Functional Variation of Neck Muscles and Their Relation to Feeding Style in Tyrannosauridae and Other Large Theropod Dinosaurs

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ABSTRACT
Reconstructed neck muscles of large theropod dinosaurs suggest influences on feeding style that paralleled variation in skull mechanics. In all examined theropods, the head dorsiflexor m. transversospinalis capitis probably filled in the posterior dorsal concavity of the neck, for a more crocodilian- than avian-like profile in this region. The tyrannosaurine tyrannosaurids Daspletosaurus and Tyrannosaurus had relatively larger moment arms for lateroflexion by m. longissimus capitis superficialis and m. complexus than albertosaurine tyrannosaurids, and longer dorsiflexive moment arms for m. complexus. Areas of dorsiflexor origination are significantly larger relative to neck length in adult Tyrannosaurus rex than in other tyrannosaurids, suggesting relatively large muscle cross-sections and forces. Tyrannosaurids were not particularly specialized for neck ventroflexion. In contrast, the hypothesis that Allosaurus co-opted m. longissimus capitis superficialis for ventroflexion is strongly corroborated. Ceratosaurus had robust insertions for the ventroflexors m. longissimus capitis profundus and m. rectus capitis ventralis. Neck muscle morphology is consistent with puncture-and-pull and powerful shake feeding in tyrannosaurids, relatively rapid strikes in Allosaurus and Ceratosaurus, and ventroflexive augmentation of weaker jaw muscle forces in the non-tyrannosaurids. Anat Rec, 2007. © 2007 Wiley-Liss, Inc.

Key words: feeding; muscle; neck; Tyrannosauridae; Theropoda; Dinosauria

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tion in *Ceratosaurus* and most other theropods. This unusual orientation of lever arms was suggestive that *Allosaurus* co-opted certain neck muscles to enhance the downward strike with the teeth of the upper jaw (Bakker, 2000).

Tyrannosaurids also display derived morphologies that have been associated with neck muscle function. As in *Allosaurus*, the tyrannosaurid nuchal crest of the parietals is tall and broad (Paul, 1988; Holtz, 2004), which indicates high leverage for large cranial dorsiflexors. Bakker et al. (1986) described differences in basituberal position and scar morphology in tyrannosaurs. Rugose scarring of the basioccipital tuberosities indicated large ventroflexors in *Daspletosaurus* and *Gorgosaurus*, whereas *Tyrannosaurus* (possibly including the described *Nanotyrannus* specimen; Bakker et al., 1986; Carr, 1999) had more anteriorly positioned and widely spaced basitubera, indicating different lever mechanics from those of other tyrannosaurids. Tyrannosaurid paroccipital processes are often laterally expansive, suggesting relatively greater leverage for lateral flexion of the head than is the case for most other theropods.

Much of this variation is suggestive of varying mechanical contributions to head movement and approaches to prey capture, apprehension, dismemberment, and deglutition. However, morphological attributes of neck muscles associated with these activities have yet to be described in detail or quantified, and their implications assessed with reference to other aspects of head and neck morphology. Herein, we compare the cranio cervical and intrinsic cervical muscle attachments in large tyrannosaurids, similarly sized carnosaurs, and the large neoceratosaurian *Ceratosaurus* (Fig. 1; abelisaurids and spinosaurids have unusual neck osteology, and will be the subject of future studies), and use these data in an assessment of feeding mechanics.

A multivariate study (Snively, 2006) assesses proportions and variation of cranio cervical moment arms in large theropods. However, that analysis does not address the relative sizes and consequent cross-sectional areas and force production of individual muscles. Three muscles, the cranial dorsiflexors m. transversospinalis capitis and m. splenius capitis, and the neck dorsiflexor m. transversospinalis cervicis, originate from the neural arches and spines of extant archosaurs. Because the cross-sectional area of homologous muscles is likely to be proportional to the size origins from morphologically homologous points, neural spine and arch height in lateral view can serve as a proxy for cross-sectional areas of these dorsiflexors.

We parsimoniously infer that for homologous and morphologically similar muscle origins, muscle cross-sectional areas in different theropods will be proportional to the size and rugosity of their origin scars (Cleuren and De Vree, 2000; Carpenter and Smith, 2001). This correlation is universally observed and inferred for human muscles, both through analysis of individual and sexual variation (Schwartz, 1995) and interspecifically (Trinkaus et al., 1991). Proximate examples occur for cranio cervical muscles among extant theropods. Zusi (1962) indicates that the linear size and area of vertebral muscle attachments is directly correlated with the size of neck muscles in lariform birds. The black skimmer (*Rynchops nigra*)
subjects its neck to high and rapid loadings as it sculls with its lower beak, and strikes and lifts prey out of the water (Bock, 1959). The skimmer has larger neural spines, more robust muscle attachments, and concomitantly larger neck muscles than gulls or terns (Fig. 2; Zusi, 1962). It is, therefore, reasonable to infer that in tyrannosaurs, the size of muscles associated with the neural spines and arches increased in bulk, both relatively and absolutely, in association with increasing size and rugosity of respective origins.

Calculated differences in muscle cross-sectional areas are unlikely to be 100% accurate, because more variables than origin area influence muscle cross-sectional size (Jasinoski et al., 2006). However, as a first approximation we can estimate relative areas of muscle cross-sections based on differences in the height of the neural complex (neural arch plus spine). By scaling theropod necks to a unit length and measuring the relative height of the neural arches and spines, we test the following hypothesis with simple statistics: 1) $H_a$: Neural arch and spine height is relatively greater in larger tyrannosaurids than in smaller ones. $H_0$: There are no significant differences in relative cervical neural arch + spine height in tyrannosaurids across their examined size range.

*Allosaurus fragilis* is included in these comparisons, although its phylogenetic remoteness from the tyrannosaurids demands cautious statistical interpretations. Descriptive results suggest other hypotheses testable by morphometric analysis. We apply these results and hypotheses to a discussion of the capabilities of theropod neck muscles for dorsiflexion, lateroflexion, ventroflexion, and stabilization during feeding activities.

**Institutional Abbreviations**

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<thead>
<tr>
<th>Institution</th>
<th>Location</th>
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<tr>
<td>AMNH</td>
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<tr>
<td>BHI</td>
<td>Hill City, South Dakota</td>
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<tr>
<td>BMRP</td>
<td>Rockford, Illinois</td>
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<tr>
<td>BYU</td>
<td>Provo, Utah</td>
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<tr>
<td>CMI</td>
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<td>Lehigh, Utah</td>
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<td>ROM</td>
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<td>TCMI</td>
<td>Indianapolis, Indiana</td>
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<tr>
<td>TMP</td>
<td>Drumheller, Alberta, Canada</td>
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<td>UMNH</td>
<td>University of Utah, Salt Lake City, Utah</td>
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<td>USNM</td>
<td>Washington DC</td>
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<tr>
<td>UUVP</td>
<td>University of Utah Vertebrate Paleontology, University of Utah, Salt Lake City, Utah (same as UMNH, different numbering scheme)</td>
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**MATERIALS AND METHODS**

**Descriptive Variation of Craniocervical Muscle Morphology in Large Theropods**

We examined and described craniocervical muscle scars on large theropod crania and cervical vertebrae to assess intertaxonomic variation (Fig. 1 depicts relationships of these theropods). Muscles were reconstructed in the extinct theropods by using the extant phylogenetic bracket of dissected birds and crocodilians (Witmer,
TABLE 1. Large theropod specimens examined for neck muscle attachments

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Specimen numbers</th>
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<tbody>
<tr>
<td><em>Abelisaurus comahuensis</em></td>
<td>MC 11098</td>
</tr>
<tr>
<td><em>Albrowasaurus sarcophagus</em></td>
<td>BYU 671/8901, ROM 5091, USNM 4734, UUVP 6000</td>
</tr>
<tr>
<td><em>Allosaurus fragilis</em></td>
<td>BYU 881/12893</td>
</tr>
<tr>
<td><em>Carnotaurus saastrei</em></td>
<td>MACN-CH 894</td>
</tr>
<tr>
<td><em>Ceratosaurus magnicornis</em></td>
<td>MWC 000, UMN 5728</td>
</tr>
<tr>
<td><em>Ceratosaurus nasicornis</em></td>
<td>USNM 4735</td>
</tr>
<tr>
<td><em>Ceratosaurus sp. small</em></td>
<td>BYU 5027, TMP 94.143.1</td>
</tr>
<tr>
<td><em>Daspletosaurus torosus, sp.</em></td>
<td>CMN 8506, FMNH PR 308, TMP 94.143.1</td>
</tr>
<tr>
<td><em>Gorgosaurus libratus</em></td>
<td>CMI 2001.89.1, ROM 1247</td>
</tr>
<tr>
<td><em>Majungatholus atopus</em></td>
<td>FMNH PR 2100</td>
</tr>
<tr>
<td><em>Monolophosaurus jiangi</em></td>
<td>IVPP 84019</td>
</tr>
<tr>
<td><em>Sinraptor dongi</em></td>
<td>IVPP 10600</td>
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<tr>
<td><em>Tubrosaurus bataar</em></td>
<td>ZPAL MgD-1/4</td>
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<tr>
<td><em>Tyrannosaurus rex</em></td>
<td>AMNH 5027, AMNH 5029, 5117; BMRP 2002.4.1, FMNH PR 2081</td>
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<tr>
<td><em>Nanotyrannus lancensis</em></td>
<td>TCM 2001.90.1, TMP 81.6.1 / CM 7541</td>
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TABLE 2. Anatomical abbreviations

