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First ceratopsid dinosaur from China and its biogeographical implications

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Ceratopsid dinosaurs represent one of the best known dinosaur groups in the Late Cretaceous, and their unquestionable fossil records are exclusively restricted to western North America. Here we report a new ceratopsid dinosaur, *Sinoceratops zhuchengensis* gen. et sp. nov., from the Upper Cretaceous Wangshi Group of Zhucheng, Shandong Province, China. Cladistic analysis places this new taxon as the only known ceratopsid from outside North America, in a basal position within the Centrosaurinae. It is considerably larger than most other centrosaurines but similar in size to basal chasmosaurines. Furthermore, it is more similar to chasmosaurines than to other centrosaurines in several features, thus blurring the distinction of the two ceratopsid subgroups. This new find not only provides significant information on the morphological transition from non-ceratopsid to ceratopsid dinosaurs, but also complicates the biogeography of the Ceratopsidae, and further demonstrates that fossil sampling has profound effects on reconstructing dinosaurian biogeography.

Late Cretaceous, Wangshi Group, Ceratopsidae, Centrosaurinae, biogeography

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Ceratopsids, or derived horned dinosaurs, are large, quadrupedal herbivorous ornithischian dinosaurs. They are among the best known dinosaur groups including famous member such as *Triceratops* [1,2]. Previously ceratopsid fossils have been known only from the Late Cretaceous deposits of the Western Interior Seaway of North America [1]. *Turanoceratops tardabilis*, a taxon based on fragmentary, unassociated material collected from the Upper Cretaceous of Uzbekistan, has been assigned to the Ceratopsidae [3,4]. This systematic proposal has been questioned [1,5,6], yet recent studies provide additional support for the ceratopsid affinity of *Turanoceratops tardabilis* [7,8]. In the summer of 2008, we opened a large quarry near Zangjiazhuang, a site located in Zhucheng, Shandong Province, China and collected numerous bones from the Upper Cretaceous Wangshi Group [9]. Most bones are referable to the largest known hadrosaurid *Shantungosaurus* as in the nearby Longgujian site [9]. However, some cranial material is apparently not derived from hadrosaurs but is referable to the Ceratopsidae. Here we report a new ceratopsid taxon based on the recovered cranial material. Given that *Turanoceratops tardabilis* is probably the sister taxon to the Ceratopsidae rather than a basal member of the group [6,10] (also see below for a detailed analysis), the new taxon represents the only known ceratopsid outside of North America [7,11,12], and its discovery has significant biogeographical implication for the Ceratopsidae.

1 Systematic paleontology

1.1 Taxonomy

Ornithischia Seeley, 1888

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Ceratopsia Marsh, 1890
Ceratopsidae Marsh, 1888
Centrosaurinae Lambe, 1915
***Sinoceratops zhuchengensis* gen. et sp. nov.**

1.2 Etymology

Sino (China) and *ceratops* (horned-face, Latinized Greek); *Zhucheng* (the place that produced the specimens described here).

1.3 Holotype

Zhucheng Dinosaur Museum (ZCDM) V0010, a partial skull with most elements of the skull roof and partial braincase.

1.4 Referred specimens

ZCDM V0011, a partial skull with much of the skull roof and most of the braincase. ZCDM V0012, partial braincase.

1.5 Type locality and horizon

Zangjiazhuang, Zhucheng, Shandong Province, China. Upper Cretaceous Wangshi Group [9].

1.6 Diagnosis

Large centrosaurine ceratopsid with at least ten robust, strongly curved horn-like processes along the posterior margin of the parietals and at least four horn-like processes on the squamosals. It is also different from other centrosaurine in the following features: a large accessory fenestra anterior to the antorbital fenestra, weakly undulated external margin of the parietals and broadly based epoccipitals.

1.7 Description and comparison

The holotype skull (Figure 1) is estimated to be 180 cm in total length (from the snout tip to the posterior end of the parietals along the midline), being one of the largest centrosaurine skulls discovered so far [1,2].

