



The anatomy of the syncervical of *Auroraceratops* (Ornithischia: Ceratopsia), the oldest known ceratopsian syncervical

Daqing Li, Eric M. Morschhauser, Hailu You & Peter Dodson

To cite this article: Daqing Li, Eric M. Morschhauser, Hailu You & Peter Dodson (2018) The anatomy of the syncervical of *Auroraceratops* (Ornithischia: Ceratopsia), the oldest known ceratopsian syncervical, *Journal of Vertebrate Paleontology*, 38:sup1, 69-74, DOI: [10.1080/02724634.2018.1510411](https://doi.org/10.1080/02724634.2018.1510411)

To link to this article: <https://doi.org/10.1080/02724634.2018.1510411>



Published online: 08 Jul 2019.



Submit your article to this journal [↗](#)



Article views: 79



View related articles [↗](#)



View Crossmark data [↗](#)



Citing articles: 1 View citing articles [↗](#)



THE ANATOMY OF THE SYNCERVICAL OF *AURORACERATOPS* (ORNITHISCHIA: CERATOPSIA), THE OLDEST KNOWN CERATOPSIAN SYNCERVICAL

DAQING LI,¹ ERIC M. MORSCHHAUSER,^{*2,3} HAILU YOU,^{4,5,6} and PETER DODSON⁷

¹Laboratory of Vertebrate Evolution and Fossil Conservation Technology, Gansu Agricultural University, 1 Yingmencun, Anning District, Lanzhou City, Gansu Province 730070, People's Republic of China, daqingli@gsau.edu.cn;

²Department of Earth and Environmental Science, University of Pennsylvania, 251 Hayden Hall, 240 South 33rd Street, Philadelphia, Pennsylvania 19104, U.S.A., eric.morschhauser@iup.edu;

³Department of Biology, Indiana University of Pennsylvania, Weyandt Hall Room 114, 975 Oakland Avenue, Indiana, Pennsylvania 15705, U.S.A.;

⁴Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, 142 Xizhimenwai Street, Beijing 100044, People's Republic of China, yuhailu@ivpp.ac.cn;

⁵CAS Center for Excellence in Life and Paleoenvironment, 142, Xizhimenwai Street, Beijing 100044, People's Republic of China;

⁶University of Chinese Academy of Sciences, 19A Yüquan Road, Beijing, 100049, People's Republic of China;

⁷School of Veterinary Medicine and Department of Earth and Environmental Science, University of Pennsylvania, 3800 Spruce Street, Philadelphia, Pennsylvania 19104-6045, U.S.A., dodsonp@vet.upenn.edu

ABSTRACT—The Early Cretaceous basal neoceratopsian dinosaur *Auroraceratops rugosus* was described based on a single skull recovered from the Gonpoquan Basin in northwestern Gansu Province, China. The genus is now known from cranial and postcranial remains representing at least 80 individuals, many of which come from the neighboring Yujingzi Basin, with an age of Aptian to earliest Albian (126–115 Ma). Among the new material were four syncervicals, representing the phylogenetically and temporally earliest occurrence of a syncervical in Ceratopsia. The anatomy of the syncervical matches that described in leptoceratopsids and protoceratopsids, with the first segment formed from a small atlas centrum, a much larger atlantal intercentrum, and a splint-like, divided atlantal neural arch. The axis bears a large hatchet-shaped neural spine and facets for a double-headed cervical rib. The centra of the first three cervical vertebrae and the first two intercentra are fused, though the boundaries of the individual elements are discernable. The relatively early temporal and phylogenetic appearance of a syncervical supports recent work that shows that the syncervical of ceratopsians is unrelated to the larger head size and cranial ornamentation characteristic of later appearing ceratopsian clades.

Citation for this article: Li, D., E. M. Morschhauser, H. You, and P. Dodson. 2019. The anatomy of the syncervical of *Auroraceratops* (Ornithischia: Ceratopsia), the oldest known ceratopsian syncervical; pp. 69–74 in Hailu You, Peter Dodson, and Eric Morschhauser (eds.), *Auroraceratops rugosus* (Ornithischia, Ceratopsia) from the Early Cretaceous of northwestern Gansu Province, China. Society of Vertebrate Paleontology Memoir 18. Journal of Vertebrate Paleontology 38(Supplement). DOI: 10.1080/02724634.2018.1510411.

INTRODUCTION

The cranial-most cervical vertebrae, neural arches, atlantal and axial intercentra, and neural spine of neoceratopsian dinosaurs are fused together in a structure called the syncervical (Campione and Holmes, 2006; Tsiuhiji and Makovicky, 2007). The syncervical has been recognized as a unique structure since early in the study of Ceratopsia (Marsh, 1891). Although the actual vertebrae composing the syncervical was debated for decades between those who considered the element to be composed of the first three cervical vertebrae (Hatcher in Hatcher et al., 1907; Brown, 1917; Lull, 1933; Brown and Schlaikjer, 1940, 1942; Sternberg, 1951; Lehman, 1989) or composed of the first four cervical vertebrae (Lull in Hatcher et al., 1907; Ostrom and Wellnhofer, 1986; Dodson and Currie, 1990; Dodson et al., 2004), there is currently a consensus that the ceratopsian syncervical is composed of the atlas, axis, third