<table>
<thead>
<tr>
<th>Name</th>
<th>Abbreviation</th>
<th>Nomenclature</th>
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<tbody>
<tr>
<td>M. transversospinalis capitis</td>
<td>m. t.cap.</td>
<td>Crocodilian</td>
</tr>
<tr>
<td>M. complexus</td>
<td>m. complexus</td>
<td>Avian</td>
</tr>
<tr>
<td>M. splenius capitis</td>
<td>m. s.c.</td>
<td>Avian</td>
</tr>
<tr>
<td>M. longissimus capitis superficialis</td>
<td>m. l.c.s.</td>
<td>Crocodilian</td>
</tr>
<tr>
<td>M. longissimus capitis profundus</td>
<td>m. l.c.p.</td>
<td>Crocodilian</td>
</tr>
<tr>
<td>M. iliocostalis capitis</td>
<td>m. i.c.</td>
<td>Crocodilian</td>
</tr>
<tr>
<td>M. rectus capitis ventralis</td>
<td>m. r.c.v.</td>
<td>Crocodilian</td>
</tr>
<tr>
<td>M. longus colli dorsalis</td>
<td>m. l.c.d./t.cerv.</td>
<td>Avian/crocodilian</td>
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<td>transversospinalis cervicis</td>
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1995). Tyrannosaurid muscle reconstructions (Snively, 2006; Snively and Russell, unpublished data) are the primary reference for identifying muscle scars of other large theropods. In most of the fossil specimens, preservation or cast resolution was sufficient to reveal the shape, size, and degree of rugosity of the muscle attachments. Specimens of *Albrowasaurus, Monolophosaurus, Abelisaurus, Majungatholus*, and two of *Ceratosaurus* were less complete or well-preserved, but otherwise had identifiable attachments. All specimens are listed in Table 1.

As detailed in the list of anatomical abbreviations given in Table 2, muscles are inferred using the crocodilian or avian nomenclature (Vanden Berge and Zweers, 1993; Cleuren and De Vree, 2000; Tsuihiji, 2005), depending on which extant taxon has attachments most closely resembling those of the large theropods. Both the avian and crocodilian names are applied to m. l.c.d./t.cerv., because their insertions on the cervical epipophyses clearly resemble those of birds, whereas their origins, from the lateral surfaces of tall neural spines along much of the neck, are inferred to be similar to those of crocodilians.

Relative Neural Spine Height in Large Theropods

To obtain a relative size index of cranial and neck dorsiflexors, neural arch plus spine heights (hereafter termed “neural complex heights”) were compared between tyrannosaurs and *Albrowasaurus*, with the necks scaled to a unit length (Table 3; Fig. 3). Specimens of a range of sizes were chosen, including a juvenile *Gorgosaurus libratus*, two adult *Daspletosaurus torosus*, two adult *T. rex*, and an adult *Albrowasaurus fragilis*. The neck of the skeleton *Gorgosaurus* was straightened when its skeleton was mounted, and the cervicals of one *Tyrannosaurus* specimen were taphonomically compressed toward each other and were not separated during preparation. This resulted in too long and too short a neck, respectively, and was corrected by selecting images of individual vertebrae in Adobe Photoshop® and aligning the zygaphophyses with 100% overlap. Necks were set to a unit length by measuring along the curvature formed by the centra in Adobe Illustrator® and scaling each neck image to the same length. Initial relative measurements of the neck of *Albrowasaurus fragilis* were based on a detailed skeletal restoration (Paul, 1988) of USNM 4734, reconstructed as articulated in a neutral posture. Subsequent examination of the specimen corroborated the accuracy of the restoration (Fig. 3D).

Measurements of neural complex height were taken between equivalent points on the images of homologous vertebrae, usually from the tip of the neural spine to a projected point between the bilateral lateral anterior bases of the neural arch, using the ruler tool in Adobe Illustrator®. Images of cervical C2-C9 were measured, because C10 was not available for one of the *Tyrannosaurus rex* specimens (BHI 3033). Pairwise t-test comparisons tested whether the average neural spine heights differed between specimens, with a two-sided confidence level initially set to 0.95 (*P* = 0.05). Because relative supracentral heights in individual animals can be considered nonindependent, *α* was manipulated downward and the confi-
dence level increased by a Dunn-Sidak adjustment:

\[ \alpha_k = 1 - (1 - \alpha)^{1/k} \]

in which \( \alpha \) is the adjusted significance value, \( \alpha \) is the original (0.05), and \( k \) is the number of comparisons. (A Dunn-Sidak correction yields a more exact and rigorous reduction in significance value than a Bonferroni adjustment.) For the three tyrannosaurid species \( k = 3 \) and \( \alpha_k = 0.01695 \). For comparison of each tyrannosaurid species with the Allosaurus specimen, and for the Daspletosaurus and Tyrannosaurus specimens with each other, \( k = 1 \) and \( \alpha_k = 0.0255 \). These values for \( k \) are legitimate given the phylogenetic proximity of the tyrannosaurs, their phylogenetic remoteness from Allosaurus (Fig. 1), and intraspecific comparisons between the tyrannosaurid specimens.

**RESULTS**

**Descriptive Patterns of Theropod Craniocervical Muscles**

Muscle attachments are described in most detail for albertosaurine tyrannosaurids, and interesting deviations from the albertosaurine origin pattern are described as they occur. Figure 4 depicts origins of neck muscles from the anterior presacral vertebrae of a representative theropod, Tyrannosaurus rex. There was little variation in the position of muscle origin sites among large theropods. The morphology of both origin and insertion sites are now described sequentially for each group (Fig. 1), beginning with albertosaurines, followed by tyrannosaurines, Allosaurus, and Ceratosaurus. These morphological data are then assessed comparatively in a systematic context, to assess variation and to relate this to its potential functional implications.

Figures are ordered inductively, first depicting insertions on specimens (as in Figs. 5 and 6) and then providing a restoration of inferred muscle morphology. In figures mapping craniocervical insertions, the occipital condyles of all specimens are scaled to the same width. This facilitates comparison of muscle moment arm lengths, and the relative size of insertions. Perspective distortion in the Allosaurus photographs exaggerates the breadth across the paroccipital processes.

**Tyrannosauridae: Albertosaurinae (Figs. 5, 7)**

*M. transversospinalis capitis (m. t.cap.)*. M. transversospinalis capitis of albertosaurine tyrannosaurids and other large theropods originated from the tips of the neural spines, and the insertion is interpreted as being along the dorsal edge of the parietals. In the albertosaurine specimens Albertosaurus sarcophagus (TMP 81.10.1), Gorgosaurus libratus (ROM 1247), and Gorgosaurus sp. (CMU 201.891), the nuchal aspect of the parietals rises far dorsally above the squamosals (present in ROM 1247 and CMU 201.891); demarcated by the squamosal articular surfaces of the postorbital and quadratojugal in TMP 81.10.1). In ROM 1247 and TMP 81.10.1, the crest appears tall relative to the breadth of the paroccipital processes. The high position of the m. t.cap. scar relative to the occipital condyle suggests strong dorsiflexive leverage for the muscle. In the Albertosaurus sarcophagus and smaller Gorgosaurus specimen (ROM 1247) the parietals are comparatively smooth in this region. How-
LARGE THEROPOD NECK FUNCTION

ever, in the larger Gorgosaurus (CMI 2001.89.1; Fig. 5) the m. t.cap. insertion is highly rugose.

Large theropods had an S-shaped neck synapomorphic for Dinosauria. In tyrannosaurs such as albertosauroids (Fig. 7), the posterior flexure of the neck is particularly acute (Holtz, 2004). In crocodilians m. t.cap. fills in the dorsal concavity formed by the ventral bowing of the entire neck, which is similar in posture to the posterior portion of the neck of theropods. The inferred origins of m. t.cap. of theropods, from the tips of most neural spines, are more similar to those of crocodilians than to the posteriorly restricted origins of the homologous m. biventer cervicis of birds (Tsujihi, 2005). It is therefore likely that m. t.cap. of albertosaurine tyrannosaurs (Fig. 7A) and other large theropods filled in the space formed by the posterior flexure of the neck as seen in crocodilians.

This differs from the condition superficially evident in birds, in which dorsal cervical musculature appears to follow the curvature of the vertebrae. However, radiographs of anseriformes (Samman, 2006) demonstrate that the muscles can partially occupy this posterior concavity. The ostensible adpression here is partly a visual consequence of the anteriorly elongate neck of birds, and partly a real effect of m. biventer cervicis being slender and intimately associated with the neck dorsiflexor, m. l.c.d.

