lateral view. B. RTMP 99.33.01 in left lateral view (B₁); costovertebral articulations, left lateral and slightly dorsal view (B₂).

vertebral articulations. Gilmore (1920) studied the basal tetanuran *Allosaurus fragilis*, and indicated that the articular end presented a roughened, beveled surface on the ventral side of the transverse process (Gilmore 1920: 38–39). Ostrom (1969) suggested that the tuberculum of the deinonychosaurian *Deinonychus antirrhopus* was articulated with the lateral extremity (not the ventral side) of the transverse process (Ostrom 1969: 82). Bakker et al. (1992: fig. 14) inferred that the rib tuberculum was articulated with the ventral surface of the distal end of the transverse process in the basal tetanuran *Torvosaurus tanneri*. However, there is room for more detailed investigation, and any inferences should reflect specific osteological landmarks.

The purpose of this study is to identify the landmark for the position of articulation on the transverse process in the costovertebral articulation of tyrannosaurids, based on infor-

mation from fossils including nearly in-situ articulated skeletons and the anatomy of extant archosaurs.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; BHI: Black Hills Institute of Geological Research, Hill City, South Dakota, USA; KPM, Kanagawa Prefectural Museum of Natural History, Odawara, Japan; NSMT (NSM), National Museum of Nature and Science (formerly National Science Museum), Tokyo, Japan; RTMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Canada; TCM, The Children's Museum, Indianapolis, USA; UT, the University of Tokyo, Tokyo, Japan.

Other abbreviations.—Presacral vertebrae are numbered from cranial to caudal, with a single-letter prefix (p), in which numbering begins with the atlas (p1), as in Brochu (2003). Corresponding ribs are abbreviated as RR (right rib) and LR (left

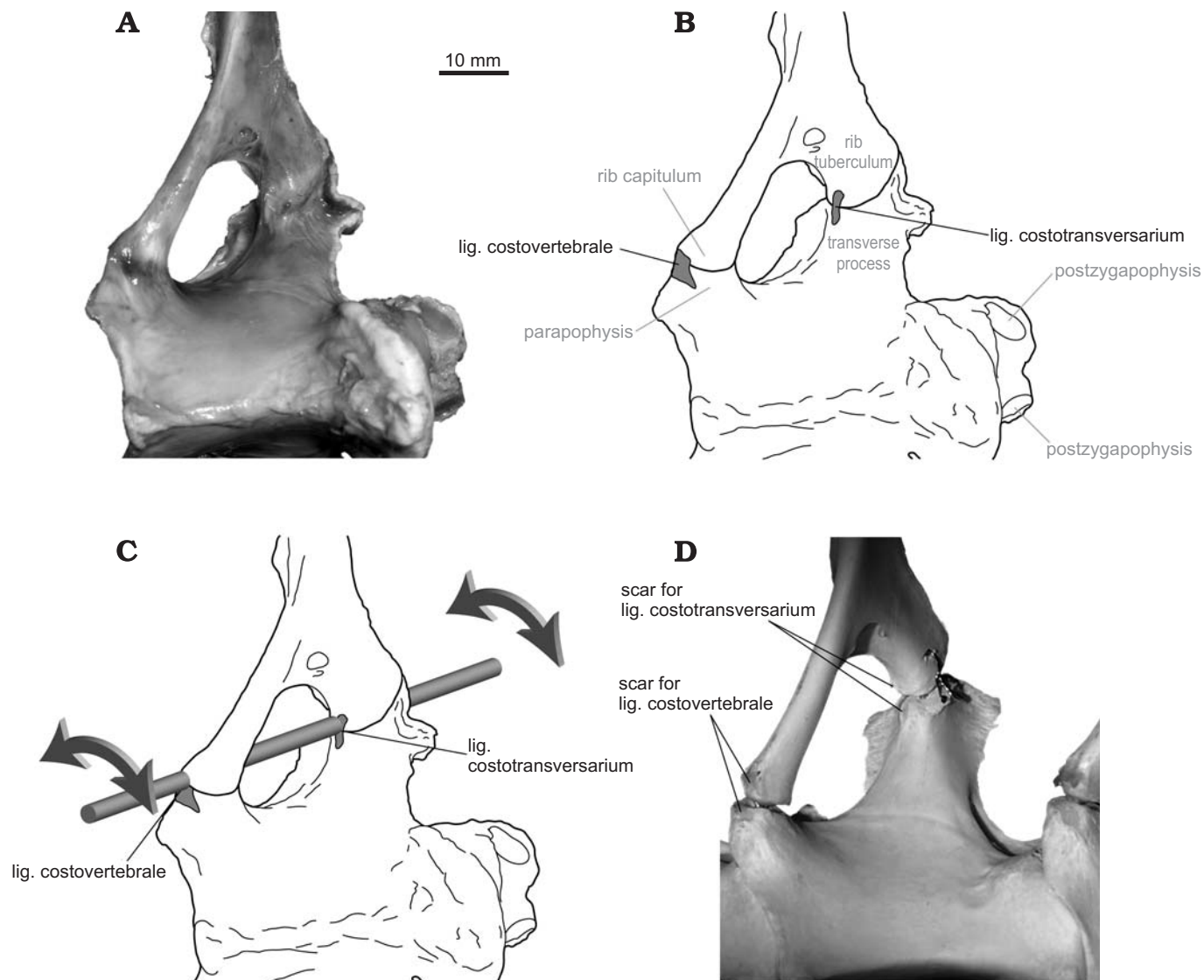


Fig. 2. Costovertebral articulation with soft tissues in Darwin's *Rhea pennata* d'Orbigny, 1834, KPM-NF2001026. The articulation between the 19th presacral vertebra (5th thoracic vertebra in Mivart 1877) and the left rib are shown. **A.** Ventral view. **B.** Line drawing of **A.** **C.** Schematic the axis of costal rotation. **D.** Skeleton after removal of soft tissues.

rib). RRp11, for example, indicates the right rib for p11; lig., ligamentum; mm, muscoli.