cervical, atlantal intercentrum, and axial intercentrum (Campione and Holmes, 2006; Tsiuhiji and Makovicky, 2007; VanBuren et al., 2015; VanBuren and Evans, 2017). Syncervical characters have figured in ceratopsian phylogenetic analyses from the beginning of modern cladistic studies of the clade (Serenó, 1984). The most recent phylogenetic analyses of the base of Neoceratopsia use several characters of the syncervical (Makovicky and Norell, 2006 [six characters]; Chinnery and Horner, 2007 [five characters]; You and Dodson, 2004 [seven characters]). Syncervicals are known from many ceratopsids, as well as from the non-ceratopsid ceratopsians *Protoceratops* (Brown and Schlaikjer, 1940), *Montanoceratops* (Brown and Schlaikjer, 1942), *Leptoceratops* (Sternberg, 1951), and *Cerasinops* (VanBuren et al., 2015).

The purpose of this study is to report on four preserved syncervicals referred to the basal neoceratopsian genus *Auroraceratops*. These represent the geologically earliest occurrence of a ceratopsian syncervical and the phylogenetically earliest diverging lineage of ceratopsians to have a syncervical (Morschhauser, 2012; VanBuren et al., 2015). Although the described syncervicals are similar to one

*Corresponding author.

Color versions of one or more of the figures in the article can be found online at www.tandfonline.com/ujvp.