M. complexus. M. complexus of tyrannosaurs is reconstructed as having originated from tall cervical epi-pophyses, and to have inserted on the posterior aspect of the squamosals. Compared with tyrannosaurine taxa, this surface is dorsoventrally restricted, as is evident in both Gorgosaurus specimens. The m. complexus insertion was relatively low and long, with a long lateral moment arm from the occipital condyle to the centroid of the attachment. Because the squamosals do not rise far dorsally above the position of the occipital condyle, they apparently had a more modest lever arm for dorsiflexion.

M. splenius capitis (m. s.c.). The medial portion of m. splenius capitis (Tsuihi, 2005) originated from the anterolateral surface of the C2 neural spine, which was exceptionally broad in albertosauroids and other tyrannosaurs. The muscle inserted on the posterior surface of the parietals. This surface varies among albertosauroid taxa, and may sometimes differ between left and right sides of the nuchal crest in the same specimen. In Albertosaurus sarcophagus (TMP 81.10.1) the surface is tall, narrow, and strongly concave medially. The insertion was somewhat broader in Gorgosaurus libratus (ROM 1247), and a large ventromedial concavity is present in the larger Gorgosaurus (CMI 2001.89.1; Fig. 5). In another large specimen identified as Gorgosaurus (AMNH 5336), Bakker et al. (1986) figured a mediolaterally extensive concavity into which m. s.c. would insert. The dorsiflexive moment arm for m. s.c appears larger in Albertosaurus sarcophagus (TMP 81.10.1) and in the ROM 1247 Gorgosaurus libratus than it is in the other Gorgosaurus specimens.

A lateral division of m. s.c. (originating from C3 and perhaps the lateral wings of the spine table of C2) may have inserted on the squamosal of albertosauroids, lateral to the caudoventral portion of the parietal and medial to the insertion of m. complexus. This insertion would have been dorsoventrally depressed, and had a laterally flexible moment arm.

M. longissimus capitis superficialis (m. l.c.s.). M. longissimus capitis superficialis originated from the distal, lateral or ventrolateral portions of the transverse processes, beginning with C5 or C6, with the posterior-most origin being from C10 or D1. This muscle inserted on the lateral extremity of the paroccipital process (the posterolateral surface of the opisthotics). The surface of this scar is rugose in all examined albertosau-
Fig. 4. Origins of major neck muscles in large theropods, mapped onto anterior presacral vertebrae [C2 (right) to D2] of Tyrannosaurus rex (right lateral view). Muscle scars include m. transversospinalis capitis (m. t.c), m. longissimus capitis superficialis/transversospinalis cervicis (m. l.c.d./t.cerv), m. complexus, m. splenius capitis (m. s.c), m. longissimus capitis profundus (m. l.c.p), m. longissimus capitis superficialis (m. l.c.s), m. iliocostalis capitis (m. i.c), m. rectus capitis ventralis (m. r.c.v). Colors indicate developmental divisions of the axial musculature: m transversospinalis (blue), m. longissimus (red), and m. iliocostalis/m. longus (green). Insertions of m. transversospinalis cervicis were posterior to the origins of m. complexus, from the anterior cervical epipophyses. Lines connect multiple origins of individual muscles; they do not represent physical continuity between scars. Some overlap was possible for origins m. i.c.s and m. i.c.p, on the transverse processes of the midcervical vertebrae. Origins of m. r.c.v. from the hypopophyses of the anterior cervicals, are partially obscured by the cervical ribs.

ines, but the rugosity is especially prominent in the large CMI 2001.89.1 Gorgosaurus (Fig. 5). The paroccipital processes are laterally expansive in this specimen, but appear narrow relative to the height of the nuchal crest in other albertosaurines. M. l.c.s, therefore, had a long moment arm for lateral flexion in CMI 2001.89.1, but apparently less leverage in the ROM 1247 Gorgosaurus and the TMP 81.10.1 Albertosaurus.

M. longissimus capitis profundus (m. l.c.p). M. longissimus capitis profundus is inferred to have originated from the transverse processes of the anterior cervicals, and to have inserted ventromedially onto the basioccipital tuberosities. A large subrectangular or teardrop shaped concavity occurs here in all three albertosaurines. This indentation is in the position expected for the insertion of m. l.c.p., but if the concavity is a pneumatic recess, then the muscle would likely have inserted lateral to it. The scar is positioned relatively farther ventrally on the Albertosaurus sarcophagus specimen than it is in the others, suggesting a relatively longer ventroflexive lever arm.

M. iliocostalis capitis (m. i.c). M. iliocostalis capitis originated from fascia surrounding the cervical rib shafts and/or from the large proximal surfaces of the posterior cervical ribs. In tyrannosaurids this muscle is interpreted as having inserted into a large triangular concavity of the ventral portion of the paroccipital process or its ventral edge (including the exoccipital medially and opisthotic laterally). This insertion is low and mediolaterally restricted in Albertosaurus sarcophagus (TMP 81.10.1)
and *Gorgosaurus libratus* (ROM 1247) compared with the broad and tall scar in the large *Gorgosaurus* (CMI 2001.89.1; Fig. 5). The center of the scar is lateral and somewhat ventral to the occipital condyle, suggesting high-gauged lateroflexion.

**M. rectus capitis ventralis (m. r.c.v.).** M. rectus capitis ventralis originated from the hypopophyses and ventral surfaces of the cervical centra. All examined albertosaurine specimens have discrete scars on the ventral surface of the basitubera for insertion of m. r.c.v. The scar is ventromedial to the insertion of m. l.c.p., and would have had the greatest ventroflexive moment arm of any of the cranio cervical muscles. The insertions of m. r.c.v. appear greatly deflected ventrad of the occipital condyle in *Albertosaurus sarcophagus* (TMP 81.10.1) and to a lesser extent in *Gorgosaurus libratus* (ROM 1247), suggesting relatively stronger ventroflexion in these animals than in the large *Gorgosaurus* (CMI 2001.89.1; Fig. 5).

**M. longus colli dorsalis/m. transversospinalis cervicis (m. l.c.d./t.cerv.).** This system of neck dorsiflexive muscles originated from the lateral surfaces of the neural spines of C4–C10, ventral to the origins of m. t.cap. The posterior neural spines are relatively shorter in albertosauines than tyrannosauines, indicating less available surface area for the origins of m. longus colli dorsalis/m. transversospinalis cervicis. As with most other large theropods, the insertions were onto posteriorly-facing scars of the anterior epipophyses, and perhaps onto the dorsal surfaces of some posterior cervical epipophyses. Insertion scars on C2 and C3 of albertosauines and other tyrannosaurids are more discrete than they are in birds or other theropods, with subcircular posterior concavities indicating stout tendons. As with crocodilians, but unlike in birds, an insertion tendon may have continued anteriorly onto the neurophyssis of C1.

Because the insertions of m. longus colli dorsalis/m. transversospinalis cervicis lie dorsal to the likely centers of intervertebral rotation, the tendons would have been conduits for dorsiflexive rotation of the anterior vertebra of each pair relative to the posterior one. Once intervertebral dorsiflexion had reached its limits, the muscles may have acted to dorsiflex the entire neck. The center of pull of the muscular system would have to be dorsal to the center of rotation of the entire system.