Terminology.—Confusion in terminology has prevented clear descriptions of vertebral and costal morphology. For example, some authors used the diapophysis as the transverse process (e.g., Lambe 1917) while others used it as the articular facet for the rib tuberculum (e.g., Wilson 1999; Brochu 2003). Terminology used in this study follows Wilson (1999) for saurischian vertebral structures. For all skeletal elements, anatomical orientations are defined in the living body.

Materials and methods

This study focuses on three-dimensionally preserved articulated skeletons of tyrannosaurids. In addition, it employs the

phylogenetic bracketing method for reconstructing the soft tissue anatomy in fossil taxa as proposed by Bryant and Russell (1992) and by Witmer (1995).

First, the ribcages of extant archosaurs (Appendix 1) were examined to identify the useful landmark for the position of articulation on the transverse process. *Rhea pennata* (Darwin's Rhea) and *Alligator mississippiensis* were dissected to examine the arrangements of soft tissues in the costovertebral articulation.

Ten well-preserved tyrannosaurid specimens (Appendix 1), including two nearly in-situ articulated skeletons, were examined. For articulated skeletons, the position of the rib relative to the corresponding vertebra was observed. For the other specimens that were fully extracted from matrix, both vertebrae and ribs were observed to identify the osteological landmark for the articular position.

An articulated skeleton of *Gorgosaurus libratus*, RTMP

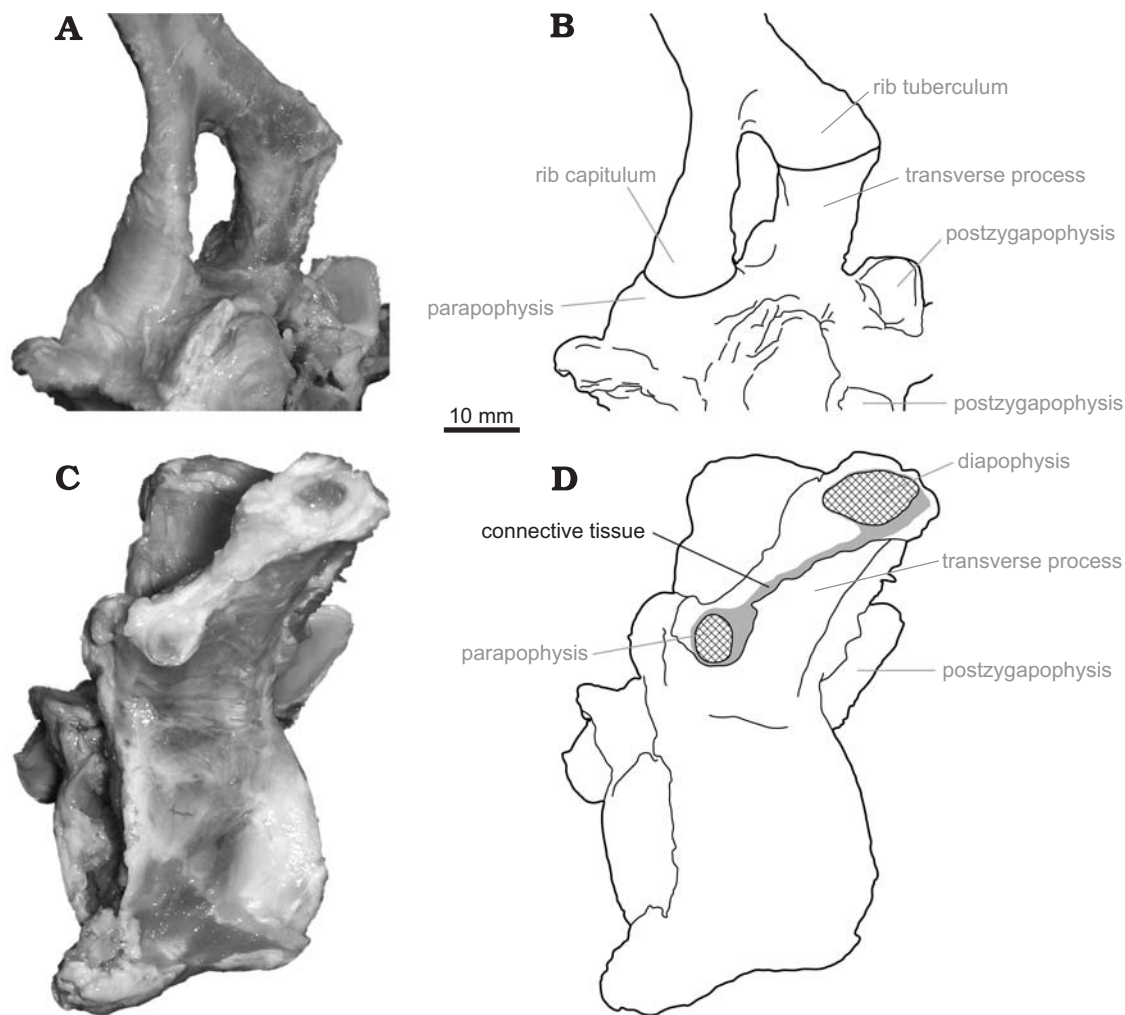


Fig. 3. Costovertebral articulation with soft tissues in *Alligator mississippiensis* Daudin, 1802, KPM-NFR000016. **A, B.** The articulation between the 10th presacral vertebra (1st thoracic vertebra in Frey 1988) and the left rib in postero-ventral view (A), and its explanatory drawing (B). **C, D.** The 12th presacral vertebra (3rd thoracic vertebra in Frey 1988) in left lateral view (C), and its explanatory drawing (D). A cross section of thin connective tissue, which binds the transverse process and the rib head, is colored in gray.

91.36.500 is nearly complete. The original skeleton was extracted from the matrix, but the author also studied a cast, RTMP 2005.00.24 (Fig. 1A), which was made prior to the extraction from the matrix to record the mode of fossil occurrence of its right side. In RTMP 2005.00.24, portions of all rib capitula and vertebral parapophyses are obscured by matrix, thus specific details of the articulations are not observable. In the anterior thoracic region, the rib articulates with the corresponding transverse process naturally, but posterior to p19, the rib is located at a slightly unnatural position due to the postmortem deformation. The position of each skeletal element was observed in the cast, RTMP 2005.00.24, and the morphological features were observed in the original skeleton, RTMP 91.36.500.