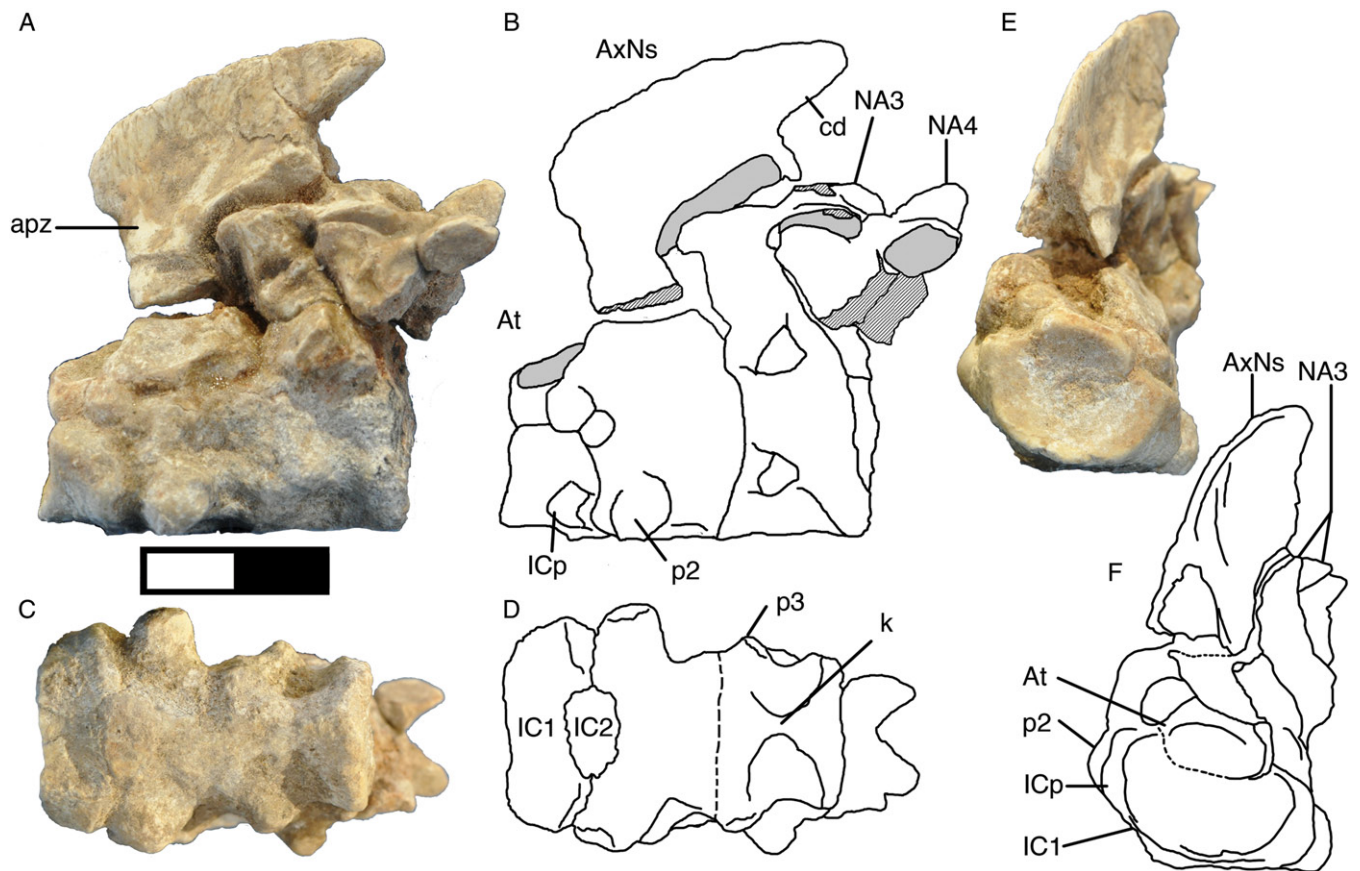


FIGURE 1. The syncervical and the articulated partial neural arch of C4 of *Auroraceratops rugosus* GSGM GJ <07>9-02/9-12 in multiple views. **A**, left lateral view; **B**, interpretive line drawing of left lateral view; **C**, ventral view; **D**, line drawing of ventral view; **E**, cranial view; **F**, line drawing of cranial view. **Abbreviations:** **apz**, possible location of axial prezygapophysis; **Axns**, neural spine of axis; **C1**, atlantal centrum (odontoid process); **C2**, axis centrum; **C3**, centrum of the third cervical vertebra; **cd**, caudal projection of axial neural spine; **IC1**, intercentrum of the atlas; **IC2**, intercentrum of the axis; **ICp**, parapophysis of atlantal intercentrum; **k**, ventral keel; **NA1**, neural arch of the atlas; **NA3**, neural arch of C3; **NA4**, neural arch of C4; **p2**, parapophysis of the axis; **p3**, parapophysis of C3. Scale bar equals 2 cm.

described by Bohlin (1953) in morphology, the latter specimen appeared to be derived from a juvenile and is now lost. The present material provides an important set of character states at a specific grade in the evolution of the ceratopsian syncervical.

For the purposes of terminology, this paper refers to the structure composed of the fused first three cervicals and the first two intercentra as the ‘syncervical.’ This structure was referred to as ‘coalesced cervicals’ in papers published during the early 20th century (Hatcher et al., 1907; Brown, 1914; Lull, 1933; Langston, 1975), and later some authors used the term ‘cervical bar’ (Lehman, 1989; Rothschild, 1997; Tsuihiji and Makovicky, 2007). We consider the term syncervical as used in Ostrom and Wellnhofer (1986) as reflecting an anatomical name constructed based upon the conventions of the broader anatomical community. In this we follow most workers on the subject from the past decade (Campione and Holmes, 2006; Tsuihiji and Makovicky, 2007; VanBuren et al., 2015).

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842, sensu Padian and May, 1993

ORNITHISCHIA Seeley, 1887, sensu Sereno, 1998

CERATOPSIA Marsh, 1889, sensu Dodson, 1997

NEOCERATOPSIA Sereno, 1986

AURORACERATOPS You et al., 2005

AURORACERATOPS RUGOSUS You et al., 2005

Institutional Abbreviation—GSGM, Gansu Geological Museum, Lanzhou, Gansu, China.

DESCRIPTION

Syncervicals are preserved in five specimens of *Auroraceratops* (GSGM GJ <07>9-03, GSGM GJ <07>9-38, GSGM GJ <09>-05, GSGM GJ <08>8-10, GSGM GJ <07>9-02/9-12). In the specimens GSGM GJ <07>9-38 and GSGM GJ <09>-05, most of the details are obscured because the skull remains articulated to the syncervical. The specimens GSGM GJ <07>9-02/9-12 include the remains of at least two individuals. Preserved with one of these specimens is a relatively complete syncervical (Fig. 1). Measurements of select specimens are listed in Table 1.

The centra of the first three vertebrae are fused in a syncervical along with the first two intercentra (Fig. 1). Although the

TABLE 1. Measurements (in mm) from several syncervicals.

GSGM GJ <07> 9-02/9-12	CENL	CDCW	CENH	TOVH	NCH	NCW	IZL	IZW	IPPW	MIDW
IC1	8.7	23.8	9.9	–	–	–	–	–	23.9	–
Atlas	+	18.5*	6.6	–	–	7.3*	–	–	–	–
Axis	13.0*	16.8*	21.2*	46.0*	11.6*	6.7*	–	11.4	28.0	15.4*
C3	14.9*	17.2	19.2*	38.3*	+	+	21.9	13.8	21.6	14.9*
GSGM GJ <07> 09-03										
IC1	8.2*	21.3*	8.5	–	–	–	–	–	20.1	–
Atlas	7.7	+	4.6	–	–	–	–	–	–	–
Axis	15.2	16.5	16.0*	+	+	+	–	+	25.4	13.4
C3	+	17.0	18.1*	+	+	+	+	+	+	12.0

(*)An asterisk indicates measurement is estimated. Crosses (+) indicate element is present, but broken. Dashes (–) indicate that the structures to measure are not naturally present on this element. **Abbreviations:** **CDCW**, caudal centrum width; **CENH**, centrum height; **CENL**, centrum length; **IPPW**, interparapophyseal width; **IZL**, interzygopophyseal length; **IZW**, interzygopophyseal width; **MIDW**, width of the vertebral centra midway along their length; **NCH**, neural canal height; **NCW**, neural canal width; **TOVH**, total vertebral height.

