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Osteological correlates of cervical musculature in Aves and Sauropoda (Dinosauria: Saurischia), with comments on the cervical ribs of *Apatosaurus*

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The cervical muscles of birds attach to specific bony features on the vertebrae. Most of these osteological correlates are also present in the cervical vertebrae of sauropod dinosaurs, which suggests similar cervical musculature in the two groups. One exception is the processus caroticus, which anchors the long ventral muscles of the bird neck but has no obvious homolog in the vertebrae of sauropods.

The absence of anterior processes of the cervical ribs has traditionally been regarded as an autapomorphy of *Apatosaurus louisae*. However, anterior processes are weakly developed or absent in some specimens of *A. ajax* and *A. excelsus*, so this character is probably less diagnostic than previously assumed.

INTRODUCTION

Sauropod dinosaurs, the largest terrestrial vertebrates, have been of continuing interest to paleobiologists because of their large size and long necks. A great deal of recent work has focused on sauropod necks and their support and mobility (Martin 1987, Frey and Martin 1997, Martin et al. 1999, Stevens and Parrish 1999). These studies have dealt mainly with the cervical osteology of sauropods. The cervical musculature of sauropods has received only limited attention to date.

As the only extant saurischian dinosaurs, birds are the closest living relatives of sauropods. Many of the osteological features of sauropod cervical vertebrae correspond to muscle attachment points in the cervical vertebrae of birds, especially ratites such as the ostrich, *Struthio camelus* Linnaeus 1758 (see Wedel and Sanders 1999, Sanders et al. 2000). This correspondence suggests that the cervical musculature of sauropods was similar to that of birds. Herein we briefly compare the cervical osteology of birds and sauropods and discuss the possible musculature of sauropod necks. We also discuss variation in the cervical ribs of *Apatosaurus* Marsh 1877 and the taxonomic utility of cervical ribs in this genus. We follow Baumel et al. (1993) for avian anatomical terminology, with supplementary information drawn from Harvey et al. (1968) and Zweers et al. (1987).

Abbreviations used in the figures are provided in Table 1.

Institutional Abbreviations: **AMNH**: American Museum of Natural History, New York; **CM**: Carnegie Museum of Natural History, Pittsburgh; **YPM**: Yale Peabody Museum, New Haven.

COMPARATIVE ANATOMY

The origins and insertions of avian neck muscles are listed in Table 2 and illustrated in Fig. 1. The correspondence of these features with their presumed homologs in sauropods is as follows:

1) The ansa costo-transversaria is the bony loop formed by the fusion of the cervical rib to the diapophysis and parapophysis, and it bounds the transverse foramen. This is present in all sauropods.

2) The tubercula ansae and cristae laterales are tubercles and crests, respectively, on the lateral faces of the ansae costotransversariae. Similar features are present in sauropods, but less well-developed, and appear as small processes on the lateral or posterior margins of the diapophyses (see Fig. 3). Wedel et al. (2000b) referred to these processes as diapophyseal tubercles.

3) The processus spinosus is the neural spine. Neural spines are present in the cervical vertebrae of all sauropods, although they are extremely low in some taxa, such as *Mamenchisaurus* Young 1954 (see Russell and Zheng 1994). Bifid neural spines are present in some ratites and in several sauropod clades.

4) The torus dorsalis is a prominent rugosity on the dorsal surface of the postzygapophyseal ramus, above the postzygapophysis itself. Similar rugosities are present above the postzygapophyses of many sauropods, and have been

Table 1. Abbreviations used in the figures.

act	ansa costotransversaria
ant	anterior process
cl	crista lateralis
cto	crista transverso-obliqua
pca	processus caroticus
pco	processus costalis
psp	processus spinosus
spol	spinopostzygapophyseal lamina
ta	tuberculum ansa
td	torus dorsalis
vlp	ventrolateral process

referred to as epipophyses (Sereno et al. 1999) or dorsal tubercles (Wedel et al. 2000b). These processes are especially prominent in *Jobaria* Sereno et al. 1999 and in long-necked taxa such as *Barosaurus* Marsh 1890, *Brachiosaurus* Riggs 1903, and *Sauroposeidon* Wedel et al. 2000a (see Wedel et al. 2000b).