Another articulated skeleton of *Gorgosaurus libratus*, RTMP 99.33.01 is incompletely prepared; however, the left side could be examined in this study (Fig. 1B). The ribcage is three-dimensionally preserved with a fully articulated gastralia basket that consists of 18 rows of gastralia. Although

the skull was covered by a plaster jacket and anterior presacrals and the pectoral girdle were incompletely prepared, vertebrae p14 to p22, the left pelvic girdle, and hind limbs were observable.

Results

Articulations in extant Archosauria

Gross anatomy of *Rhea pennata*.—Each articulation between rib capitulum and parapophysis is covered by a fibrous membrane. The fibrous membrane covers approximately one third of the surface of the succeeding anterior centrum. On the anteroventral side of each joint, there is a thickening of the joint capsule, which forms a collateral ligament, namely the lig. costovertebrale (Fig. 2), as described by Baumel and Raikow (1993) and Yasuda (2002). The rib tuberculum articulates ventrally with the distal end of the transverse process.

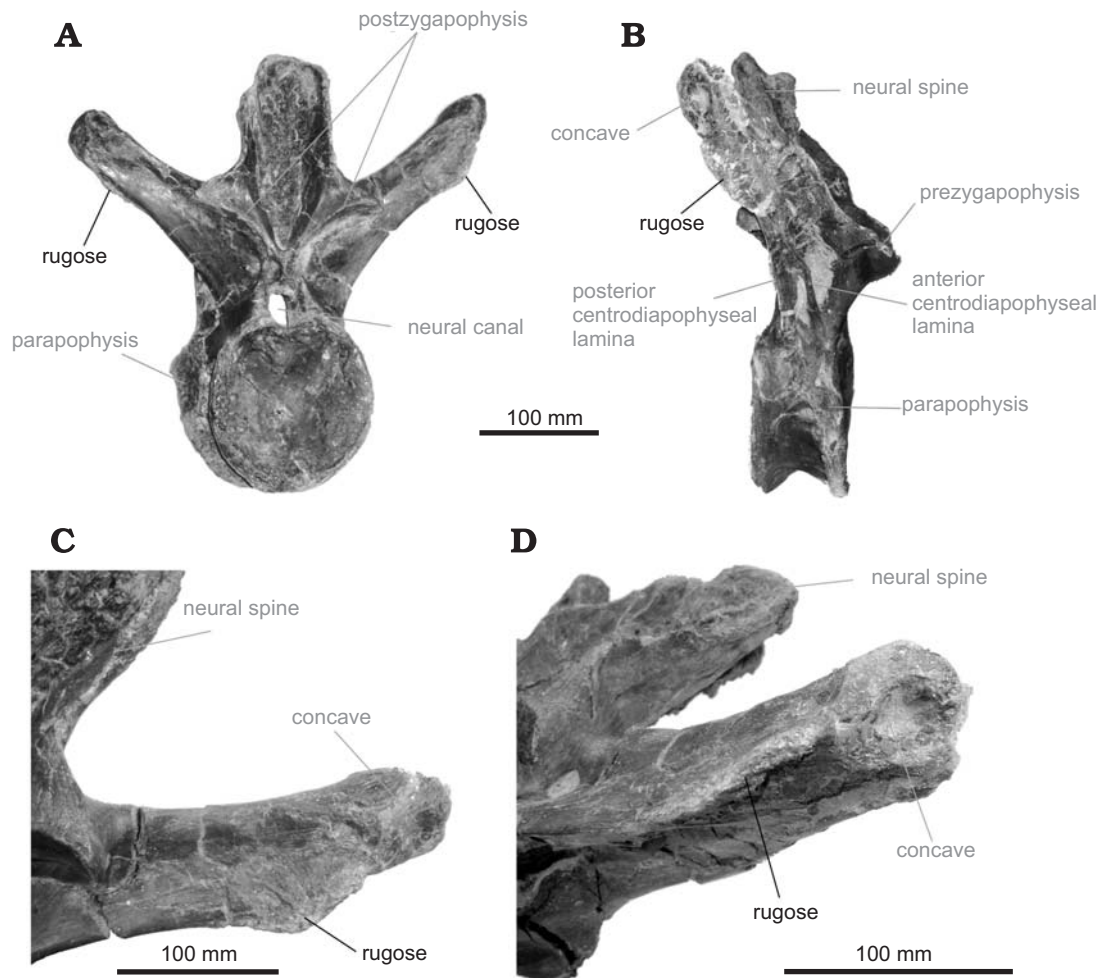


Fig. 4. Anterior thoracic (possibly p13) vertebra of tyrannosaurid dinosaur *Daspletosaurus torosus* Russell, 1970, RTMP 2001.36.01 from the Campanian Oldman Formation of Milk River, Manyberries, Alberta, Canada. **A.** Posterior view. **B.** Right lateral view. **C.** Right transverse process in posterior view. **D.** Right transverse process in lateroventral view.

On the anteroventral side of each joint, there is a thickening of the joint capsule, which forms the lig. costotransversarium (Fig. 2), as described by Yasuda (2002) in *Gallus gallus* (Chicken). Both the lig. costovertebrale and the lig. costotransversarium are located approximately along the orientation of the axis of each hinge joint which consists of two articulations between a vertebra and a bicapitate rib head (Fig. 2C), and as a result, these ligaments scarcely stretch during costal rotation.

There is a vascularized thin membrane across each foramen (foramen transversarium) formed by a vertebra and a bicapitate rib. Epaxial muscles, namely mm. intertransversarii and mm. levatores costarum (Vanden Berge and Zweers 1993), attach to the distal part of the transverse process and dorsal part of the rib.

The skeleton of *Rhea pennata* bears distinct scars for both the lig. costovertebrale and the lig. costotransversarium (Fig. 2D). The scars are marked as rugosities.