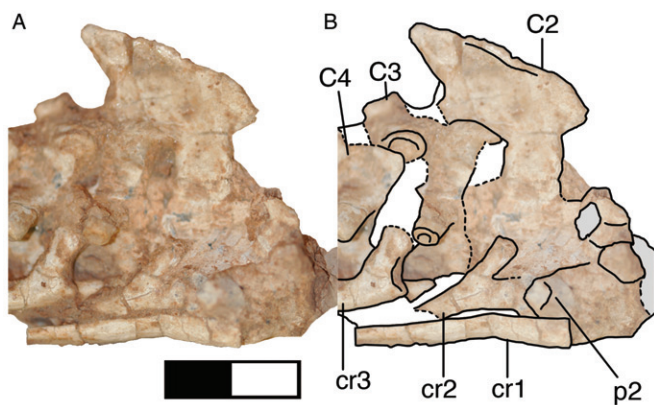


FIGURE 2. The syncervical of GSGM GJ <08> 8-10. **A**, photograph in left lateral view; **B**, interpretive line drawing. **Abbreviations:** **C2**, axis; **C3**, the third cervical vertebra; **C4**, the fourth cervical vertebra; **cr1**, first cervical rib; **cr2**, second cervical rib; **cr3**, third cervical rib; **p2**, parapophysis of the axis. Scale bar equals 2 cm.

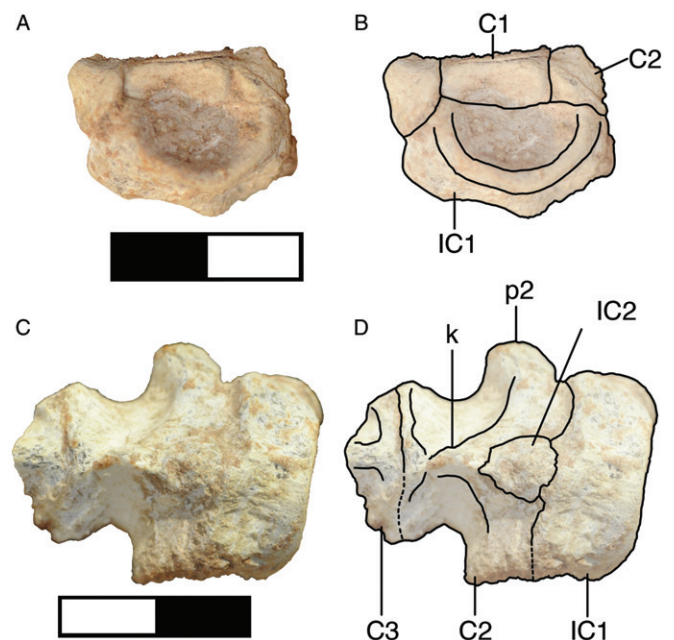


FIGURE 3. The syncervical of *Auroraceratops rugosus* GSGM GJ <07> 9-03. **A**, cranial view; **B**, interpretive drawing of cranial view; **C**, ventral view; **D**, interpretive drawing of ventral view. **Abbreviations:** **C1**, atlantal centrum; **C2**, axis centrum; **C3**, centrum of the third cervical vertebra; **cd**, caudal projection of axial neural spine; **IC1**, intercentrum of the atlas; **IC2**, intercentrum of the axis; **k**, ventral keel; **p2**, parapophysis of the axis. Scale bar equals 2 cm.

individual elements are fused together, the sutures between them are still visible. The structure of the syncervical is consistent with the interpretation that the first element is an atlantal centrum (the odontoid of some) lying over an atlantal intercentrum (Campione and Holmes, 2006; Tsuihiji and Makovicky, 2007). Specimen GJ <09>-05 is missing the atlantal and axial neural arches, which provides a dorsal view of the syncervical in articulation with the occipital condyle. The anterior surface of the syncervical is concave for receiving the occipital condyle. The caudal articular surface on the syncervical is flat. The intervertebral foramen between the axis and the third cervical is large and oval.

The atlantal neural arch is not preserved in many specimens (Figs. 1, 2). We follow Campione and Holmes (2006) in considering this the result of disarticulation and nonpreservation of the typically delicate atlantal arch components. The base of the atlantal arch is preserved in GSGM GJ <09>-03, although the atlantal arch itself is broken on both sides. Based on the preserved cross-sections, the lateral walls of the arch would have been very slender. A space of ~3 mm lies between the broken base of the atlantal arch and the cranial edge of the axial arch. However, the atlantal centrum is noticeably mediolaterally narrower than the underlying intercentrum. This leaves two

flattened areas lateral to the atlantal centrum but cranial to the cervical rib articulations (Fig. 1E). It is possible that these facets were the areas of articulation of the neural arches, which would have allowed the arches to contact both the atlantal centrum and the atlantal intercentrum, as proposed by Tsuihiji and Makovicky (2007) for *Leptoceratops*.

The atlantal centrum makes up approximately one-third of the rostral-most segment (Fig. 2A). The cranial surface of the centrum is gently concave (Figs. 1E, 3A). The centrum widens caudally in two knob-like lateral processes (Fig. 1E), which are not as strongly developed as in *Protoceratops* (Brown and Schlaikjer, 1942; Tsuihiji and Makovicky, 2007). The neural canal is very wide over the atlantal centrum.