5) The crista transverso-obliqua is a low crest that runs from the processus spinosus to the torus dorsalis. In sauropods the processus spinosus and torus dorsalis are connected by the spinopostzygapophyseal lamina (Wilson 1999). The crista transverso-obliqua of birds is a muscle attachment feature. The spinopostzygapophyseal lamina of sauropods bounds a pneumatic fossa and is the only cortical surface available for muscle attachment between the processus spinosus and torus dorsalis.

6) The processus caroticus is one of a pair of processes on the ventral surface of the centrum that bound the carotid fossa on either side. The processes carotici are ventrally directed and sometimes inclined anteriorly. They arise from the ventral cortex at the junctions of the parapophyses with the centrum. No feature occupies the equivalent position in sauropod vertebrae.

7) The processus costalis is the cervical rib. The cervical ribs of birds are typically short, and rarely extend beyond the ends of their respective centra. Cervical rib length appears to be related to body size, and the largest taxa, such as *Struthio*, have the longest cervical ribs. All sauropods have cervical ribs. Many taxa have very long cervical ribs that run beneath several centra and form overlapping bundles (e.g., *Sauroposeidon*; see Wedel et al. 2000b). The cervical ribs of *Apatosaurus* are more similar to those of birds in being very short and robust. In birds, the anterior terminus of each cervical rib consists of a broad, blunt surface called the caput of the cervical rib (Zweers et al., 1987). This feature is not to be confused with the capitulum, which connects the cervical rib to the parapophysis of the centrum. The caput of the avian cervical rib does not extend forward as a free process, as do the anterior processes of the cervical ribs in most sauropods. In some specimens of *Apatosaurus* the cervical ribs lack anterior processes. This absence is unusual among sauropods and is discussed in more detail below.

8) The processus ventralis corporis is a ventrally-directed crest descending from the midline of the centrum. This feature is most prominent in the posterior cervical vertebrae, and is often formed by the medial fusion of the processes carotici posterior to the point at which the carotid arteries diverge from the carotid sulcus as they approach the thorax. In CM 879, a specimen of *Haplocanthosaurus* Hatcher 1903, a low ridge is variably present on the ventral surface of the centrum between the parapophyses. It is unclear whether this ridge corresponds to the processus ventralis corporis of birds, and similar processes are absent in the cervical vertebrae of all other sauropods that we have examined.

The short muscles of the avian cervical system are the Mm. intercristales, Mm. interspinales, and Mm. intertransversarii, which connect the cristae transverso-obliquae, processes spinosi, and ansae costotransversariae, respectively, of adjacent vertebrae. The neural spines and cervical rib loops (ansae costotransverariae) of sauropods often bear rugosities and tubercles, and probably served to anchor homologous muscles (Fig. 2). As discussed above, the avian crista transverso-obliqua occupies the same position as the spinopostzygapophyseal lamina of sauropods. Homologs of the avian Mm. intercristales may have connected the spinopostzygapophyseal laminae of adjacent vertebrae in sauropods.

The long muscles of the avian cervical system consist of a dorso-lateral group, the M. ascendens cervicalis and M. lon-

Table 2. Origins and insertions of the cervical musculature of birds. Information drawn from Zweers et al. (1987) and Baumel et al. (1993). Muscles appear in the order discussed in Baumel et al. (1993); muscles inserting on the skull are not included.