**Tyrannosauridae: Tyrannosaurinae (Figs. 6, 8, 9)**

**M. transversospinalis capitis (m. t.cap.).** The origins of m. transversospinalis capitis were probably relatively more extensive in tyrannosaurines than albertosauines, because the posterior neural spines are taller. This is especially evident in specimens of *Daspletosaurus* (CMN 8505, FMNH PR 308) and *Tyrannosaurus rex* (BHI
Fig. 6. Craniocervical muscle scars on occiputs of tyrannosaurine tyrannosaurids A: Daspletosaurus torosus (CMN 8505; 1.0 meter from the premaxilla to the posterior-most extent of the opisthotics). B: Tyrannosaurus rex (AMNH 5119; scale bar = 10 cm). C: Tyrannosaurus rex (FMNH PR 2081; 1.4 meters from the premaxilla to the posterior-most extent of the opisthotics). Lateral images of the specimens show the location of some muscle scars in context. Abbreviations are as in Figure 4. FMNH PR 2081 is crushed dorsoventrally and partly reconstructed for symmetry; its lateral skull reconstruction is restored as undistorted. Ambiguous insertions of m. splenius capitis are designated with a question mark. Color coding and abbreviations are as in Figure 4.
Fig. 7. Schematic lateral reconstruction of neck muscles in the albertosaurine tyrannosaurid Gorgosaurus sp. (CMI 2001.89.1); the cervical rib on C10 is restored. Intervertebral muscles are omitted. A–C: The first image (A) depicts the superficial muscles, and B and C represent successively deeper layers. Blue, muscles of the transversospinalis system; red, longissimus system; green, iliocostalis system.
Fig. 8. A–C: Lateral flesh reconstruction of neck and jaw musculature of Tyrannosaurus rex (A), Allosaurus fragilis (B), and Ceratosaurus nasicornis (C). Tendinous attachments are rendered as white. Neck muscle abbreviations are as in Figure 4. B: In Allosaurus fragilis, the novel course of m. longissimus capitis superficialis is evident. In Ceratosaurus m. longissimus capitis profundus and m. rectus capitis ventralis are restored as robust, based on the large size of their insertions. M. transversospinalis capitis has a relatively small insertion on the parietals in Ceratosaurus, and this muscle is restored here as slender compared with that in Tyrannosaurus and Allosaurus. Jaw muscle contractions are: m. a.m.e. med. = m. adductor mandibulae externus medialis. m. a.e.s., m. adductor mandibulae externus superficialis; m. a.e. post., m. adductor mandibulae posterior; m. dep. mand., m. depressor mandibulae; m. pt. ant., pterygoideus anterior/dorsalis; m. pt. post., m. pterygoideus posterior/ventralis.
Fig. 9. Schematic dorsal reconstructions of neck muscles in large theropods, with intervertebral muscles omitted. Most abbreviations are as in Figure 4 (m. epi.-cap. med., m. epistropheo-capitis medialis), and color-coding and superficial-to-deep conventions are as in Figure 7. A–C: Juvenile Tyrannosaurus rex, reconstructed from measurements and photographs of BMRP 2002.4.1. The occiput and some cervicals are restored after adult specimens. Tendons of m. l.c.d./t.cerv. (B, right) would insert onto the anterior epipophyses posteroventral to the origins of m. complexus (B, left). M. l.c.d./t.cerv. is shown here overlying these structures to emphasize the course of the entire muscle complex. D: Adult Tyrannosaurus rex (AMNH 5027; skeleton after Paul, 1988), showing the breadth of the neck muscles (in black) relative to other depicted theropods. E–G: Neck muscles of Allosaurus fragilis, overlying a skeletal reconstruction of UNNM 4734 modified from Paul (1988). One part of the m. l.c.d./t.cerv. system is shown (F), with origins from posterior neural arches and insertions onto the posterior surfaces of the anterior epipophyses. H–J: Ceratosaurus nasicornis, with muscles overlying a skeletal reconstruction of USNM 4735 modified from Paul (1988). Note the narrow insertions of m. t.cap. compared with those in Allosaurus fragilis (E–G) and Tyrannosaurus rex (A–D). In E–J, a ligament may have been present in the depicted locations of m. epistropheo-capitis medialis.
3033), but is obscured in other T. rex specimens because the neural arches below the spines appear proportionally large (AMNH 5027). The insertion of the muscle onto the nuchal crest of the parietals is broad in the tyrannosaurines Daspletosaurus torosus (CMN 8505), Daspletosaurus specimens FMNH PR 308 and TMP 94.143.1 (a juvenile), and Tyrannosaurus rex (AMNH 5027, 5029, 5117; BHI 3033, CMNH 7541 [juvenile], FMNH PR 2081, MOR 555, TMP 81.6.1). This indicates a mediolaterally extensive insertion for m. t.c.p., compared with that of Albertosaurus sarcophagus (TMP 81.10.1) and Gorgosaurus libratus (ROM 1247).

The parietal scar is highly rugose in all specimens except for Daspletosaurus torosus (CMN 8505) and the largest and smallest Tyrannosaurus rex (FMNH PR 2081 and CMNH 7541). The scar is also rough in specimens of Tarbosaurus bataar (especially in ZPAL MgD-I/4), as described by Hurum and Sabath (2003). In some Tyrannosaurus rex specimens (AMNH 5027, 5029, 5117) the rugosity has extremely high relief reminiscent of nuchal scarring on the occiput of large prosobodontians. The size and rugosity of the m. t.c.p. scar in tyrannosaurines indicates a large, powerful muscle, but its dorsiflexive leverage appears lesser than in albertosaurines relative to the breadth of the skull.

M. complexus. In posterior view tyrannosaurine squamosals are relatively more dorsoventrally extensive than those of albertosaurines, indicating a more dorsoventrally extensive insertion of m. complexus. Because the squamosals are more laterally extensive (concomitant with the broader paroccipital processes), the insertion area may have been relatively greater in tyrannosaurines than in albertosaurines. The origins of m. complexus on the epiphyseal appear relatively larger in tyrannosaurines than in albertosaurines. Larger attachments may have been associated with a muscle belly of a larger cross-sectional area (as seen in lariforms: Zusi, 1962) than in albertosaurines. Leverage for lateroflexion, and especially dorsiflexion, by m. complexus appear generally greater for m. complexus of tyrannosaurines vs. albertosaurines. An exception is found in a narrow-skulled adult Daspletosaurus (FMNH PR 308), which displays a shorter m. complexus lever arm for lateral flexion than that of other large tyrannosaurines.

The scar is not well-delineated in most tyrannosaurine specimens, and the extent of m. complexus attachment to the squamosals is ambiguous. In many Tyrannosaurus rex specimens the squamosals form a posterior apical ridge that runs ventrolaterally. In one T. rex specimen (TMP 81.6.1) a discrete ridge-like scar occurs there. This may indicate mineralization of the tendon of m. complexus. The region in variable in Daspletosaurus, appearing either flat (CMN 8050) or ridge-like (FMNH PR 308).

M. splenius capitis (m. s.c.). As with albertosaurines, the shape of the m. s.c. insertion on the parietals varies between specimens, and even between left and right sides of the same specimen. This is presumably the result of either taphonomic distortion or developmental variation. It ranges from nearly circular in Tyrannosaurus rex AMNH 5027, BHI 3033, and FMNH 2081 to sub-triangular on the left parietal of Daspletosaurus torosus CMN 8505 and right parietal of Tyrannosaurus rex AMNH 5119. The scar is more mediolaterally extensive in tyrannosaurines than it is in the albertosaurines Albertosaurus sarcophagus TMP 81.10.1 and Gorgosaurus libratus ROM 1247. However, the tyrannosaurine m. s.c. scar does not appear broader than that of the large Gorgosaurus CMI 2001.89.1, except that in most Tyrannosaurus rex specimens. M. s.c. inserted dorsal to the occipital condyle in all tyrannosaurids, and would have had a strong dorsiflexive lever arm. In all tyrannosaurines, the lateral breadth of the parietals may have given m. s.c. a longer lever arm for lateral flexion than was the case for albertosaurines.

A possible attachment for a lateral division of m. splenius capitis occurs on the squamosal, ventromedial to the insertion of m. complexus. This region is better delineated in tyrannosaurines than is in albertosaurines. At this position a lateral belly of m. s.c. would have a long moment arm for lateral flexion. Because the insertion was dorsal to the occipital condyle, the muscle could have acted in dorsiflexion as well, although this moment arm would be shorter than that for lateral flexion. Alternatively, this region may be part of the insertion area of m. complexus.

M. longissimus capitis superficialis (m. l.c.s.). The paroccipital processes appear proportionally broader in tyrannosaurines than albertosaurines (validated by statistical results: Snively, 2006), and the insertion of m. l.c.s. had a correspondingly long moment arm for lateroflexion. This moment arm was especially large relative to skull length in Tyrannosaurus rex specimens. While the juvenile Daspletosaurus (TMP 94.143.1) and the type of Daspletosaurus torosus (CMN 8505) have broad paroccipital processes, another adult Daspletosaurus (FMNH PR 308) has a posteriorly narrow skull. The moment arm for m. l.c.s. in this animal would have provided for weaker lateral flexion than is the case for other large tyrannosaurines.

Rugosity of the m. l.c.s. insertion is different between some tyrannosaurine specimens and the albertosaurines. The scar is invariably large in area and discrete, but has a smoother, bumpier texture in Tyrannosaurus rex and the type of Daspletosaurus torosus (CMN 8505), when compared with the parallel striations seen in most albertosaurines and the juvenile Daspletosaurus (TMP 94.143.1).

M. longissimus capitis profundus (m. long. cap. prof). A concave scar on each basioccipital tuberosity of tyrannosaurines resembles that inferred as the m. l.c.p. insertion in albertosaurines, and would have a similar moment arm for ventroflexion. The scar appears more laterally placed in tyrannosaurines than in albertosaurines, reflecting a longer lever arm for lateral flexion by m. l.c.p.

M. iliocostalis capitis (m. i.c.). The triangular insertion of m. i.c. is mediolaterally broader in tyrannosaurines than in albertosaurines (including the large Gorgosaurus CMI 2001.89.1), with the exception of the narrow-skulled Daspletosaurus (FMNH PR 308). The moment arm for lateral flexion would have been generally longer, for lower-squared leverage with higher out force but potentially less out velocity when turning the head.
**M. rectus capitis ventralis (m. r.c.v.).** In tyrannosaurs, the insertion of m. r.c.v. is in the same position as it is in albertosaurines, ventral to the concave insertion of m. l.c.p. M. r.c.v. would have had the greatest ventroflexive lever arm of any of the craniocephalic muscles. As for m. l.c.p., the insertion is more laterally placed than it is in albertosaurines, indicating greater potential for lateral flexion.