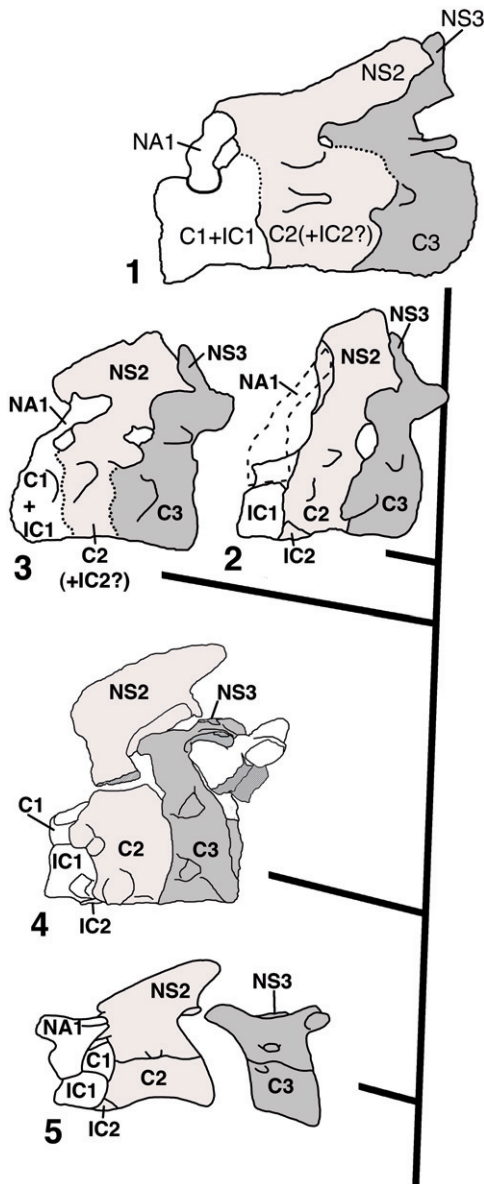


FIGURE 4. Diagrammatic illustrations of the atlas, axis, third cervical, and associated intercentra of several Ornithischian dinosaurs illustrating the state changes in the development of this structure (modified from Tsuihiji and Makovicky, 2007). 1, *Triceratops*; 2, *Protoceratops* (possible first neural arch position indicated by dashed outline); 3, *Montanoceratops*; 4, *Auroraceratops*; 5, *Hypsilophodon*. All images are in left lateral view and are not to scale. **Abbreviations:** C1, atlantal centrum; C2, axis centrum; C3, centrum of the third cervical vertebra; IC1, intercentrum of the atlas; IC2, intercentrum of the axis; NA1, neural arch of the atlas; NS2, neural spine of the axis; NS3, neural spine of the third cervical vertebra.

The atlantal intercentrum lies ventral to the atlantal centrum and makes up approximately two-thirds of the total volume of the first segment in the syncervical (Figs. 1, 3). Cranially, the first intercentrum forms a shallow rim on the articular surface for the occipital condyle. Laterally on the atlantal intercentrum, there is a small tubercle, which serves as the parapophysis, the articulation point for the head of the first cervical rib (Fig. 2). This articulation point is near the large and bulbous parapophysis for cervical rib 2 (Fig. 1A, C). Specimen GJ <08> 8-10 (Fig. 2) clearly shows that two ribs are present at

the level of the parapophysis of the axis, with one rib articulating with the vertebra and another extending further cranially. The intercentrum is smoothly convex ventrally, with no indications of the ventral ridge seen on the more caudal cervical vertebrae (Fig. 3). A small canal appears to exit from the back of the articular surface of the intercentrum. The small, wedge-shaped axial intercentrum is located just caudal to the atlantal intercentrum and ventral to that large and bulbous parapophysis (Figs. 1C, D, 3).

The axial neural spine is hatchet-shaped (Fig. 1A). Its dorsal margin is convex rostrally and pointed caudally where it tapers dorsal to the neural spine of cervical 3. This triangular tapering dorsal process, which is detached from the postzygapophyses, is not preserved in *Protoceratops*, *Montanoceratops* (Tsuihiji and Makovicky, 2007), or *Leptoceratops* (Campione and Holmes, 2006). Two very shallow, cranioventrally oriented depressions lie high on each side of the axial neural spine. The depressions are bordered by a steep, semicircular step cranioventrally, and the floor of the fossae gradually merges with the lateral surface of the neural spine caudodorsally. These depressions may represent the prezygapophyseal facet for the atlantal neural arch, as described for *Protoceratops* and *Leptoceratops* (Campione and Holmes, 2006; Tsuihiji and Makovicky, 2007). Ventral to the neural spine are two elongate, rectangular, and ventrolaterally angled postzygapophyseal facets. The caudal ends of the postzygapophyseal facets are associated with a step in the ventral margin of the neural spine, marking the caudal end of its main portion. This step in the ventral margin of the axial spine also forms the cranial end of the tapering caudal projection. The neural canal is tall and triangular over the axis (Fig. 1E). A faint sutural line is present between the neural arch and the centrum on specimen GSJB <09>-8.

The centrum of the axis is fused to the third cervical in fully adult specimens, although the sutures can still be discerned (Fig. 1A, B). The relatively small axial diapophysis lies caudoventrally to the bulbous articular surface on the caudal portion of the atlantal centrum. At present, it is not clear whether the parapophysis of the axis lies on the neural arch or on the axial centrum. The sutures in that area are obscured by cracking (Fig. 1A). The parapophysis is large (0.5 cm in diameter) and projects approximately 2 mm from the body of the centrum, giving the centrum an hourglass-shaped outline when viewed ventrally. The ventral surface of the axial centrum also bears a distinct keel (Fig. 3).