Muscle	Origin	Insertion
M. ascendens cervicalis	Ansa costotransversaria	Torus dorsalis
M. longus colli dorsalis	Processus spinosus	Torus dorsalis
Mm. intercristales	Crista transverso-obliqua	Crista transverso-obliqua
Mm. interspinales	Processus spinosus	Processus spinosus
Mm. intertransversarii	Tubercula ansae Cristae laterales	Tubercula ansae Cristae laterales
M. flexor colli medialis	Processus caroticus Processus costalis	Proc. ventralis corporis Processus costalis
M. flexor colli lateralis	Tubercula ansae Cristae laterales	Processus costalis
M. longus colli ventralis	Processus caroticus Proc. ventralis corporis	Processus costalis

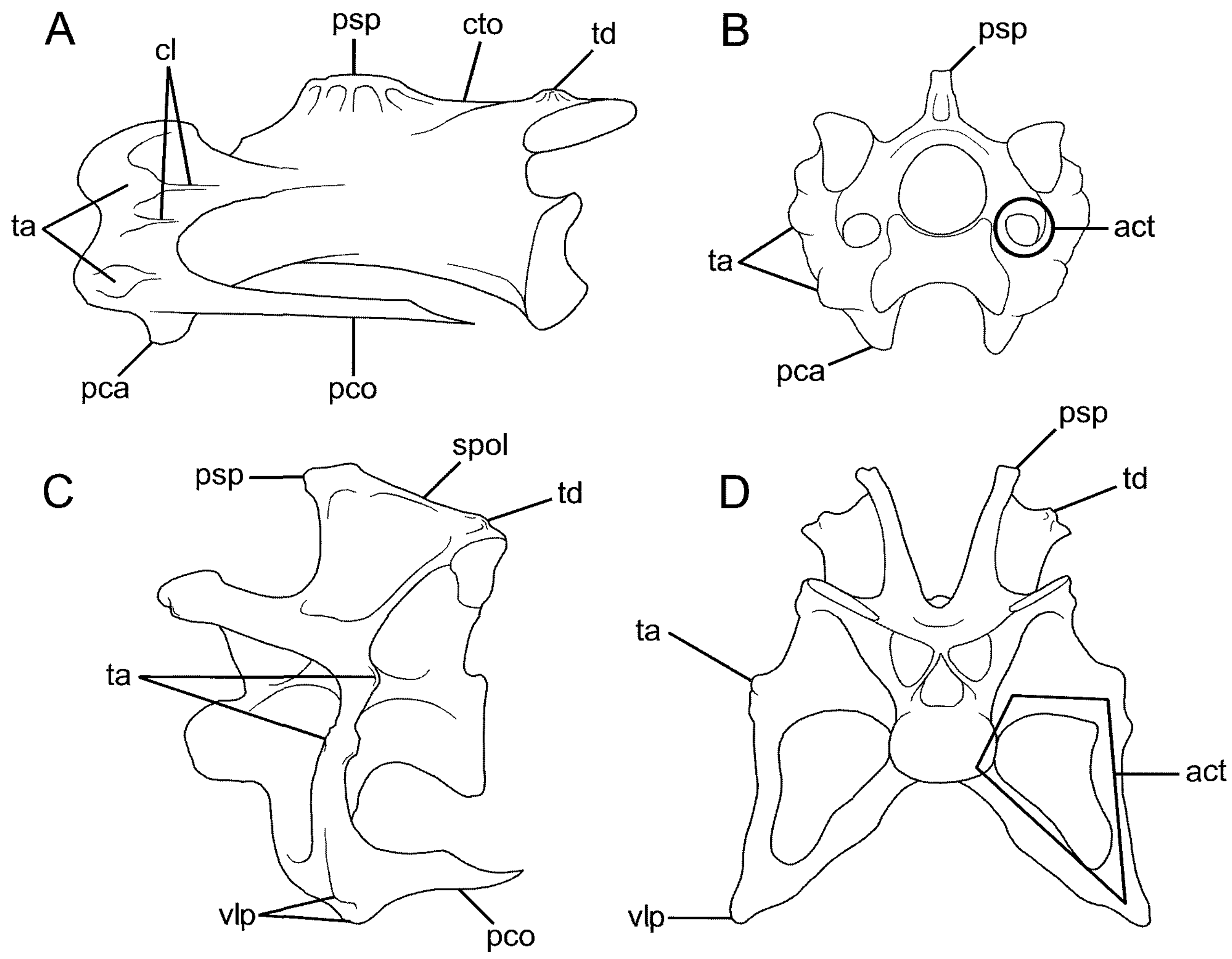

Fig. 1. Cervical vertebrae of *Struthio camelus* and *Apatosaurus louisae*, with muscle attachment points labeled (C and D traced from Gilmore 1936:pl. 24). **A.** A mid-cervical vertebra of *S. camelus* in left lateral view. **B.** A mid-cervical vertebra of *S. camelus* in anterior view. **C.** C10 of *A. louisae* in left lateral view. **D.** C10 of *A. louisae* in anterior view.