**M. longus colli dorsalis/m. transversospinalis cervicis (m. l.c.d./t.cerv.)**. M. l.c.d./t.cerv. origins from the posterior neural spines of adult tyrannosaurus specimens [including Daspletosaurus CMN 8505 and FMNH PR 308 and Tyrannosaurus AMNH 5027, BHI 3033, BM(NH) R7994: Osborn (1905)] appear proportionally taller than they do in albertosaurines or other large theropods. This indicates a relatively larger potential origination area in any other large theropod, save for the carnivore Acrocanthosaurus atokensis (Currie and Carpentor, 2000; Harris, 1998).

The insertions of m. longus colli dorsalis/m. transversospinalis cervicis were onto the posterior surfaces of the cervical epipophyses, as described for albertosaurines, indicating similar intervertebral and whole-neck dorsiflexion. The posterior concavity of insertion on the C2 epipophysis is especially discrete in *Tyrannosaurus rex*.

**Carnosauria: Allosaurus fragilis** (Figs. 8–11)

**M. transversospinalis capitis (m. t.cap.).** As in tyrannosaurs, *Allosaurus fragilis* has broad parietales with a discrete posterodorsal surface, interpreted to be the insertion site of m. t.cap. The attachment is less rugose than it is in tyrannosaurs. This may indicate a weaker attachment, and a muscle belly with a relatively smaller cross-section and force generation than in m. t.cap. of tyrannosaurs. The scar’s position dorsal to the occipital condyle indicates that m. transversospinalis capitis in *A. fragilis* was an effective dorsiflexor.

The supraoccipital of *Allosaurus fragilis* has a strong, wedge-like projection (Madsen, 1976) that extends posteriorly from the parietals. The projection can be rugose in large specimens (as in UUVP 6000 and BYU 671/8901), especially on its dorsal surface, which strongly indicates attachment of soft tissues. There are three major candidates for the attaching structure: a medial tendon of m. transversospinalis capitis, part of m. splenius capitis (similar to m. epistropheo-capitis medialis of crocodylians), or a ligament from the anterodorsomedial surface of the C2 neural spine. If t. cap. inserted on the projection, it indicates a topology similar to that of crocodylians (Tsuihiji, 2005), which have lateral and medial tendons for different portions of m. t.cap. *Allosaurus fragilis* would differ from crocodylians, however, in having a large insertion for the lateral tendon of m. t.cap. on the nuchal crest of the parietals.

The height of the parietal crest and supraoccipital projection vary substantially in different specimens of *Allosaurus fragilis*, being tall in UUVP 6000 and low in ROM 12868. This suggests that capability for cranial dorsiflexion was variable between individuals.

**M. complexus.** The inferred insertion of m. complexus of *Allosaurus fragilis* resembles that of the type specimen of *Daspletosaurs torosus* (CMN 8505): a large, flat area on the posterior surface of the squamosal. This surface is tall and triangular in *A. fragilis*, and the attachment for m. complexus would be narrower than it was in tyrannosaurs. The height of the insertion above the occipital condyle indicates a substantial lever arm for dorsiflexion. However, the moment arm for lateral flexion appears longer than that for dorsiflexion. Insertion morphology of m. complexus, therefore, more closely resembles that of tyrannosaurine tyrannosaurs, but its lever arm mechanics appear to more closely approximate those of albertosaurines.

**M. splenius capitis (m. s.c.).** A large concave area on the posterior surface of the parietales is interpreted as the main insertion of m. splenius capitis, lateral and ventrolateral to the posterior projection of the supraoccipital and ventromedial to the dorsal insertion of m. t.cap. This insertion is more consistently shaped from specimen to specimen, and the left and right insertions are more consistently symmetrical, than seen in tyrannosaurs. M. s.c. would have had a strong moment arm for dorsiflexion. However, the moment arm for lateral flexion appears relatively smaller than it was in tyrannosaurs, the parietal nuchal crests of which are wider than those of *A. fragilis*.

The likely insertion of m. complexus takes up most of the posterior surface of the squamosal of *A. fragilis*. This would restrict the potential insertion area for a lateral division of m. s.c. Because the neural spine of C3 is narrower in *Allosaurus* than it is in tyrannosaurs, origination area would be smaller as well. If present, a lateral division of m. s.c. likely constituted a minor portion of the craniocephalic musculature of *A. fragilis*.

If a muscle originating medially to m. s.c. from the axis inserted onto the posterior projection of the *Allosaurus* occiput, it may have been similar to m. epistropheo-capitis medialis of crocodylians. M. splenius capitis as described here would have resembled the crocodilian m. epistropheo-capitis lateralis.

**M. longissimus capitis superficialis (m. l.c.s.).** M. longissimus capitis superficialis of *Allosaurus fragilis* would have inserted on the lateral edge of the paroccipital process, and had a substantial moment arm for lateral flexion. The attachment is less rugose than it is in most tyrannosaurid specimens. In *Allosaurus* specimens in which this insertion is well preserved, such as ROM 12868 and the right side of UUVP 6000, the paroccipital processes slope ventrolaterally so that the m. l.c.s. scar lies well below the occipital condyle. Corroborating Bakker’s (2000) observations, this arrangement is unique among examined theropods and appears to be reflective of a strong ventroflexive moment arm of the muscle.

**M. longissimus capitis profundus** (m. long. cap. prof). The basitubera of some specimens of *Allosaurus fragilis* have distinct lateral and medial projections. M. longissimus capitis profundus inserted on the lateral division. The morphology of this bifurcation varies among *A. fragilis* specimens; in BYU 671/8901 the lateral projection is larger and more laterally offset than it is in UUVP 6000. In all examined *A. fragilis* specimens m. l.c.p. has a large ventroflexive moment arm, but those with a more lateral insertion likely had greater leverage for lateral flexion. The bifurcation of the basitubera is unique to *Allosaurus* among examined theropods.

**M. iliocostalis capitis** (m. i.c.). The insertion of m. iliocostalis capitis in *Allosaurus fragilis* is inferred as having
been onto a rectangular depression on the ventral portion of
the paroccipital process. This differs from the more triangu-
lar pattern of insertion present in most tyrannosaurs. The
muscle would have had moment arms for lateral flexion and
some capacity for ventroflexion, although these would be
less extensive than the respective capabilities of m. l.c.s.

**M. rectus capitis ventralis (m. r.c.v.).** A discrete
insertion for m. rectus capitis ventralis is present on the
posteroventral surface of the medial projection of the basi-
tubera. The insertion is ventral to the occipital condyle,
and the associated muscle imparted ventroflexion along
with m. l.c.s. and m. l.c.p.
Fig. 11. Schematic lateral reconstruction of neck muscles of Allosaurus fragilis overlying a skeletal reconstruction of USNM 4734 modified from Paul (1988). Intervertebral muscles are omitted. Color coding and superficial-to-deep conventions are as in Figure 7, and abbreviations follow Figures 4 and 9. M. longissimus capitis superficialis (A) may have more closely followed the contour of the neck than depicted here. A ligament may have been present in the depicted location of m. epistropheo-capitis medialis.
**M. longus colli dorsalis/m. transversospinalis cervicis (m. l.c.d./t.cerv.).** Slips of this muscular system originated from the lateral surfaces of the neural spines and inserted on the epipophyses, as they did in tyrannosaurids, and functioned similarly to promote cervical dorsiflexion. The neural spines were lower relative to neck length than they were in adult tyrannosaurids, but appear more extensive anteroposteriorly than they do in all tyrannosaurids except some *Tyrananosaurus rex* specimens. On the cervicals of *Allosaurus*, striated scars on the lateral surfaces of posterior neural spines are restricted to the dorsal half of the spine. The relative bulk of the muscle in the two groups is difficult to compare with reference to the size of the origins, although the insertion tendons may have been relatively smaller in *Allosaurus* than they were in tyrannosaurids. Because the cervicals of *Allosaurus* were strongly opisthocoelous, intervertebral dorsiflexion may have had greater excursion than in tyrannosaurids, but this must be tested by examining the range of motion at the zygapophyses (Samman et al., 2006).

**Neoceratosauria: Ceratosaurus (Figs. 8, 9, 12, 13)**

**M. transversospinalis capitis (m. t.cap.).** The origins of *m. transversospinalis capitis* in *Ceratosaurus* are bracketed as having been tendinous from the dorsal surfaces of the neural spines. Osteoderms, closely associated with the neural spines in *Ceratosaurus nasicornis* (USNM 4735), resided within the skin and superficial fascia covering the muscle, and would have been dorsally displaced by it during life. This interpretation could be falsified or complicated if histological evidence points to close connection between the osteoderms and neural spines.