The neural arch of C3 is not fused to the axial neural arch. The low spinous process of the neural arch of C3 appears to fit completely inside and underneath the arch of the axis. The third cervical of *Montanoceratops* has a long neural spine (Brown and Schlaikjer, 1942; Tsuihiji and Makovicky, 2007). It is entirely possible that a larger neural spine exists for *Auroraceratops* but is covered by the well-preserved axial neural spine. A large, ovate, and dorsomedially inclined prezygapophysis is present on the third cervical. On specimen GSJB <09>-8 the long axis of the ovate articular surface of the prezygapophyses slopes cranially at about 30° from the horizontal. The caudal extent of the prezygapophysis nearly overlaps that of the cranial extent of the postzygapophyses on C3. The postzygapophyses are oval facets with a length of approximately 1 cm. The pedicels of the arches of C3 are inclined dorsocranially. Subadult *Protoceratops* and *Montanoceratops* have vertically or caudally inclined pedicels (Brown and Schlaikjer, 1942; Tsuihiji and Makovicky, 2007), in contrast to the cranially inclined pedicels of *Auroraceratops*. The elongate and ventrally curving diapophysis of C3 clearly sits above the centrum and on the neural arch (Fig. 2). The centrum of the third cervical is craniocaudally shorter than that of the axis. An elevated parapophysis is located cranially and ventrally on the centrum of C3, at the

same level as the axial parapophysis (Fig. 1C–D). The ventral surface of the centrum of C3 bears a distinct keel (Fig. 3).

The partial neural arch of C4 is still articulated with C3 in GSGM GJ <07> 9-02/9-12 (Fig. 1A,B). The arch of C4 bears a low neural spine. The morphology of the pre- and postzygapophyses are the same on C4 as on C3. The pedicels of the neural arch of C4 slope dorsocranially.

DISCUSSION AND CONCLUSIONS

The basal neoceratopsian *Auroraceratops rugosus* possesses a syncervical consisting of the atlantal centrum, atlantal intercentrum, axial centrum, axial intercentrum, and cervical 3, with their centra fused but distinguishable (Figs. 1, 4). The atlantal centrum is small, forming approximately one-third of the total volume of the first segment of the syncervical, whereas the atlantal intercentrum forms the bulk of the articular surface (Fig. 1E) and bears a lateral tubercle for the attachment of the long, thin, single-headed first cervical rib (Fig. 2). The atlantal neural arches are partially preserved in one specimen, and articular facets indicate their location in other specimens. A small, ovate axial intercentrum is located between the atlantal intercentrum and the axial centrum. The axis has the largest centrum in the syncervical, and it bears two facets on each side for a double-headed cervical rib (Fig. 1A, B). The axial neural spine is large and hatchet-shaped, with an elongate, tapering caudal projection extending from above the caudal end of the postzygapophyses over the neural spine of the third cervical. The third cervical centrum is craniocaudally shorter than that of the axis and is ventrally keeled. The neural arch of C3 is strongly cranially inclined. The parapophysis and diapophysis are clearly separated, with the pendant diapophysis fully migrated onto the neural arch (Fig. 1B).

The oldest age assigned to previously described ceratopsian syncervicals belongs to a *Protoceratops andrewsi* from Ukhaa Tolgod (Tsuihiji and Makovicky, 2007). The *Protoceratops*-bearing localities of the Ukhaa Tolgod, Bayn Dzak, and Tugrugyyn Shireh localities (Brown and Schlaikjer, 1940) have been referred to the Campanian (maximum 83.6 ± 0.2 Ma) (Dashzeveg et al., 2006; Dingus et al., 2008; Cohen et al., 2013). *Auroraceratops* from the Yujingzi Basin has been assigned an Aptian to earliest Albian age, between 126 and 115 Ma (Suarez et al., 2019), making this the oldest reported occurrence of a ceratopsian syncervical (VanBuren et al., 2015). Phylogenetic work also shows that *Auroraceratops* is the earliest diverging lineage in Neoceratopsia to preserve a syncervical (Fig. 4) (Morschhauser, 2012; VanBuren et al., 2015; Morschhauser et al., 2019). *Auroraceratops*, as a non-leptoceratopsid, non-coronosaur basal neoceratopsian (Morschhauser et al., 2019), provides a clearer picture of the basal condition of the neoceratopsian cervical series than previous specimens afforded. The material described here demonstrates that a reduced axial centrum and a tall, hatchet-shaped axial neural spine first appeared early in the history of Neoceratopsia. VanBuren et al. (2015) and VanBuren and Evans (2017) examined the possible functional role of the ceratopsian syncervical. VanBuren et al. (2015) concluded that the syncervical could not have been an adaptation to larger head size, or intraspecific combat in ceratopsians. Important to their conclusions was the fact that the syncervical first appeared in *Auroraceratops*, a taxon with a small overall body size, relatively small skull, and which lacks the cranial ornamentation that is often associated with hypotheses of cranial combat (Farlow and Dodson, 1975; Farke, 2014; VanBuren et al., 2015, and references therein). VanBuren and Evans' (2017) survey of extant amniotes with syncervicals also found that many taxa that possess syncervicals also engage in