As in many other ceratopsid specimens [1,2], the cranial sutures are obscured and thus no preserved elements could be precisely defined by their borders. The skull has a typical ceratopsid profile (Figure 2), being anteriorly narrow and posteriorly much wider in dorsal view [1]. The fused parietals of the holotype are 105 cm in the maximum transverse width. Also similar to other ceratopsids [13], the snout is proportionally long (estimated to be about 70% of the basal skull length). As in ceratopsids, the orbit is small (estimated to be less than 15% of the basal skull length) and its long axis is nearly vertically oriented, different from the proportionally larger orbit with an anteroposteriorly oriented long axis in most more basal ceratopsians [5]. Similar to other ceratopsids, the infratemporal fenestra is small in size and is located considerably ventral to the orbit, though not to the degree seen in most other ceratopsids [1]. Similar to other ceratopsids, a highly reduced antorbital fenestra is present along the posterodorsal border of the maxilla. A second fenestra, much larger in size, is located anterior to the antorbital fenestra, as in an unnamed basal centrosaurine, and

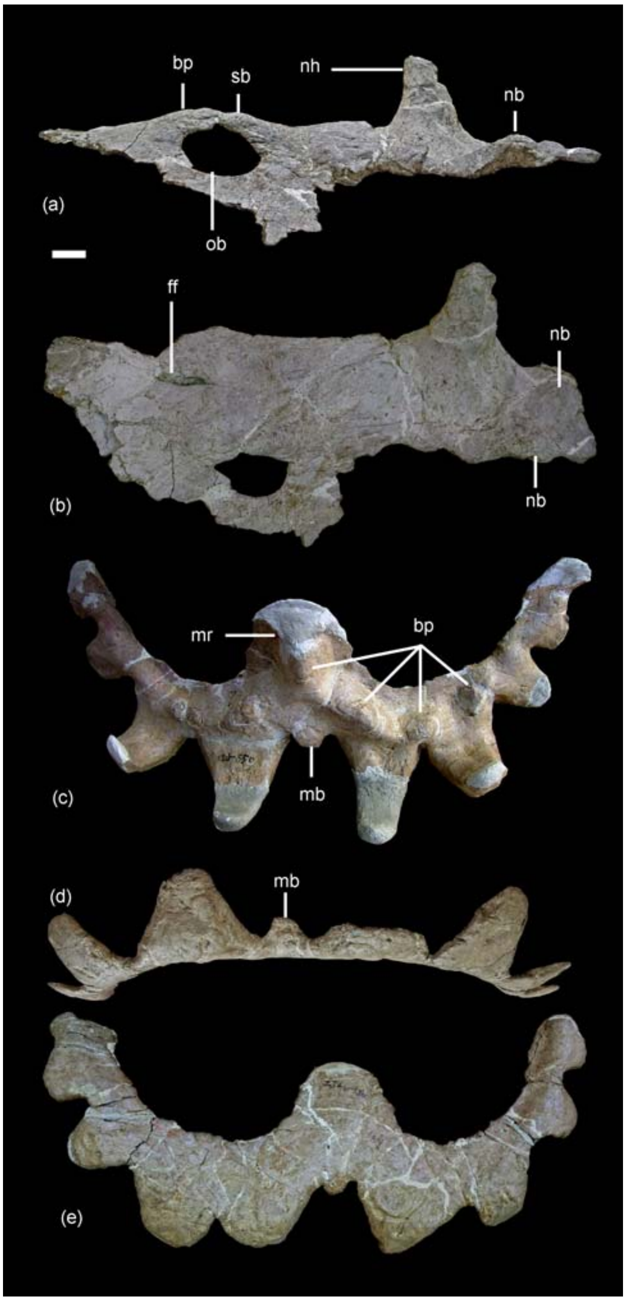

Figure 1 Photograph of *Sinoceratops zhuchengensis* holotype. ZCDM V0010 skull in right lateral (a) and right laterodorsal (b) views; ZCDM V0010 parietals in dorsal (c), posterior (d), and ventral (e) views. Abbreviations: bp, bump; ff, frontal fontanelle; mb, median bump; mr, midline ramus; nb, nasal bump; nh, nasal horn; ob, orbit; pb, postorbital bump; sb, supraorbital bump. Scale bar = 8 cm for (a), (b) and 6 cm for (c), (d), and (e).