gus colli dorsalis, and a ventral group, the M. flexor colli lateralis and medialis and the M. longus colli ventralis. The dorso-lateral muscles originate on the neural spines and transverse processes and insert on the tori dorsales. The tori dorsales are therefore the primary anchor points through which the extensor muscles exert force on the cervical skeleton. The prominent tori dorsales of many sauropods, especially the long-necked taxa, indicate that homologous extensor muscles were probably well-developed in sauropods (Fig. 2). The ventral muscles of the avian neck originate on the processes carotici and costales and insert on the processes costales and the processes ventrales of the centra. The cervical ribs of sauropods almost certainly served as insertions for the equivalent muscles.

The absence of processes carotici and processes ventrales in sauropods is puzzling and warrants further investigation. This absence is particularly puzzling because all of the other muscle attachments in avian cervical vertebrae can be readily identified in the vertebrae of sauropods. The processes carotici and processes ventrales of birds serve as origins for the M. flexor colli medialis (in part) and M. longus colli ventralis. In the absence of similar processes in sauropods, where did the long ventral muscles of the neck originate? This question will probably remain unanswered until we have a better understanding of the evolution of cervical musculature in archosaurs and can frame the problem in a more complete phylogenetic context. We are therefore pleased to note ongoing work by Tsuihiji (2001, 2002) on the evolution of cervical musculature in diapsids, which promises much valuable information.

THE CERVICAL RIBS OF *APATOSAURUS*

The cervical ribs of some specimens of *Apatosaurus* lack anterior processes (Fig. 3). This absence of anterior processes has traditionally been considered a synapomorphy of *A. louisae* Holland 1915 (see Gilmore 1936, McIntosh 1990). However, the anterior processes are only weakly developed on certain cervical vertebrae of YPM 1980, the holotype of