head-lift digging. Although this is highly improbable in larger ceratopsids (VanBuren and Evans, 2017), fossorial behavior has been hypothesized in smaller ceratopsians (Longrich, 2010). Fossorial behavior is known in at least one taxon of ornithomimid comparable in size to *Auroraceratops* (Varricchio et al., 2007). With the current lack of information about cervical anatomy from other early-appearing neoceratopsian species, testing hypotheses of adaptational or functional drivers in the formation of the syncervical is not possible. More specimens of other non-coronosaur, non-leptoceratopsid neoceratopsians will be needed to determine the precise timing and context of the transition from the basal (unfused) condition of the atlas-axis complex to the syncervical.

ACKNOWLEDGMENTS

We thank R. Irmis for his editorial help and T. Tsuihiji and an anonymous reviewer for their comments on the manuscript. We thank A. Tumarkin-Dertatzian and H. Pfefferkorn for reading early drafts of this work. This research was generously funded by several Penn Paleobiology Summer Stipend grants (2009–2010), a Jurassic Foundation grant, and a National Geographic Young Explorer's Grant to E.M.M. A portion of this work was completed while E.M.M. was participating in the 2009 East Asia and Pacific Summer Institutes program jointly administered by the National Science Foundation and the Chinese Ministry of Science and Technology. This research was also funded by grants from the National Science Foundation (1024671) to P.D., from the National Natural Science Foundation of China (41072019) and the basic outlay of scientific research work from Ministry of Science and Technology (J1003) to Y.H., and the Gansu Geological Museum to L.D.

LITERATURE CITED

- Bohlin, B. 1953. Fossil reptiles from Mongolia and Kansu. Reports from the Scientific Expedition to the North-western Provinces of China under Leadership of Dr. Sven Hedin Publication 37:1–113.
- Brown, B. 1914. *Leptoceratops*, a new genus of Ceratopsia from the Edmonton Cretaceous of Alberta. Bulletin of the American Museum of Natural History 33:567–580.
- Brown, B. 1917. A complete skeleton of the horned dinosaur *Monoclonius*, and description of a second skeleton showing skin impressions. Bulletin of the American Museum of Natural History 37:281–306.
- Brown, B., and E. M. Schlaikjer. 1940. The structure and function of *Protoceratops*. Annals of the New York Academy of Sciences 40: 133–266.
- Brown, B., and E. M. Schlaikjer. 1942. The skeleton of *Leptoceratops* with the description of a new species American Museum Novitates 1169:1–15.
- Campione, N. E., and R. Holmes. 2006. The anatomy and homologies of the ceratopsid syncervical. Journal of Vertebrate Paleontology 26:1014–1017.
- Chinnery, B. J., and J. R. Horner. 2007. A new neoceratopsian dinosaur linking North American and Asian taxa. Journal of Vertebrate Paleontology 27:625–641.
- Cohen, K. M., S. C. Finney, P. L. Gibbard, and J.-X. Fan. 2013. The ICS International Chronostratigraphic Chart. Episodes 36:199–204.
- Dashzeveg, D., L. Dingus, D. B. Loope, C. C. Swisher III, T. Dulam, and M. R. Sweeney. 2006. New stratigraphic subdivision, depositional environment, and age estimate for the Upper Cretaceous Djadokhta Formation, Southern Ulan Nur Basin, Mongolia. American Museum Novitates 3498:1–31.
- Dingus, L., D. B. Loope, D. Dashzeveg, C. C. Swisher III, C. Minjin, M. J. Novacek, and M. A. Norell. 2008. The geology of Ukhaa Tolgod (Djadokhta Formation, Upper Cretaceous, Nemegt Basin, Mongolia). American Museum Novitates 3616:1–40.