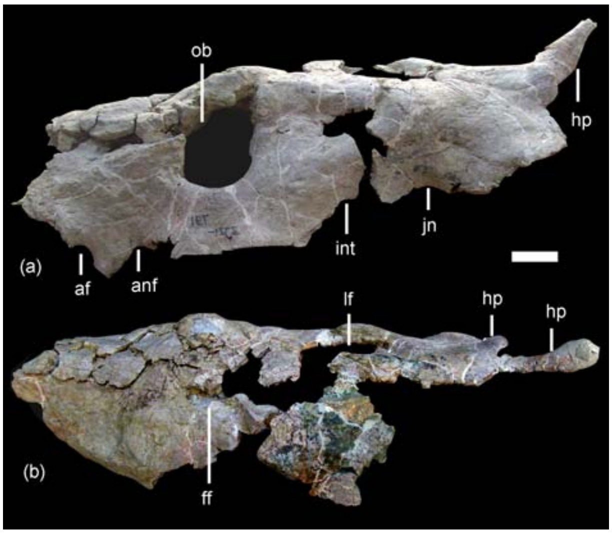

Figure 2 Photograph of *Sinoceratops zhuchengensis* ZCDM V0011. Skull in left lateral (a) and dorsal (b) views. Abbreviations: af, accessory fenestra; anf, antorbital fenestra; ff, frontal fontanelle; hp, horn-like process; int, infratemporal fenestra; jn, jugal notch; lf, lateral fenestra; ob, orbit. Scale bar = 10 cm.

derived non-ceratopsid neoceratopsian *Zuniceratops*, *Bagaceratops*, and *Magnirostris* [10,12,14,15].

The lacrimal is fused to the adjacent elements and thus its borders are not clear. The bone texture indicates, however, that the lacrimal is reduced in size. The nasals are fused to each other. A relatively small nasal horn is located about the mid-length of the snout. It is slightly curved posteriorly and transversely compressed. It is about twice as long anteroposteriorly as wide transversely at the cross section. In the holotype, the mostly preserved nasal horn is about 30 cm tall and about 25 cm in basal length. One relatively prominent bump is located anterolateral to the nasal horn and a less prominent one located anterior and slightly lateral to the nasal horn.

The jugal contributes a large portion of the cheek, but its contact relationships to the adjacent elements are not clear due to the obscured sutures. However, it must have a large contact with the squamosal as in other ceratopsids [2] inferred from the general morphology of the postorbital area and at the junction area of the jugal, squamosal and the postorbital is a large, shallow depression. The postorbital bears no horn-like structure, but a very weak postorbital bump is present, which is located over posterodorsal corner of the orbit. Anterior to this bump is an even weaker supraorbital bump, which is located over the anterodorsal corner of the orbit.

The fused frontals bear a frontal fontanelle along the midline, which is located medial to the postorbital bump. Similar to that of other centrosaurines [1], it is elongate anteroposteriorly and narrow transversely. Posterolateral to the frontal fontanelle are a pair of large, deep depressions which are fenestrated along their lateral border (lateral fenestra), a feature variably seen in some ceratopsid specimens.