There are several nonexclusive candidates for the insertion of *m. transversospinalis capitis*. Unlike *Allosaurus* and tyrannosaurids, *Ceratosaurus* lacks a broad nuchal crest that would support a large tendinous insertion. Instead, the parietals of *Ceratosaurus* slope ventrolaterally on either side of a caudally rugose, posterior projection of the supraoccipital (like that present in *Allosaurus*). The parietals may bear a midline, dorsal posterior projection above the supraoccipital, as do those of *Ceratosaurus magnicornis* (MWC 0001), or grade posteroventrally into the supraoccipital (the large *Ceratosaurus* sp. A: BYU 881/12893). The posterior projection, consisting of either configuration of bones, is similar to the parietal eminence identified in the abelisaurid neoceratosaurians *Majungatholus atopus* and *Carnotaurus sastrei* (Sampson et al., 1998). It is possible that *m. t.cap.* had a medial insertion on the posterior projections of the parietal and/or supraoccipital, and a lateral insertion onto the ventrolaterally sloping ridges of the parietals. The axis (C2) of *Ceratosaurus* has a strong medial ridge (UUVP 1053), the prespinal ridge of Madsen and Welles (2000), that corresponds with the supraoccipital projection. It is, therefore, possible that a C2-supraoccipital ligament spanned the gap between these elements, and that the insertion of *m. t.cap.* was limited to the parietals. Alternately, a muscle similar to *m. epipreposeo-capitis* medialis of crocodilians may have inserted here, originating from the medial portion of the axial neural spine. In either case, this medially laterally concentrated insertion of *m. t.cap.* was more like that of the narrow tendinous insertion seen in crocodilians and birds than the broad insertion of *Allosaurus* and tyrannosaurids.

The insertion of *m. t.cap.* in *Ceratosaurus* was dorsal to the occipital condyle, in a position enabling it to effect dorsiflexion. The lever arm does not appear to be relatively as long as that of *Allosaurus* and tyrannosaurids.

**M. complexus.** *M. complexus* of *Ceratosaurus* is inferred to have inserted on the posterior surface of the squamosal. The surface provides a substantial area evident in BYU 881/12893; from its posterior apex it slopes anteromedially in dorsal view. The insertion is both dorsal and quite lateral to the occipital condyle, indicating strong dorsiflexive and lateroflexive moments.

The origin of *m. complexus* in all of these theropods is inferred to have been from the anterior cervical epipophyses. While relatively narrower than those of tyrannosaurids, the epipophyses of *Ceratosaurus* have prominent anterodorsal rugosities on C2–5, and are especially tall in C3 and C4 of *Ceratosaurus denticulatus* (UUVP 1053, 6863, 6865). The strong rugosity and large anterior surface area of most of these origins indicates that *m. complexus* of *Ceratosaurus* may have had a large cross-sectional area, and contracted with substantial force for dorsi- and lateroflexion.

**M. splenius capitis (m. s.c.).** The insertion of *m. splenius capitis* in *Ceratosaurus* was onto the posterior surface of each parietal, ventral to the ventrolaterally running ridge of insertion of *m. t.cap.* The insertion is variable in shape, ranging from subrectangular (BYU 881/12893) to triangular (MWC 0001). Individual variation or taphonomic distortion may have contributed to these differences. BYU 881/12893 is more robust than other specimens, and the subrectangular shape of its scar may best represent the in vivo condition of the m. s.c. insertion.

Because *m. splenius capitis* inserted above the occipital condyle in *Ceratosaurus* it was positioned to dorsiflex the cranium. Its moment arm appears to be relatively shorter than that of *Allosaurus* and tyrannosaurids, which have tall nuchal surfaces of the parietals.

**M. longissimus capitis superficialis (m. l.c.s.).** Although rugosity is not evident on the lateral portion of the paroccipital processes in *Ceratosaurus*, *m. l.c.s.* is inferred to have inserted here by bracketing *Ceratosaurus* between crocodilians and tyrannosaurids. The insertion would be directly lateral to the occipital condyle and effect lateroflexion, but because the cranium is narrow, the moment arm appears relatively shorter than it is in other large theropods.

**M. longissimus capitis profundus (m. l.c.p.).** The basioccipital tuberosities of *Ceratosaurus* (BYU 883/12893, USNM 4735) appear relatively larger than they do in any other examined theropod. A large teardrop-shaped scar for *m. longissimus capitis profundus* is present just ventrolateral to the occipital condyle. The large insertion area may indicate large cross-sectional area of the muscle, and relatively more forceful contraction for ventral and ventrolateral flexion.
**M. iliocostalis capitis (m. i.c.).** The insertion of m. iliocostalis capitis in *Ceratosaurus* was onto a triangular concavity, tapering ventrolaterally along the ventral portion of each paroccipital process. The opisthotics are less laterally extensive in *Ceratosaurus* than they are in *Allosaurus* and especially tyrannosaurids, and the m. i.c. scar consequently appears relatively smaller than it is in these other large theropods. Because the centroid of the scar is

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**Fig. 12.** Craniocervical muscle insertions on *Ceratosaurus* specimens **A:** BYU 881/12893. **B:** A cast of MWC 0001. Scale bars = 10 cm. The lateral skull reconstruction (after Paul, 1988) shows the location of some muscle scars in context. Color-coding and abbreviations are as in Figure 4.
Fig. 13. Schematic lateral reconstruction of neck muscles of Ceratosaurus nasicornis, overlying a skeletal reconstruction of USNM 4735 modified from Paul (1988). Intervertebral muscles are omitted. Coloring and abbreviations are as in Figure 4, and superficial-to-deep conventions are as in Figure 7. A ligament may have been present in the depicted location of m. epistropheo-capitis medialis.
lateral to the occipital condyle and has a short moment arm, contraction of m. i.c. is inferred to have caused high-gear leg flexion of the cranium in *Ceratosaurus*.

*M. rectus capitis ventralis (m. r.c.v.).* A large and discrete reniform scar is present on the posteroventral surface of the basiubera in *Ceratosaurus*, and is especially evident in BYU 883/12893. This is inferred to be the insertion of *m. rectus capitis ventralis*. As with *m. i.c.p. of Ceratosaurus*, the large size of this insertion suggests that *m. r.c.v.* had a large cross-sectional area. The ventral position of the attachment relative to the occipital condyle would have imparted high ventroflexive leverage to the action of its associated muscle.

*M. longus colli dorsalis/m. transversospinalis cervicis (m. l.c.d./t.cerv.).* The morphology of *m. longus colli dorsalis/m. transversospinalis cervicis of Ceratosaurus* was similar to that of tyrannosaurids and *Allosaurus*. As in *Allosaurus*, rugosity of the lateral surfaces of the posterior neural spines is limited to the dorsal portion of each surface (e.g., Gilmore, 1920: plate 20). These are interpreted to be the sites of origin of *m. l.c.d./t.cerv.* in both taxa.

The insertions and inferred actions of *m. longus colli dorsalis/m. transversospinalis cervicis* vary from specimen to specimen of *Ceratosaurus*. Insertions would be on the epipophyses, as in other theropods. These are tall, with high inferred dorsiflexive leverage in anterior cervicals of *Ceratosaurus dentisulcatus* (UUVP 1053, 6963, 6965), but lower in a specimen identified as C3 of *Ceratosaurus nasicornis* (USMN 4735: Gilmore, 1920). The epipophyses of C1 are long in the latter specimen; if *m. l.c.d./t.cerv.* inserted onto these, the moment arm for dorsiflexion would be relatively long.

### Relative Heights of the Neural Complex in Large Theropod Necks

The preceding results bear on moment arm proportions of cranio cervical muscles. Variation in the inferred size of the muscles *m. trans. cap* and the intrinsic neck muscle *m. trans. cerv.* emerges from relative heights of the neural complex, when tyrannosaurid and *Allosaurus* necks are scaled to the same length. Measurements of relative heights of the neural complex of the tyrannosaurid are given in Table 1. *Allosaurus* measurements are from a drawn figure (Paul, 1988), and statistics derived from them must be considered more tentative. At the 95% confidence level, relative neural arch + spine heights in all the tyrannosaurid genera were significantly different from each other. The relative heights in *Daspletosaurus* were significantly greater than in the juvenile *Gorgosaurus* specimen (*P* = 0.0288), and the heights in either *Tyrannosaurus* specimen were, in turn, significantly greater than those of either *Daspletosaurus* neck (0.0001515 > *p*). *Daspletosaurus* and *Tyrannosaurus* had significantly taller neural complexes than *Allosaurus*, but the heights were statistically indistinguishable in the *Allosaurus* and *Gorgosaurus* specimens (*P* = 0.533). Neural spine heights were also statistically indistinguishable in the respective specimen pairs of *Daspletosaurus* (*P* = 0.6577) and *Tyrannosaurus* (*P* = 0.4347).

With Dunn-Sidak-adjusted *α* = 0.01695, relative neural complex heights of the *Tyrannosaurus* specimens were still significantly greater than those of the other theropods (*P* < 10e-5). However, the heights in *Daspletosaurus* were not significantly greater than in the *Gorgosaurus* at *α* = 0.01695, or the *Allosaurus* at the Dunn-Sidak-adjusted *α* = 0.0253.