- Dodson, P. 1997. Neoceratopsia; pp. 473–478 in P. J. Currie, and K. Padian (eds.), *Encyclopedia of Dinosaurs*. Academic Press, San Diego, California.
- Dodson, P., and P. J. Currie. 1990. Neoceratopsia; pp. 593–618 in D. B. Weishampel, P. Dodson and H. Osmólska (eds.), *The Dinosauria*. California University Press, Berkeley, California.
- Dodson, P., C. A. Forster, and S. D. Sampson. 2004. Ceratopsidae; pp. 494–513 in D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*, second edition. University of California Press, Berkeley, California.
- Farke, A. A. 2014. Evaluating combat in ornithischian dinosaurs. *Journal of Zoology* 292:242–249.
- Farlow, J. O., and P. Dodson. 1975. The behavioral significance of frill and horn morphology in ceratopsian dinosaurs. *Evolution* 29:353–361.
- Hatcher, J. B., O. C. Marsh, and R. S. Lull. 1907. *The Ceratopsia*. U.S. Geological Survey Monograph 49:1–300.
- Langston, W., Jr. 1975. The ceratopsian dinosaurs and associated lower vertebrates from the St. Mary River Formation (Maestrichtian) at Scabby Butte, southern Alberta. *Canadian Journal of Earth Science* 12:1576–1608.
- Lehman, T. M. 1989. *Chasmosaurus mariscalensis*, sp. nov., a new ceratopsian dinosaur from Texas. *Journal of Vertebrate Paleontology* 9:137–162.
- Longrich, N. 2010. The function of large eyes in *Protoceratops*: a nocturnal ceratopsian; pp. 308–327 in M. J. Ryan, B. J. Chinnery-Allgeier, and D. A. Eberth (eds.), *New Perspectives on Horned Dinosaurs: The Royal Tyrell Museum Ceratopsian Symposium*. Indiana University Press, Bloomington, Indiana.
- Lull, R. S. 1933. A revision of the Ceratopsia or horned dinosaurs. *Memoirs of the Peabody Museum of Natural History* 3(3):1–175.
- Makovicky, P. J. and M. A. Norell. 2006. *Yamaceratops dorngobiensis*, a new primitive ceratopsian (Dinosauria: Ornithischia) from the Cretaceous of Mongolia. *American Museum Novitates* 3530:1–42.
- Marsh, O. C. 1889. A new family of horned Dinosauria from the Cretaceous. *American Journal of Science* 36:477–478.
- Marsh, O. C. 1891. The gigantic Ceratopsidae, or horned dinosaurs of North America. *Geological Magazine* 8:193–199.
- Morschhauser, E. M. 2012. The anatomy and phylogeny of *Auroraceratops* (Ornithischia: Dinosauria) from the Yujingzi Basin of Gansu Province, China. Ph.D. dissertation, University of Pennsylvania, Philadelphia, Pennsylvania, 629 pp.
- Morschhauser, E. M., H. You, D. Li, and P. Dodson. 2019. Phylogenetic history of *Auroraceratops rugosus* (Ceratopsia: Ornithischia) from the Lower Cretaceous of Gansu Province, China; pp. 117–147 in H. You, P. Dodson, and E. Morschhauser (eds.), *Auroraceratops rugosus* (Ornithischia, Ceratopsia) from the Early Cretaceous of northwestern Gansu Province, China. *Society of Vertebrate Paleontology Memoir* 18. *Journal of Vertebrate Paleontology* 38(Supplement).
- Ostrom, J., and P. Wellnhofer. 1986. The Munich specimen of *Triceratops* with a revision of the genus. *Zitteliana* 14:111–158.
- Owen, R. 1842. Report on British fossil reptiles. Part II. Reports of the British Association for the Advancement of Science 11:60–204.
- Padian, K., and C. L. May. 1993. The earliest dinosaurs. *New Mexico Museum of Natural History & Science Bulletin* 3:379–381.
- Rothschild, B. M. 1997. Dinosaurian paleopathology; pp. 426–448 in J. O. Farlow and M. K. Brett-Surman (eds.), *The Complete Dinosaur*. Indiana University Press, Bloomington, Indiana.
- Sereno, P. C. 1984. The phylogeny of the Ornithischia: a reappraisal; pp. 219–226 in W.-E. Reif and F. Westphal (eds.), *Third Symposium on Mesozoic Terrestrial Ecosystems, Short Papers*. Attempto Verlag, Tübingen, Germany.
- Sereno, P. C. 1986. Phylogeny of the bird-hipped dinosaurs (Order Ornithischia). *National Geographic Research* 2:234–256.
- Sereno, P. C. 1998. A rationale for phylogenetic definitions, with application to the higher-level taxonomy of Dinosauria. *Neues Jahrbuch für Geologie und Palaontologie, Abhandlungen* 210:41–83.
- Sternberg, C. M. 1951. Complete skeleton of *Leptoceratops gracilis* Brown, from the upper Edmonton member on Red Deer River, Alberta. *Bulletin of the National Museum of Canada* 123:225–255.
- Tsuihiji, T., and P. J. Makovicky. 2007. Homology of the neoceratopsian cervical bar elements. *Journal of Paleontology* 81:1132–1138.
- VanBuren, C. S., and D. C. Evans. 2017. Evolution and function of anterior cervical vertebral fusion in tetrapods. *Biological Reviews* 92:608–626.
- VanBuren, C. S., N. E. Campione, and D. C. Evans. 2015. Head size, weaponry, and cervical adaptation: testing craniocervical evolutionary hypotheses in Ceratopsia. *Evolution* 69:1728–1744.
- Varricchio, D. J., A. J. Martin, and Y. Katsura. 2007. First trace and body fossil evidence of a burrowing, denning dinosaur. *Proceedings of the Royal Society B: Biological Sciences* 274:1361–1368.
- You, H., and P. Dodson. 2004. Basal Ceratopsia; pp. 478–493 in D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*, second edition. California University Press, Berkeley, California.
- You, H., D. Li, Q. Ji, M. C. Lamanna, and P. Dodson. 2005. On a new genus of basal neoceratopsian dinosaur from the Early Cretaceous of Gansu Province, China. *Acta Geologica Sinica (English Edition)* 79(5):593–597.

Submitted on February 4, 2016; revisions received October 14, 2017; accepted February 3, 2018.

Memoirs editor: Randall Irmis.