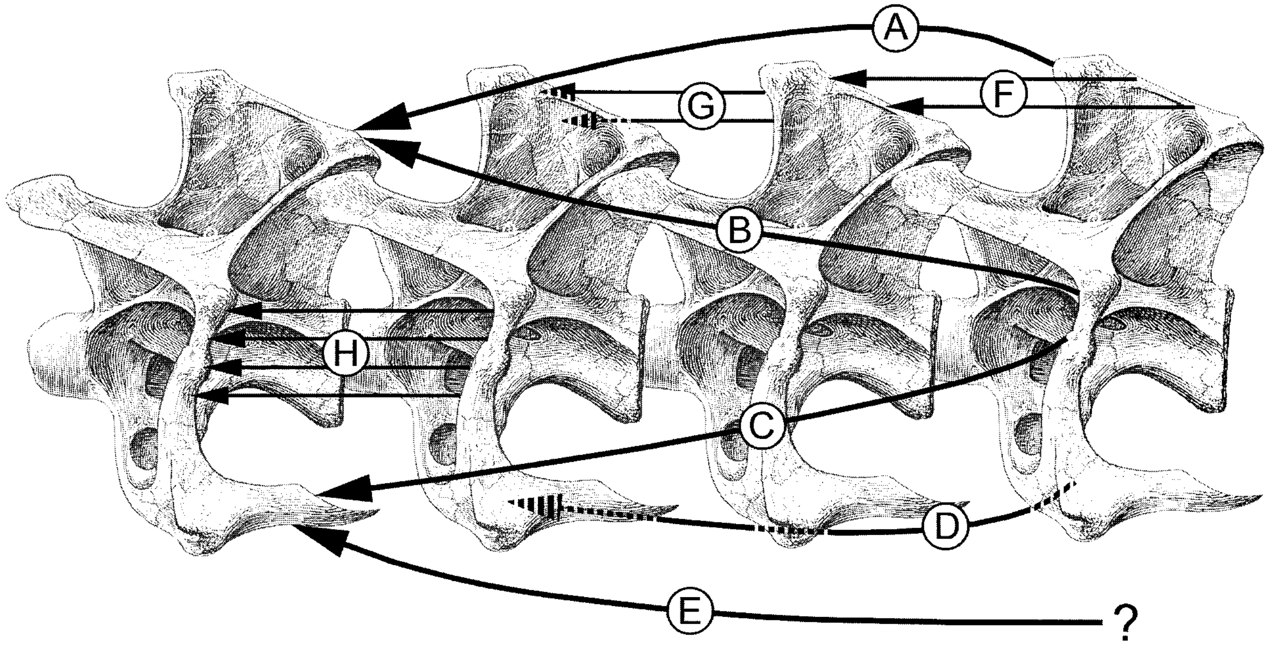

Fig. 2. Possible connections of the cervical musculature of sauropods, based on the neck muscles of birds. The stylized neck segment is shown in left lateral view. Dashed arrows indicate muscles passing medially behind bony structures. **A.-E.** Muscles that span multiple segments. In birds, most of these muscles have multiple slips and they may attach to some vertebrae but not others (see Zweers et al. 1987:fig. 7). For simplicity, only a single course is illustrated here, but readers are cautioned that the actual musculature was probably much more complex. **A.** M. longus colli dorsalis. **B.** M. cervicalis ascendens. **C.** M. flexor colli lateralis. **D.** M. flexor colli medialis. **E.** M. longus colli ventralis. In birds, this muscle originates from the processes carotici, which are absent in the vertebrae of sauropods (see discussion in text). **F.-H.** Single segment muscles. **F.** Mm. intercristales. **G.** Mm. interspinales. **H.** Mm. intertransversarii. Vertebrae modified from Gilmore (1936:pl. 24).

A. excelsus Marsh 1879 (see Fig. 3C). Furthermore, anterior processes are present in YPM 1860, the holotype of *A. ajax* Marsh 1877, but absent in YPM 1861, a cervical vertebra from the same quarry that has been referred to *A. ajax* (see McIntosh 1995). Therefore, the presence or absence of anterior processes is probably not useful for discriminating species of *Apatosaurus.*

Cervical ribs of *Apatosaurus* that lack anterior processes typically bear one or more small bony processes on their ventral margins (Fig. 3). Gilmore (1936:196) described ventrolateral processes in the cervical vertebrae of CM 3018, the holotype of *A. louisae*, and stated that each of these processes "doubtless served as the attachment of one of the powerful intervertebral muscles." They are also present in cervical vertebra YPM 1861 of *A. ajax.* Because these ventrolateral processes occur on cervical ribs that lack anterior processes, it is possible that both types of processes correspond to the same muscle and simply represent alternate attachments. However, the processes in a cervical vertebra of *A. ajax* face more posteriorly than anteriorly (Fig. 3E), and a vertebra of *A. excelsus* bears processes that face ventromedially rather than ventrolaterally (Fig. 3D). It is doubtful that all of these processes correspond to the same muscle or muscles. In birds, different muscles attach to the medial and lateral sides of the cervical ribs, and a single bony feature may serve as the attachment for more than one muscle. For example, the M. flexor colli mediales originate from and insert on the medial surfaces of the cervical ribs, and the laterally-facing tubercula ansae and cristae laterales serve as attachments for both the Mm. intertransversarii and the M. flexor colli laterales. For the present, it may be impossible to determine which of these muscles were associated with the various processes of *Apatosaurus* cervical ribs.