### DISCUSSION

**Osteological Correlations Indicate Variance in Functional Morphology of Respective, Individual Neck Muscles**

Several morphological trends are evident from descriptive and quantitative analysis of theropod neck muscles. These are evident from osteological commonality and differences among large theropod clades and measurements of inferred moment arms of cranio cervical muscles. The most consistent correlation between morphology and neck action in the examined theropods is dorsiflexion by *m. s.c.* While its insertions on the parietals differ in shape and size, they have moment arms for moderate dorsiflexion in all the examined theropods.

Other aspects of dorsiflexion were more variable. Tyrannosaurids have tall parietals, and rugose scarring for the *m. t.cap. dorsiflexor* (juvenile and adult specimens of most taxa). Rugosity indicates that the muscle pulled with considerable force on the insertion; coupled with high leverage, this suggests notably strong dorsiflexion by *m. trans. cap* in tyrannosaurids. The height of the parietals in *Carnotaurus* and *Majungatholus* indicates high leverage for dorsiflexion by *m. t.cap.*, and breadth of the insertion in *Allosaurus* (and *Sinraptor*) indicates a large tendon and a powerful muscle pull. These large carnivores, abelisaurids, and especially tyrannosaurids appear to have been capable of powerful dorsiflexion by *m. t.cap.*, albeit by different combinations of mechanisms. In contrast, *Ceratosaurus* and *Monolophosaurus* did not have tall or broad parietals, and *m. t.cap.* was less effective in low-gear dorsiflexion.

*Ceratosaurus*, carnosaurs, and tyrannosaurine tyrannosaurids have squamosals that are vertically extensive above the occipital condyle. Dorsiflexion by *m. complexus* would have strongly augmented that by *m. t.cap.*, compensating for relative weakness of *m. t.cap.*-generated dorsiflexion in *Ceratosaurus* and *Monolophosaurus*, and enhancing overall dorsiflexive power in the other taxa. Conversely, the squamosals are low in albertosaurine tyrannosaurids (and *Carnotaurus sastrei*), indicating that *m. complexus* contributed more weakly to dorsiflexion than it did in most large theropods. The low squamosals artifically suggest taller parietals in albertosaurines than tyrannosaurines and better leverage of *m. t.cap.* However, moment arm measurements and PCA scores (Snively, 2006) contradict this visual impression, and indicate similar leverage for this muscle in all tyrannosaurids. The moment arm is proportionally long in *Tyrannosaurus rex*, indicating capacity for powerful dorsiflexion that is visually obscured by the great lateral extent of the paroccipital processes and squamosals. Squamosal morphology also influences the capacity of *m. complexus* for lateral flexion, in concert with influences from epipophysis morphology and the muscle’s corresponding origins from these structures. The breadth across the squamosals in tyrannosaurids, especially *Tyrannosaurus rex*, suggests stronger leverage for lateroflexion than in other theropods. In albertosaurines this
large moment arm for lateral flexion indicates a greater role in this function than for dorsiflexion.

Cranial ventroflexion entails straightforward inference in large theropods. Several osteological features indicate varied solutions for powerful ventroflexion. *Allosaurus* had the most novel morphology for this action, with ventral deflection of the paroccipital processes imparting a ventroflexive moment arm to m. longissimus capitis superficialis (Bakker, 2000). *Sinraptor dongi* and *Gorgosaurus libratus* (ROM 1247) appear to have ventrally extensive basitubera, providing high leverage for ventroflexive muscles. *Ceratosaurus* has massive basitubera with large insertions of m. l. cap. prof. and m. r.c.v., indicating that these muscles were large and effective ventroflexors.

This study confirms Bakker et al.'s (1986) observations of anteriorly placed and laterally extended basitubera in *Tyrannosaurus rex* (possibly subsuming *Nanotyrannus lancensis*; Carr, 1999). The precision of our measurement protocol probably underestimates the ventroflexive moment arms of muscles attaching to the basitubera of *T. rex*. The measurement in all specimens was orthogonal to the long axis of the skull if it was placed on a substrate, which is accurate for specimens with vertical basitubera. However, with the cranium in this position, the basioccipitals slant anteroventrally in *T. rex*. Orientation of the occipital condyle and semicircular canals (Witmer et al., 2005) indicate a ventroflexed neutral posture of the *T. rex* cranium, which would bring the basitubera into a vertical orientation, resembling that of the other theropods. Measurements of m. l.c.p. and m. r.c.v. moment arms from the occipital condyle to the basituberal insertions would more accurately reflect ventroflexive capability of these muscles on *T. rex* specimens when the head was held in a neutral posture.

**Tyrannosaurus rex Had Relatively Large Dorsiflexor Origins**

Judged by t-test results for relative heights of the neural spines, the relative size of tyrannosaurid dorsiflexors increased with increasing absolute body size at the 95% confidence level, corroborating hypotheses 3) Ha: Neural arch and spine height is relatively greater in larger tyrannosaurids than in smaller ones. The *T. rex* specimens have significantly taller neural complexes than the other tyrannosaurids at the Dunn-Sidak-adjusted confidence level of 98.305%. At this level the *Daspletosaurus* heights are not significantly greater than those of *Gorgosaurus or Allosaurus*, and in this case we cannot reject the null hypothesis 3) H0: There are no significant differences in cervical neural arch + spine height in tyrannosaurids. However, the average relative heights of neural complexes in *Daspletosaurus* are more than 32% greater than those of the juvenile *Gorgosaurus*. This appears to have biological significance, if not statistical significance at this sample size. We predict that a larger sample of vertebrae from *Daspletosaurus* and *Gorgosaurus* specimens, of the same body size as these individuals, will increase statistical confidence in relative height differences in neural complexes.

All of these theropods have correlates for dorsiflexor origins that are similar in position and morphology, but that vary in size. The neural complexes in the *Tyrannosaurus* specimen are 2.45 times the relative height of those in *Gorgosaurus*. A *Tyrannosaurus* neck scaled down to the length of the *Gorgosaurus* specimen would have six times the dorsiflexor cross-sectional area. This assumes isometric scaling of anteroposterior lengths of the neural complexes. For this dimension, one *T. rex* specimen averaged 1.466 times that of *Gorgosaurus* (Table 1) when the necks are scaled to the same length. This indicates an even greater discrepancy in relative origin areas and muscle cross-sections than those calculated from relative neural complex height.

In absolute terms the *Tyrannosaurus* specimen was approximately 1.5 times as long as the *Gorgosaurus*, indicating dorsiflexor muscles capable of exerting at least nine times the force. While the adult *Tyrannosaurus* was a proportionally bulkier animal, it is likely that its ability to accelerate its head and neck by means of dorsiflexion did not degrade to the extent expected from its much greater mass.

The *Allosaurus* specimen has relative neural complex heights equivalent to those of the juvenile *Gorgosaurus*. However, most of its neural complexes are relatively larger in the anteroposterior dimension, and the entire body of the *Allosaurus* specimen is larger (7.4 vs. 5.9 meters: Paul, 1988; Henderson and Snively, 2003). The dorsiflexors of the *Allosaurus* specimen were probably somewhat larger in cross-section than those of the *Gorgosaurus* individual.

**Neck-Modulated Feeding Actions of Large Theropods**

**Dorsiflexion.** M. transversospinalis capitis and m. splenius capitis were effective craniocephalic dorsiflexors in all of these theropods, and m. transversospinalis cervicis effected neck dorsiflexion. With tall nuchal crests (Paul, 1988), tyrannosaurids and abelisaurids had long dorsiflexion in levers for the craniocephalic muscles, and rugosity of the m. t.cap. insertion indicates high force input from this muscle. M. complexus would have effectively augmented dorsiflexion in examined large theropods other than *Carnotaurus* and albertosaurine tyrannosaurids.

The tall cervical epipophyses of abelisaurids imparted large moment arms for intervertebral dorsiflexion, but the line of action for m. transversospinalis cervicis and m. cervicales ascendentes had a strong ventral component. With less of a horizontal component of muscle force perpendicular to their dorsiflexive moment arm, their force for dorsiflexion may have been more limited than in other theropods. This hypothesis has yet to be tested quantitatively.

**Vento flexion.** Large theropods had varying capacity for cranial ventroflexion, and those that display correlates for powerful ventroflexion achieved it by different mechanisms. Although tyrannosaurids do not display particularly effective leverage for ventroflexion, the scar for m. l.c.p. is discrete in all examined specimens, and the insertion for m. r.c.v. is relatively larger than that of *Allosaurus*, so these muscles may have been fairly large. However, tyrannosaurids do not appear to be particularly specialized for ventroflexion, a condition shared with abelisaurids and the carnivore *Monolophosaurus jiangi*.

In contrast, other carnosaurs show strong morphological specialization for ventroflexion. *Allosaurus* was capable of ventroflexion by bilateral contraction of m. l.c.s., and *Sinraptor* has long moment arms for m. l.c.p. and m.
r.c.v. While the neoceratosaurian Ceratosaurus does not have a long moment arm for these muscles, the robustness of its ventroflexor insertions indicates large muscles, and perhaps powerful, high-hegared ventroflexion.