Other avian skeletons.—The skeletons of *Struthio camelus* (Ostrich, uncatalogued UT), *Grus vipio* (White-naped Crane,

NSMT PO 004), *Phalacrocorax filamentosus* (Japanese Cormorant, NSMT PO 14), and *Pygoscelis adeliae* (Adelie Penguin, NSMT PO 486) exhibit the scar for the lig. costotransversarium, and these scars align approximately along the rotational axis for the rib. Vertebrae of *S. camelus* (uncatalogued UT) also bears scars for the lig. costovertebrale.

In *S. camelus* (uncatalogued UT) and *P. adeliae* (NSMT PO 486), the dorsal part of the distal end of the transverse process is well-ornamented with rugosity, although the articular surface for the rib is located at the more ventral position.

Gross anatomy of *Alligator mississippiensis*.—In the anterior thoracic region represented by p10–11 (Fig. 3A, B), each rib bears widely separated bicapitate rib heads, and the foramen transversarium is occupied by mm. intertransversarii. In both the capitular and the tubercular joints, the joint capsule is almost uniform in thickness. In the posterior thoracic region represented by p12 and the more posterior vertebrae, the notch of the rib head reduces in size, and the dorsal edge of rib head aligns with the ventral edge of the corresponding transverse process, as described by Frey (1988). A thin con-

nective tissue, which binds the transverse process and the rib head, runs continuously between the joint capsules in the capitular and the tubercular joints (Fig. 3C, D).

Other crocodylian skeletons.—In the skeleton of *Caiman crocodilus* (Spectacled Caiman, NSMT PO 423 and 424), the geometry of the costovertebral articulation varies greatly along the vertebral column. The arrangement of the parapophysis and the diapophysis is suddenly changed from a perpendicular pattern to a horizontal pattern, between p11 and p12 (comparable to second and third thoracic vertebrae in the description of *Alligator sinensis*, by Cong et al. 1998) as in *Alligator mississippiensis*. Simultaneously, the notch of the rib head changes in size at the point between p11 and p12. Posterior to p12, the notches are much smaller than more anterior ones. In both types of vertebrae and ribs, there are no distinct scars for the lig. costovertebrale nor the lig. costotransversarium seen in avian skeletons.

Articulated tyrannosaurid skeletons

RTMP 91.36.500.—Anterior to p10, the transverse process is oriented almost ventrally, and the rib tuberculum articulates with the anteroventral surface of the transverse process. In p11, the transverse process is oriented lateroventrally, and the corresponding right rib tuberculum articulates with it anterodorsally. RRp11 possesses widely separated heads unlike the more anterior ribs, and the tuberculum articulates with its dorsal surface.

In p12, the transverse process is oriented laterodorsally, and its distal end forms an inverted-triangular surface that directed laterally (Fig. 1A₂). The distal surface and its dorsal side are rugose. RRp12 possesses a dorsally projected tuberculum, and the notch between the capitulum and the tuberculum is smaller than that of the RRp11. The tuberculum articulates with the posteroventral side of the distal inverted-triangular surface on the transverse process.

Vertebra p13 possesses an inverted-triangular surface on the distal end of transverse process (Fig. 1A₂). The dorsal, ventral, and anteroventral parts of the distal end are rugose, but the posteroventral surface is relatively smooth. The rugosity extends to the distal portion of the posterior centrodiaepophyseal lamina. RRp13 possesses a square tuberculum that projects slightly laterally. The antero-posterior width of the tuberculum is approximately equal to the width of the posteroventral side of the inverted-triangular surface on the corresponding transverse process. The small lateral projection of the tuberculum overhangs the posteroventral side of the distal inverted-triangular surface on the transverse process.

In p14 and p15, each transverse process possesses an inverted-triangular surface, and the corresponding rib possesses a square tuberculum with a triangular anterolateral projection (Fig. 1A₂). The tuberculum articulates 4 mm medioventrally in p14 and 7 mm medioventrally in p15 from the posteroventral side of the distal inverted-triangular surface on the transverse process.

In p16, p17, and p18, each transverse process also possesses an inverted-triangular surface, but the triangle is compressed dorso-ventrally, in comparison with more anterior presacrals. RRp16–p18 possess triangular wedge-shaped tubercula, which are located medioventral to the posteroventral sides of the distal inverted-triangular surfaces on the corresponding transverse processes. RRp19 was slightly dislocated from the natural position of the articulation with the transverse process, due to postmortem deformation. The rib possesses a faintly anterolaterally projected tuberculum, but the dorsal portion is covered by matrix. The rib tuberculum is located in a medioventral position relative to the posteroventral side of the distal inverted-triangular surface on the transverse process. In p20 and p21, the rib tuberculum is covered by matrix. In the fossil, the rib tuberculum does not contact the corresponding transverse process, but the tuberculum is positioned medioventral to the posteroventral side of the distal inverted-triangular surface on the vertebral transverse process. P22 is the most posterior vertebra that is not covered by the iliac blade. The transverse process also possesses a dorso-ventrally compressed inverted-triangular surface, but the surface faces anterolateral unlike the other presacrals. The rib tuberculum articulates with the ventral apex of the distal inverted-triangular surface.

RTMP 91.36.500 also provides detailed rib morphology, which allows identification of the ribs in other disarticulated specimens. The anterior and posterior intercostal ridges (sensu Bakker et al. 1992) on the rib shaft gradually change their proportions along the body axis. From p11 to p22, the more anterior rib possesses a more distinct posterior intercostal ridge and a less distinct anterior intercostal ridge, whereas the more posterior rib possesses a more distinct anterior intercostal ridge and a less distinct posterior intercostal ridge. Also, the shape of the distal end of the rib shaft is changed along the body axis. The ribs for p11 and p12 possess tapered distal ends. The ribs for p13, p14, and p15 possess expanding and rugose distal ends. From p16 to p19, the ribs possess medio-laterally compressed thin distal ends. The ribs for p20, p21, and p22 possess tapered distal ends.