The bony frill is composed of the squamosals anterolaterally and the parietals in the rest areas as in other centrosaurines. Also similar to most other centrosaurines [1], the relatively short squamosal has a postquadrate portion about twice as long as the prequadrate portion. It borders the infratemporal fenestra dorsally and posterally to exclude the postorbital from the fenestra. As in other ceratopsids [1], the squamosal is constricted posterior to the infratemporal fenestra to form a jugal notch. At least two relatively straight horn-like processes, which are oriented lateroposterodorsally, are present along the lateral margin of the squamosal. Each parietal bears at least five horn-like, curved processes along its posterior and lateral margins. They are short, robust, and oriented posterodorsally, with the medial ones more prominent than the lateral ones. As in other centrosaurines [1], the horn-like processes are somewhat imbricate in arrangement. The fused parietals are slightly indented posteriorly along the midline at the posterior margin and more similar to chasmosaurines [1], the external margin of the parietals is relatively weakly undulated. Also similar to chasmosaurines [1], the epoccipitals are broad based, with the adjacent ones contacting each other. The posterior and particularly lateral ramus is narrow in dorsal view compared to the midline ramus. The latter is triangular in cross-section, bearing a relatively broad sagittal crest as in other centrosaurines [1]. There are at least 10 prominent bumps along the dorsal surface of the posterior ramus and lateral ramus of the fused parietals and one on the posterodorsal surface at the midline. These bumps are more prominent close to the midline than laterally. Smaller bumps are also present on the dorsal surface of the midline ramus. There are two large parietal fenestrae, the lateral borders of which are oriented anterolaterally as in other centrosaurines [1].

The braincase elements are firmly fused to the skull roof and as in other ceratopsids [1], the braincase is located anterior to the parietals. The occipital condyle is large, measuring about 90 cm in diameter in ZCDM 0012.

2 Discussion

We investigated the systematic position of *Sinoceratops zhuchengensis* by scoring it into a recently published dataset for ceratopsid phylogeny [16]. We also add *Turanoceratops*, a taxon claimed to be a basal ceratopsid [7], and *Albertaceratops*, a recently described basal centrosaurine [17], into the dataset (Table 1). The data matrix was analyzed using the NONA (ver 2.0) software package [18] and formatting and character exploration was performed in WinClada [19]. The analysis protocol consisted of 1000 Tree Bisection and Regrafting tree searches followed by branch swapping. Settings included collapsing unsupported branches and counting all states in polymorphic codings. Other settings includ-

Table 1 Scorings for *Sinoceratops*, *Albertaceratops*, and *Turanoceratops*

Taxa	Scoring
Sinoceratops	???????????????1[12]010111-1??1?11111????111???100101??????????????????????????
Albertaceratops	11??????????1??1201?10101?112??11[01]1?1???111?010---1?????1??11??????????????0??
Turanoceratops	????????????????0???101?0???11??????????????????????????0??111??????????????

ing the character ordering follow [16]. The analysis resulted in 2 equally most parsimonious trees with a length of 101 steps, the strict consensus of which is shown below (Figure 3). Our analysis on this dataset places *Sinoceratops zhuchengensis* within the Centrosaurinae. Derived features uniting *Sinoceratops zhuchengensis* and other centrosaurines include short parietosquamosal frill, squamosal much shorter than parietal, and parietal epoccipital modified into large horns [1,17]. However, in *Sinoceratops zhuchengensis*, the parietal margin imbrication is not evident and the parietal epoccipital at locus 2 is posterodorsally directed rather than medially directed as in other centrosaurines [1,17]. These features suggest that *Sinoceratops zhuchengensis* lies in a basal position within the Centrosaurinae as indicated by our analysis (Figure 3).

Estimated to have a skull of 180 cm long, *Sinoceratops zhuchengensis* is among the largest centrosaurines and is much larger than other basal centrosaurines in size [17]. Comparatively, chasmosaurines are in general larger than centrosaurines in body size and the size disparity is more evident between the basal members of the two groups [2]. However, the discovery of *Sinoceratops zhuchengensis* removes this size disparity. Besides, *Sinoceratops zhuchengensis* is more similar to chasmosaurines than to other centrosaurines in several features, including weakly undulated external margin of the parietals and broadly based epoccipitals, thus further blurring the distinction of the two ceratopsid subgroups.