**Lateroflexion.** Large theropods display less variety in adaptations for lateroflexion than for ventroflexion. M. ilio-costalis capitis, inferable as inserting just lateral to the occipital condyle in all examined theropods, was positioned for high-hegared lateroflexion that would impart high velocity to the rostrum. However, Cleuren and De Vree (2000) note that the crocodilian m. i.c. is electromyographically active primarily during rotation of the cranial bone on the long axis. The capacity of other muscles for lateroflexion is less ambiguous. With their wide occiput tyrannosauriids (especially tyrannosaurs) were capable of notably powerful lateroflexion by m. longissimus capitis superficialis, but the muscle had a long moment arm for lateroflexion in most other taxa as well.

In albertosaurine tyrannosauriids, abelisaurids, and especially Ceratosaurus, m. complexus was important for augmenting lateroflexion by m. l.c.s. This muscle would have enhanced lateroflexion in Majungatholus, carnosaurs, and tyrannosauriids. tyrannosauriids, but also had strong dorsi-flexive leverage.

**Stabilization.** Electromyography of crocodilians (Cleuren and De Vree, 2000) indicates the importance of antagonistic muscle contraction in stabilizing neck joints when other muscles are performing work. The ventroflexors m. longissimus capitis profundus and m. rectus capitis ventrals are especially important for stabilizing the head against excessive dorsi-flexion by m. transversospinalis capitis and m. transversospinalis cervicis. These damping effects are inferable for cranio-cervical muscles of extinct theropods. In taxa without specialization for strong ventroflexion but with correlates of powerful dorsi-flexion (abelisaurids and tyrannosauriids), M. l.c.p. and m. r.c.v. may have been more extensively involved in stabilization than in performing posive work for ventroflexion.

**Concluding Inferences: Feeding Profiles of Large Theropods Based on Neck Muscle Function**

Figures 8 and 9 depict comparisons of superficial neck musculature of large theropods, and highlight variation in their feeding apparatus. Large theropods are classifiable into feeding styles based on the morphology of their necks, skulls, inferred musculature, and inferred cranio-cervical kinematics. These are not exclusive functional classifications and, like extant birds and crocodilians, large theropods were undoubtedly versatile in their feeding strategies. However, specializations suggest differential adeptness for certain strategies in different clades of theropods.

**Tyranosauroid: Puncture and pull/shake feeders.** This strategy has been suggested for tyrannosauriids based on tooth marks, tooth morphology, and finite element analysis (Erickson and Olsen, 1996; Erickson et al., 1996; Rayfield, 2004). The strategy would involve puncturing the soft tissues and bones of prey, and pulling to excise the tissues from the prey’s body. Powerful dorsi-flexion would have facilitated the latter function. The long moment arms for latero-flexion in tyrannosauriids, and particularly in Tyrannosaurus rex, would have facilitated uniquely powerful lateral flexion for excising flesh.

While not as adept as tyrannosauriids at powerful side-ways movements of the head, albertosaurine tyrannosauriids and other large theropods could have used latero-flexion for tearing as well. When on land, crocodilians tear flesh effectively by tugging sideways (Cleuren and De Vree, 2000; the aquatic “death roll” practiced by crocodilians is unlikely for terrestrial-specialized theropods). Aside from Osteolaemus and some alligatoroids, the crocodilian occiput appears no broader relative to skull length than in most theropods, which would have leverage for lateroflexion similar to that of most crocodilians.

**Allosaurus and Sinraptor: Strike and tear/pull feeders.** This style of feeding (Holz, 2002) would involve powerful ventroflexion to draw the upper teeth through flesh, and to strike downward at prey with the cranial dentition (Bakker, 2000; Rayfield et al., 2001). Both Allosaurus and Sinraptor display correlates of powerful ventroflexive kinematics that would facilitate cutting flesh with the upper dentition. Tall squamosals and moderately wide occiputs indicate the muscular versatility to pull by latero- and dorsi-flexion as well, actions similar to, if less powerful than, those of tyrannosauriids.

Strong opistho-coely of the cervical vertebrae, and a similar ball-and-socket atlanto-occipital joint, would have rendered the neck of Allosaurus especially maneuverable. With this mobility, and with relatively shorter in levers for cranio-cervical muscles than in tyrannosauriids, Allo-saurus appears to have been capable of rapid and high-exursion movements of its head and neck. This would be valuable for striking rapidly at smaller prey, as suggested by Rayfield et al. (2001), although bite marks on Stegosaurus plates indicate that Allosaurus attacked large prey as well (Carpenter et al., 2005).

**Ceratosaurus: Slice and rake feeder.** With its large ziphodont teeth and inferred large muscles for ventroflexion, Ceratosaurus may have raked its upper teeth through prey similarly to large carnosaurs. With a large inferred m. l.c.p., and especially a large m. r.c.v. acting on a modest in lever, strikes or cutting action with the upper teeth would have been high-hegared, rapid actions. Large origins of m. complexus indicate a large muscle cross-section and high force production. Coupled with short moment arms, high force indicates that m. complexus of Ceratosaurus effected particularly rapid and powerful head dorsi-flexion and latero-flexion. Short moment arms for most other muscles would have enabled rapid, although not particularly forceful, movements of the head.

Several osteological correlates of jaw muscles indicate a more forceful bite in Ceratosaurus than would be expected from the modest size of its adductor chamber. A deep, subcircular scar on the parietals just anterior to the supratemporal fenestra indicates a strong origin for m. pseudotemporalis (sensu Molnar, 1973), an anterodorsally positioned jaw adductor. The pterygoid flanges of Cerato-saurus are rugously striated, indicating a stout origin for m. pterygoideus posterior/ventralis that loops pulley-like around the saurian mandible (Holliday and Witmer,
This muscle is responsible for the powerful bites of crocodilians that lack a large adductor chamber (Cleuren and De Vree, 2000), and biomechanical methods can test for similar power in *Ceratosaurus*.

The diversity of neck, head, and appendicular morphologies in large theropods suggests differing degrees of specialization and constraint on feeding style. Large tyrannosaurids had bulkier, less mobile necks than other theropods, with muscles capable of exerting high torques during feeding. This indicates powerful feeding actions within the limits of neck mobility, but also a more stable platform than in other theropods for gripping flesh and tearing, through actions of the hind limbs and inertia of the prey. The forelimbs of tyrannosaurids are reduced in size and possess only two digits with phalanges (Holtz, 2004). While the forelimbs were strong in some tyrannosaurids (Carpenter and Smith, 2001; Carpenter, 2002), they were diminished in their ability to grasp and wound prey compared with those of other coelurosaurids and most carnosaurs (Giffin, 1990; Senter and Robins, 2005). Relative capacities of the feeding apparatus and forelimbs correlate with adaptations for speed and agility in tyrannosaurids (Holtz, 1995; Snively and Russell, 2002, 2003), and the corresponding potential to outmaneuver and bite into large prey.

*Ceratosaurus* and its abelisaurids relatives share short manual digits and forelimbs, and a large cnemial crest of theibia that presumably facilitated powerful knee extension during locomotion. These morphologies suggest that large neoceratosaurs approached prey with rapid acceleration to relatively low speeds, and little engagement with the forelimbs. *Ceratosaurus*’s large, ziphodont teeth, lighter neck than that of abelisaurids, and high-gear cranio cervical moment arms suggest that it used rapid, slashing strikes with its jaws when engaging large prey. This biting method is analogous to that seen in Komodo monitors (Auffenberg, 1981), and differs from the more crocodilian-like biting style inferred for tyrannosaurids.

In contrast to these short-armed theropods, *Allosaurus* appears to have been less specialized for locomotor speed but perhaps more versatile in its feeding capabilities. The legs of *Allosaurus* and other carnosaurs are relatively shorter than those of tyrannosaurids, and these animals were probably slower and less maneuverable relative to body size (Holtz, 1995; Henderson and Snively, 2003; Snively and Russell, 2003; Snively et al., 2004). However, *Allosaurus* appears to have had exceptional neck mobility, effective leverage for cranio cervical muscles, and large forelimbs with massive unguals that were effective in both gripping and raking through flesh (Carpenter, 2002). By using the jaws, neck, and forelimbs (Giffin, 1990) synchronously, *Allosaurus*, morphologically similar carnosaurs (Senter and Robins, 2005), and basal tetanurines such as *Tarbosaurus*, could have made use of multiple weapons when dispatching prey in the “strike and tear” mode proposed by Holtz (2002). As Senter and Robins (2005) note for the carnosaur *Acrocanthosaurus atokensis*, limited anterior range of motion of the forelimbs indicates initial engagement with the jaws and subsequent use of the arms.

Powerful forelimbs and a highly mobile neck (Holtz, 2002; Holtz et al., 2004) suggest similarity in the amount of forelimb use between derived carnosaurs and much smaller macropredaceous dromaeosaurs. In contrast, tyrannosaurids and large neoceratosaurs more likely attempted to outmaneuver prey for dispatch by the jaws alone. The combination of great power in tyrannosaurid necks, high strengths of their head skeleton, and the bone-splintering capabilities of their jaws and teeth were evidently unique to Tyrannosauridae among large theropods.

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LARGE THEROPOD NECK FUNCTION