RTMP 99.33.01.—LRp14–p15 are much longer than the more posterior ribs, and the distal rib shaft intersects with the dorsal portion of the gastralia series. The distal end of LRp15 is rugose. LRp16 is abruptly shorter than the more anterior ribs, and the distal end is rugose.

From p17 to p21, the costovertebral articulations were observable, and each rib tuberculum articulates slight medially with the ventral surface of the distal end of the corresponding transverse process (Fig. 1B₂). Each transverse process bears a compressed inverted-triangular surface on the distal end, and the surface is rugose. There is a small notch on the anterior edge of the left ilium, and the distal end of the vertebral transverse process of p22 is settled in the space. In p22, the distal end of the transverse process forms a compressed inverted-triangular surface, and the corresponding rib tuberculum articulates ventrally with it.

Disarticulated skeletal elements

Vertebrae.—The p10 of NSM PV 20425 (*Tyrannosaurus rex*) possesses the slightly ventrally directed transverse process, whereas p11 possesses a almost dorsally directed transverse process, as shown in Osborn (1916: pl. 27) and in RTMP 85.62.01 (*Daspletosaurus* sp.). On the other hand, the shift occurs between p11 and p12 in RTMP 91.36.500 (*Gorgosaurus libratus*). Osborn (1906: 288) described these two vertebrae as “cervico-dorsals”. Similarly, there are minor differences in the morphological shift between cervical and anterior thoracic vertebrae in other tyrannosaurids. Therefore, below is a summary of the transition along the body axis.

NSM PV 20425 (*T. rex*) preserves vertebrae from p10 to p12. In p10, the parapophysis is positioned on the anterior and ventral rim of the centrum and faces posteriorly. The transverse process bears anterolaterally facing inverted-triangular surface on its distal end. In p11, the parapophysis lies on the ventral position on the anterior edge of the centrum and faces lateroposteriorly. In p12, the parapophysis is positioned further dorsally and faces more laterally than in p11. TCM 2001. 89. 1 (*G. libratus*) and RTMP 85.62.01 (*D. sp.*) exhibit almost the same features. One vertebra of RTMP 2001.36.01 (*Daspletosaurus torosus*) represents an anterior thoracic element, and there is a rugose ridge on the ventral surface of the distal part of each transverse process. The rugosity extends dorso-ventrally and slightly antero-posteriorly on the posterior centrodiapophyseal lamina, and ends at the distal end of the transverse process. There is a postero-ventrolaterally facing shallow concavity at the lateral end point of this rugosity. The orientation of the rugose ridge is almost parallel to that of the line between the concavity on the transverse process and the parapophysis.

From p13 to p18 of NSM PV 20425 (*T. rex*), little variation is observable within the series, although left transverse processes are not preserved from p14 to p18. From p19 to p21, the transverse processes of the both sides are not preserved. In p13, the parapophysis is positioned on the centrum, whereas posterior to p14, the parapophysis lies on the ventral part of the neural arch. Between p13 and p21, the parapophysis faces laterally and slightly posteriorly. There is a rugose ridge on the posterior centrodiapophyseal lamina of each transverse process, as mentioned for the more anterior vertebra of the specimen. These rugosities, represented by RTMP 2001.36.01 (*D. torosus*; Fig. 4A, B), are observable in all individuals examined in this study. At the distal end of the rugose ridge of RTMP 2001.36.01, there is a posteroventrolaterally facing shallow concavity at the lateral endpoint of the rugosity on each transverse process (Fig. 4C, D). The orientation of the rugose ridge is approximately parallel to the line between the concavity on the transverse process and parapophysis.

Ribs.—Tyrannosaurid thoracic ribs exhibit gradual transitions in morphology from anterior to posterior, as mentioned for the two articulated skeletons. Therefore, the order of isolated ribs is identifiable in well-preserved conditions.

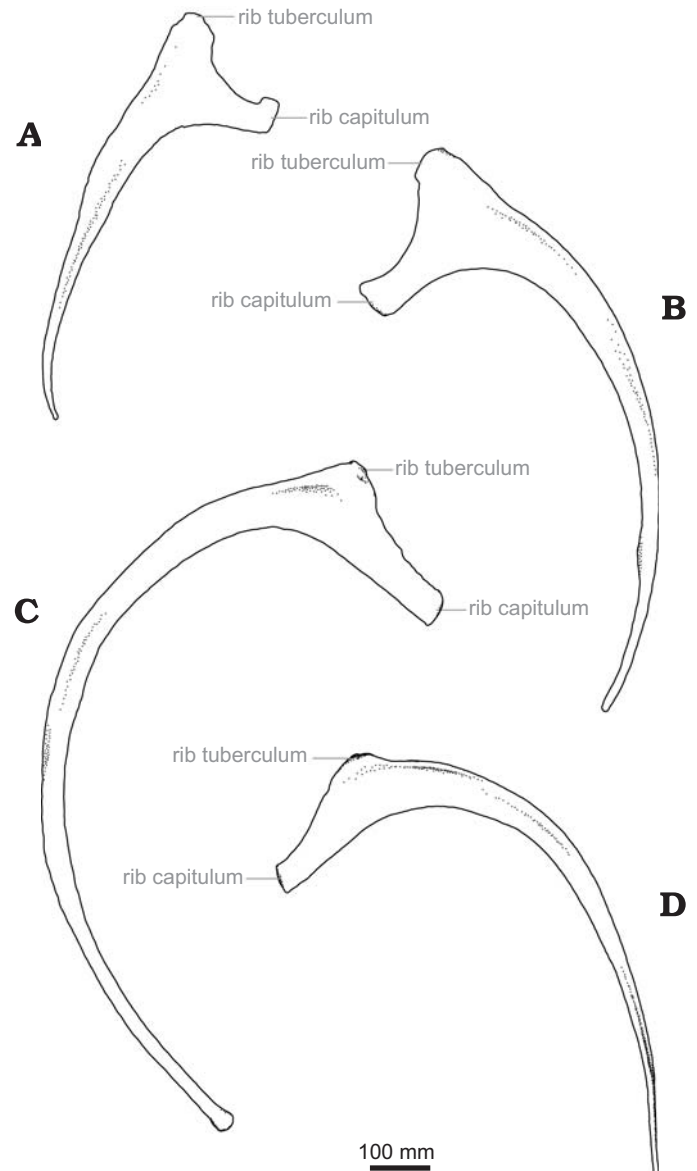


Fig. 5. Thoracic ribs of *Tyrannosaurus rex* Osborn, 1905, NSM PV 20425 from the Maastrichtian Hell Creek Formation of Buffalo, South Dakota, USA, in posterior view. **A.** Left rib for p11. **B.** Right rib for p12. **C.** Left rib for p15. **D.** Right rib for p18.