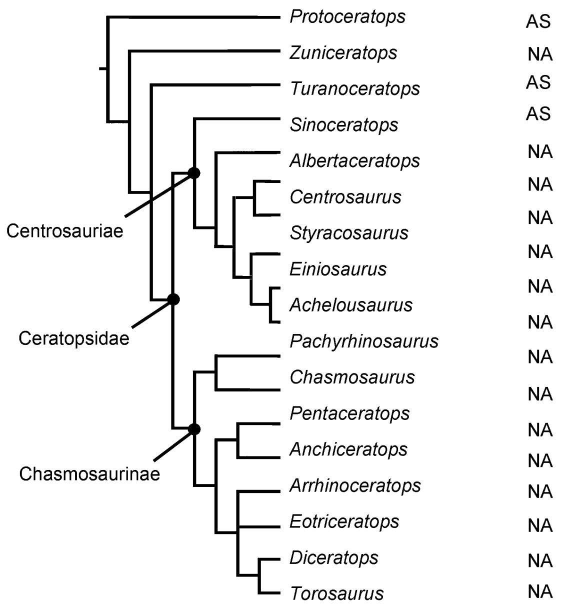

Figure 3 The phylogeny and geographical distribution of derived neoceratopsians. The analysis of a dataset in [16] with 3 taxa added resulted in 2 equally most parsimonious trees with a length of 101 steps (CI = 0.80 and RI = 0.88). AS, Asia; NA, North America.

Sinoceratops zhuchengensis also shortens the morphological gap between non-ceratopsid and ceratopsid dinosaurs. For example, its infratemporal fenestra is located in a position between the relatively dorsally located one in more basal ceratopsians and extremely ventrally located one in other ceratopsids [1]; it has a large, accessory fenestra anterior to the antorbital fenestra, as in several taxa that are most closely related to the Ceratopsidae [14]. These features suggest a more complex pattern during the transition to the Ceratopsidae. The last feature particularly indicates that some salient features have only a brief phase in ceratopsian evolution.

Although *Turanoceratops* has been recently suggested to be the most basal known chasmosaurine [7], our analysis rejects this systematic hypothesis. In our analysis, *Turanoceratops* is in a position more derived than *Zuniceratops* as suggested by previous analysis [7], but is placed outside the Ceratopsidae. It lacks several ceratopsid synapomorphies including presence of a nasal ornamentation and reduced secondary ridges on maxillary and dentary teeth, though it has double-rooted teeth. *Sinoceratops zhuchengensis,* suggested by our analysis, is therefore the only known ceratopsid from outside the western North America.

The absence of ceratopsids in Asia has been an intriguing issue in dinosaurian biogeography given that all other dinosaur groups found in Late Cretaceous deposits of North America are also seen in Asia, such as the Tyrannosauridae, Ornithomimidae, Troodontidae, Alvarezsauridae, Hardrosauridae, Pachycephalosauria, Ankylosauridae, and most recently the Nodosauridae [12,20,21]. A quantitative study indicates that ceratopsians have dispersed much less than other dinosaur groups around them [12] partially due to the endemic nature of the Ceratopsidae, the most speciose clade of the Ceratopsia. This has been attributed to the absence of preferred paleoenviroments, the insufficient fossil sampling or a combination of both these factors [12]. The discovery of the basal centrosaurine *Sinoceratops zhuchengensis* suggests that the latter factor might be the main reason for the rarity of the group in Asia, though limited ceratopsid preferred paleoenviroments must have also contributed to this. Extensive collecting has recently filled the record of several dinosaurian groups in Asia in case of the Ceratopsidae and Nodosauriae [20], or in North America in case of the Alvarezsauridae [21,22]. These discoveries provide significant new information on the dinosaurian biogeography. Given the ceratopsian phylogeny presented in Figure 3, the Ceratopsidae is more likely to have originated in Asia and migrate to North America. Multiple dispersal events occurred in the ceratopsian evolution and all these dispersals might be from Asia to North America. Such a dispersal pattern has also been suggested for some other dinosaur groups such as the derived Ornithomimosauria and Tyrannosauroidea [23, 24].

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