CONCLUSIONS

A review of avian cervical musculature reveals that most of the osteological correlates of specific muscles are also present in the vertebrae of sauropods. One exception is the processus caroticus, which is absent in sauropods. The origins of the long muscles of the ventral neck are therefore uncertain in sauropods, and more work will be required to resolve this problem. The absence of anterior processes of the cervical ribs has traditionally been one of the characters used to diagnose *Apatosaurus lousiae* to the exclusion of other species of *Apatosaurus.* Anterior processes are variably absent in *A. ajax* and *A. excelsus*, which casts doubt on the utility of this character. Taxonomists should treat cervical rib characters with caution, given the variation in cervical rib morphology in *Apatosaurus.*

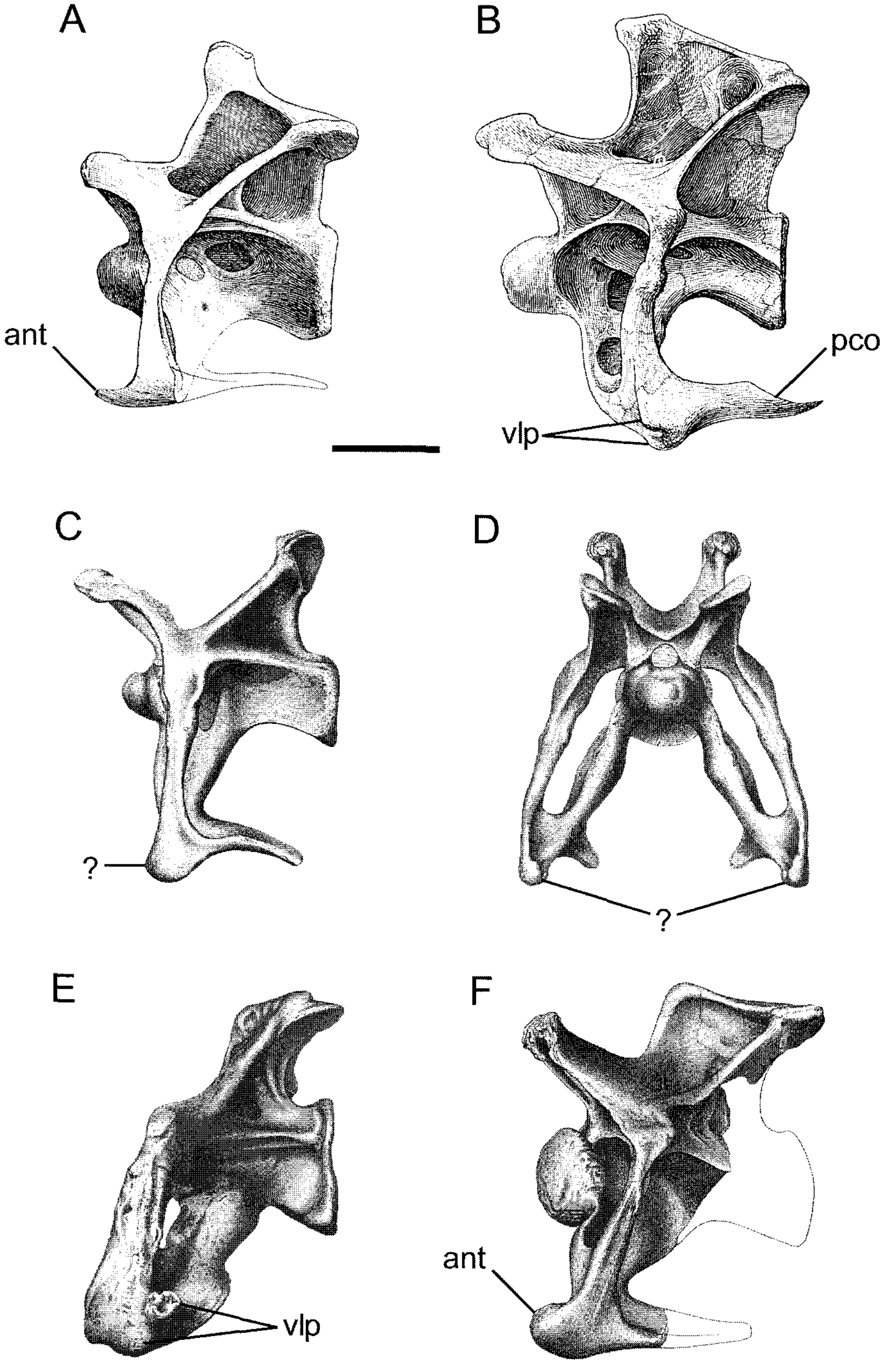

Fig. 3. Cervical vertebrae of *Apatosaurus* showing the variation in cervical rib morphology, scale bar = 20 cm. All vertebrae are shown in left lateral view, except for **D**, and at the same scale. **A.** C10 of *A. excelsus* (CM 563, modified from Gilmore 1936:pl. 31) is typical of most sauropod cervical vertebrae in having well developed anterior processes. **B.** C10 of *A. louisae* (CM 3018, modified from Gilmore 1936:pl. 24) lacks anterior processes, but it has prominent ventrolateral processes. **C.** C8? of the *A. excelsus* holotype (YPM 1980, modified from Ostrom and McIntosh 1966:pl. 12) has large processes that project ventromedially. These are probably not equivalent to the ventrolateral processes of *A. louisae*, because different muscles attached to the medial and lateral surfaces of the cervical ribs. **D.** The same vertebra in anterior view. **E.** A posterior cervical vertebra of *A. ajax* (YPM 1861, modified from Ostrom and McIntosh 1966:pl. 15) is similar to vertebrae of *A. louisae* in having ventrolateral processes rather than anterior processes. Note that at least one of these processes faces posteriorly rather than anteriorly. **F.** Another posterior cervical vertebra of *A. ajax* (YPM 1840, modified from Ostrom and McIntosh 1966:pl. 14) has robust anterior processes. The vertebrae shown in **E** and **F** are from the same quarry and, possibly, the same individual (see McIntosh 1995). Although anterior processes are consistently absent in *A. louisae* (e.g., AMNH 460 and CM 3018), they are variable in both *A. excelsus* and *A. ajax*, and we consider the taxonomic utility of anterior processes to be suspect.