In comparison to the more anterior ribs, the ribs for p11 display a dramatic change in length, as observed in RTMP 91.36.500 (*G. libratus*). RRp11 of NSM PV 20425 (Fig. 5A) possesses a dorso-ventrally long oval capitulum, and a dorsally projected and dorsomedially faced tuberculum. The posterior surface of the tuberculum forms a rugose triangular surface. In the ribs for p12 (Fig. 5B), each notch between capitulum and tuberculum is reduced.

The ribs for p13, p14, and p15 (Fig. 5C) are characterized by great length and expanded rugose distal end, as shown in RTMP 91.36.500 and RTMP 99.33.01 (*G. libratus*). RTMP 81.10.01 (*Albertosaurus sarcophagus*), RTMP 85.98.01 (*A. sarcophagus*), RTMP 94. 12. 602 (*G. libratus*), TCM 2001. 89. 1 (*G. libratus*), RTMP 2001.36.01 (*D. torosus*), and NSM

PV 20425 (*T. rex*) preserve ribs numbered from p13 to p15, and share some features, namely, dorso-ventrally long oval capitulum, dorsally projected tuberculum, and well-developed posterior intercostal ridge. There is a distinct rugose ridge just medial to the tuberculum on the dorsal edge of the neck of each rib (Fig. 6), as noted in Brochu (2003).

In ribs posterior to p16 (Fig. 5D), the tuberculum is poorly developed. Instead, the rugosity near the tuberculum is well developed.

Discussion

Two articulated fossil skeletons, namely RTMP 91.36.500 and RTMP 99.33.01 demonstrate that the dorsally projected tuberculum of the thoracic rib articulates with the ventral or posteroventral side of the distal end of the transverse process in tyrannosaurids. In addition, on the basis of the anatomy of extant archosaurs and the osteological features in tyrannosaurid skeletons, the scars for the lig. costotransversarium can be securely identified on the distal part of transverse process and on the part just medial to the rib tuberculum in tyrannosaurids.

The tyrannosaurid osteological features that are the best explained as the scars for the lig. costotransversarium are consistent with the rib arrangement of two articulated skeletons. There is a rugose ridge on the distal part of the posterior centrodiapophyseal lamina of the transverse process in most of the specimens examined in this study. The distinct rugosity is also developed near the rib tuberculum on the dorsal edge of the rib neck. On the basis of these two features, when capitulum and tuberculum settle in parapophysis and the ventral side of the transverse process respectively, the rugosity on the rib neck and the rugose ridge on the transverse process become aligned with one another.

Rhea pennata (Aves) possesses a ligament (lig. costotransversarium) between the transverse process and the tuberculum, and a scar for the ligament on the skeleton is widely distributed within extant avian taxa. There are no distinct connective tissues at the sites other than the lig. costotransversarium in archosaurian crown groups (Frey 1988; Baumel and Raikow 1993: figs. 5, 10; Vanden Berge and Zweers 1993; Yasuda 2002: 141, pl. 3; Organ 2006), thus the relationship between avian and tyrannosaurid structures passes the tests of homology (Patterson 1982). On the other hand, crocodylians, the other archosaurian group that phylogenetically brackets the Tyrannosauridae, possess neither distinct ligament (Frey 1988) nor osteological scar. These lines of evidence indicate that the condition of the extant crown group node bracketing the Tyrannosauridae, consisting of Aves and crocodylians, is equivocal. In a functional context, the ligament in Aves aligns along the axis of costal rotation (Fig. 2C), thus facilitating the costal rotation and simultaneously reinforcing the articulation. In tyrannosaurid skeletons, the orientation of the rugose ridge on the transverse process is approximately parallel to that of the line between the two pivots on the vertebra. Provided that

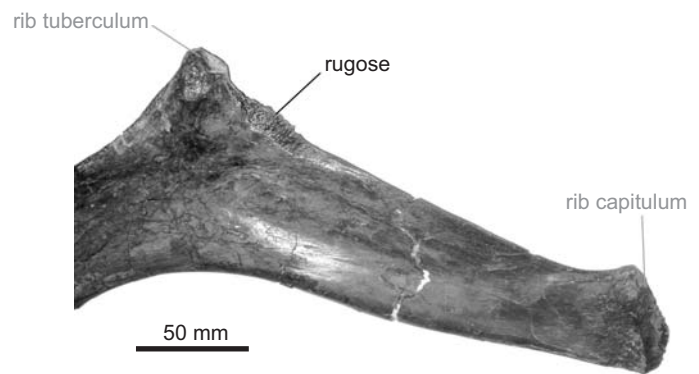


Fig. 6. Anterior thoracic rib of tyrannosaurid dinosaur *Daspletosaurus torosus* Russell, 1970, RTMP 2001.36.01 from the Campanian Oldman Formation of Milk River, Manyberries, Alberta, Canada, in posterior view. The rib head is shown.

the rugose ridge was a scar for the lig. costotransversarium, the ligament accomplished reinforcement of the articulation without interfering with the costal rotation around a single axis. Accordingly, the location of the scar for lig. costotransversarium supports the hypothesis that the ligament performed the same function in tyrannosaurids as it does in the Aves. Therefore, the presence of the lig. costotransversarium connecting the transverse process and the rib neck in the Tyrannosauridae (Fig. 7) represents a level II inference (sensu Witmer 1995).

The interpretation that the rib tuberculum articulates with the ventral surface of the transverse process in tyrannosaurids is inconsistent with a previous interpretation proposed by Lambe (1917), and complements the anatomy described by Brochu (2003). Both Lambe (1917) and Brochu (2003) relied on the possible articular facet on the rib tuberculum, although the shape of the tuberculum is usually ambiguous. Thus, the interpretation presented here that is based on both the articulated skeletons and the potential soft tissue anatomy bears better probability. This study yielded more precise observations than those of Maleev (1974), and provides additional support for the reconstruction by Maleev (1974). The shift of the articular position for the rib tuberculum in the last few presacral vertebrae (Maleev 1974) is also supported.

Among other dinosaurs, Norman (1986) described the ornithischian *Iguanodon atherfieldensis* as bearing an antero-ventrally directed recess on the transverse process and a rugosity on the posterodorsal edge of the rib neck, and interpreted these osteological features as the scars for a ligament to bind the rib firmly against the transverse process. Furthermore, in the dromaeosaurid *Saurornitholestes* (RTMP 88.121.39), each thoracic rib possesses a rugosity at the site just medial to the tuberculum on the dorsal edge of the rib neck. Although the existence of the vertebral scar is unconfirmed in this study, this taxon probably also possesses the ligament system at the tubercular articulation. In addition, some specimens of *Allosaurus* (*A. fragilis*, AMNH FR 666; *A. sp.*, AMNH FR 813; *A.*

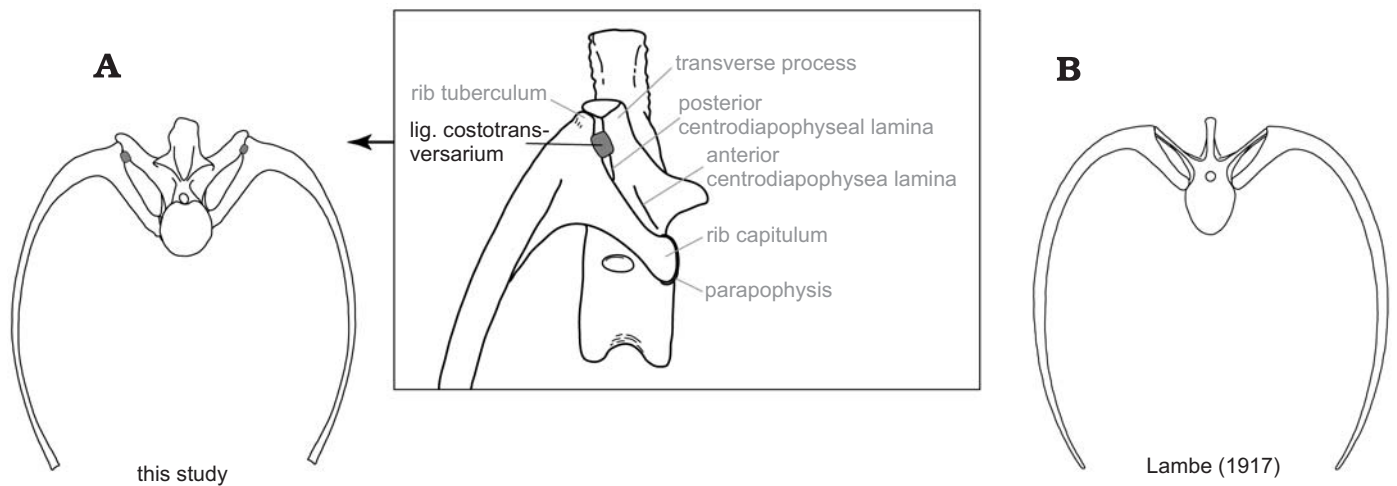


Fig. 7. The schematic structure of the costovertebral articulation in the Tyrannosauridae. **A.** The reconstruction in this study in posterior view and in right lateral view. **B.** The reconstruction by Lambe (1917) in posterior view. The rib tuberculum articulates with the ventral surface of the distal part of the transverse process in this study, whereas the rib articulates with the lateral extremity of the transverse process in Lambe (1917).