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ERRATUM

to Wedel and Sanders. 2002. *PaleoBios* 22(3):1-6.

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Since the publication of Wedel and Sanders (2002), two errors in the text have come to our attention. The first concerns the presence or absence of the process ventralis corporis in sauropods, and the second concerns Gilmore's (1936) statements regarding the cervical ribs of *Apatosaurus.*

Institutional abbreviations: **CM** or **C.M.**, Carnegie Museum of Natural History, Pittsburgh.

The avian process ventralis corporis is a bony ridge that descends from the midline of the ventral surface of the centrum. In our recent paper, we stated that a similar low ridge was variably present in *Haplocanthosaurus* but unknown in other sauropods (Wedel and Sanders 2002:2). However, according to Upchurch (1998), a the presence of midline keels on the ventral surfaces of the cervical centra is primitive for Sauropoda, and the character is present in *Barapasaurus*, *Shunosaurus*, *Omeisaurus*, *Mamenchisaurus*, *Patagosaurus*, *Dicraeosaurus*, *Lapparentosaurus*, and *Phuwiangosaurus.*

In addition, we misquoted Gilmore (1936). We said that Gilmore (1936:196) described ventrolateral processes in the cervical ribs of *Apatosaurus louisae*, and that he stated that each process "doubtless served as the attachment of one of the powerful intervertebral muscles" (Wedel and Sanders 2002:4). Actually, the text on p. 196, including the line that we quoted, refers to the bony knobs that sit between the bifurcated neural spines of *Apatosaurus.* Gilmore (1936) described the cervical ribs of *A. louisae* on pp. 209 and 212, where he stated, "In none of the cervical ribs of this specimen [CM 3018] is there a forwardly projecting end as in *Diplodocus*, or as in many of the ribs of No. 563 C.M., see Pl. XXXI. There is, however, a heavy blunt projection that extends downward and slightly backward." It is these "heavy blunt projections" that we referred to as ventrolateral processes.

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