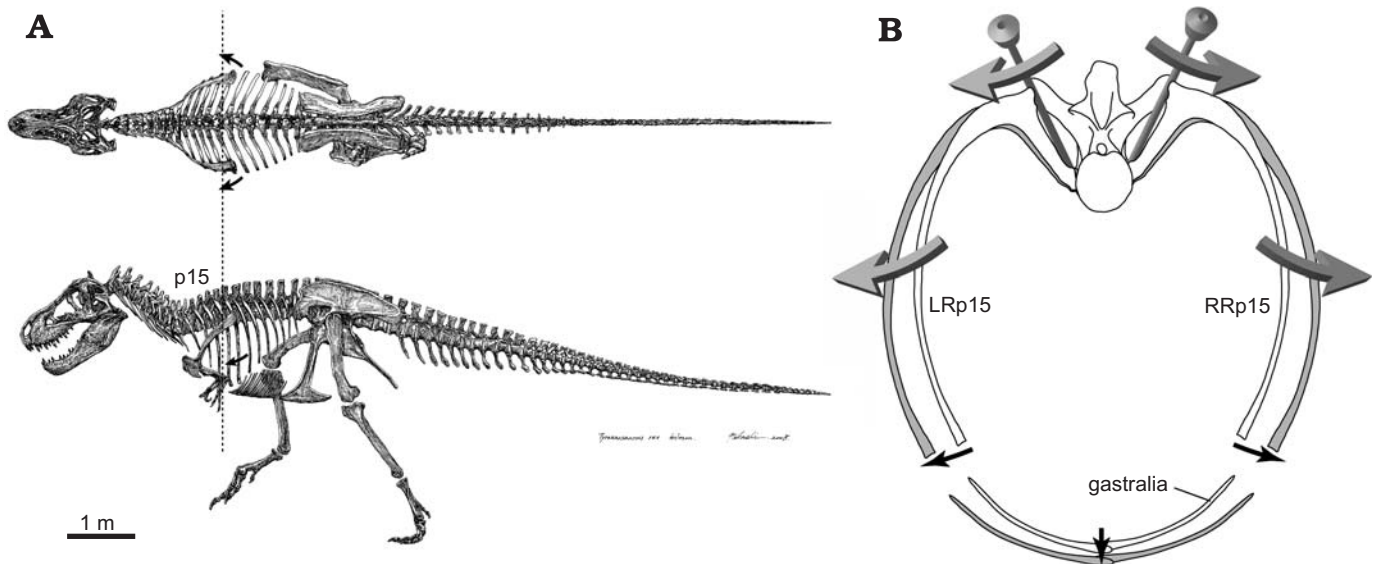


Fig. 8. Thoracic kinematics in the Tyrannosauridae. **A.** Skeleton of *Tyrannosaurus rex* in dorsal and left lateral views (reconstruction courtesy of Takashi Oda), showing the level of p15 (broken line). Arrows indicate movements of ribs during inspiration. **B.** Transverse section of the tyrannosaurid ribcage at the level of p15 in posterior view. Large three-dimensional arrows indicate the costal rotation during the shift from the expiration (white ribs) to the inspiration (shaded ribs) modes. Small plane arrows indicate the projections of the movements on the transverse plane. The rotational axis for the rib and the rib outline are based on RTMP 2001.36.01 (*Daspletosaurus torosus*).

sp., AMNH FR 680) exhibit the rugose scar on the ventral side of the distal part of the transverse process. Therefore, in general the articular position for the tuberculum on the vertebra is identifiable on the basis of the direction of the scar for lig. costotransversarium, and this landmark is useful for measuring the orientation of the rotational axis for the rib in non-avian theropods.

The orientation of the rotational axis for the rib is one of the main factors in thoracic kinematics. In tyrannosaurids, the rotational axis for the rib is oriented relatively dorso-ventrally, and thus lateral excursion is always larger than ventral excursion during costal aspiration (Fig. 8). On the other

hand, different patterns of the rotational axis are seen among other taxa. More extensive research on the rotational axis for the rib in both non-avian and avian theropods and the form-function relationship between costovertebral articulation and thoracic kinematics is necessary.

Conclusions

Observation of two nearly in-situ articulated skeletons and isolated skeletal elements of tyrannosaurids revealed that the rib tuberculum articulated with the ventral or posteroventral

side of the inverted-triangular surface on the distal end of the transverse process. In addition, a rugose scar for the lig. costotransversarium, that connects the rib tuberculum with the transverse process, was identified at the corresponding positions of both the rib neck and the vertebral transverse process. The scar for the ligament is recognizable in extant birds, but not in extant crocodylians. Therefore, this connective tissue may exist at level II inference (sensu Witmer 1995). The scar for the ligament is recognizable in other dinosaurian taxa, and thus is useful for identifying the articular facet for the rib tuberculum and the orientation of the rotational axis for the rib.

Acknowledgements

I express my greatest gratitude to Leon Claessens (Holy Cross College, Worcester, USA), Patrick O'Connor (Ohio University, Athens, USA), and Makoto Manabe (NSMT) for revising the earlier draft in detail, and to Takanobu Tsuihiji (NSMT), Lawrence Witmer (Ohio University), Peter Makovicky (Field Museum of Natural History, Chicago, USA), Norihisa Inuzuka (UT), Peter Larson (BHI), Tatsuo Oji (UT), and Kazushige Tanabe (UT) for their meaningful comments and helpful advises. Mathew Wedel (University of California, Merced, USA) and an anonymous referee critically reviewed the manuscript. Also, I appreciate the assistance of Donald Brinkman and James Gardner (RTMP); Neal Larson (BHI); and Mark Norell and Jack Conrad (AMNH). Hajime Taru and Mitsuharu Oshima provided the opportunities to dissect crocodylians and birds at KPM. Simon Darroch (UT) helped to correct grammatical errors of the manuscript. Takashi Oda (Seian University of Art and Design, Ohtsu, Japan) kindly provided the reconstruction of *T. rex*. This study was financially supported by the University of Tokyo, Research Grant Program (2005, 2006), the Jurassic Foundation (2006) and Research Fellowships from the Japan Society for the Promotion of Science (2007–2010).

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Appendix 1

List of specimen examined in this study.

Taxon	Species	Specimen number	Note
Tyrannosauridae	<i>Albertosaurus sarcophagus</i>	RTMP 81.10.01	
	<i>Albertosaurus sarcophagus</i>	RTMP 85.98.01	
	<i>Daspletosaurus torosus</i>	RTMP 2001.36.01	
	<i>Daspletosaurus</i> sp.	RTMP 85.62.01	
	<i>Gorgosaurus libratus</i>	RTMP 91.36.500 (original fossil) RTMP 2005.00.24 (cast of 91.36.500 in not fully prepared condition)	nearly in-situ articulated skeleton
	<i>Gorgosaurus libratus</i>	RTMP 94.12.602	
	<i>Gorgosaurus libratus</i>	RTMP 99.33.01	nearly in-situ articulated skeleton
	<i>Gorgosaurus libratus</i>	TCM 2001.89.1	
	<i>Tyrannosaurus rex</i>	NSM PV 20425 (cast of Black Hills Institute of Geological Research, Hill City, South Dakota (BHI) 3033)	original fossil (BHI 3033) were examined
	tyrannosaurid cf. <i>G. libratus</i>	RTMP 86.144.01	juvenile (Currie, 2003)
Aves	<i>Rhea pennata</i> (Darwin's Rhea)	KPM-NF2001026 (entire specimen)	11 years old and 25 kg in weight
	<i>Struthio camelus</i> (Ostrich)	uncatalogued UT	
	<i>Grus vipio</i> (White-naped Crane)	NSMT PO 004	
	<i>Phalacrocorax filamentosus</i> (Japanese Cormorant)	NSMT PO 14	
	<i>Pygoscelis adeliae</i> (Adelie Penguin)	NSMT PO 486	
Crocodilia	<i>Alligator mississippiensis</i>	KPM- NFR000016 (entire specimen)	
	<i>Caiman crocodilus</i> (Spectacled Caiman)	NSMT PO 424	
	<i>Caiman crocodilus</i>	NSMT PO 443	