A New Basal Hadrosauroid Dinosaur (Dinosauria: Ornithopoda) with Transitional Features from the Late Cretaceous of Henan Province, China

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Abstract

Background: Southwestern Henan Province in central China contains many down-faulted basins, including the Xixia Basin where the Upper Cretaceous continental sediments are well exposed. The Majiacun Formation is a major dinosaur-bearing stratigraphic unit that occurs in this basin.

Methodology/Principal Findings: A new basal hadrosauroid dinosaur, Zhanghenglong yangchengensis gen. et sp. nov., is named based on newly collected specimens from the middle Santonian Majiacun Formation of Zhoujiagou Village, Xixia Basin. Two transitional features between basal hadrosauroids and hadrosaurids are attached to the diagnosis of the new taxon, namely five maxillary foramina consisting of four small scattered ones anteroposteriorly arranged in a row and a large one adjacent to the articular facet for the jugal, and dentary tooth crowns bearing both median and distally offset primary ridges. Zhanghenglong also displays a unique combination of plesiomorphic and derived features of hadrosaurids, and is clearly morphologically transitional between basal hadrosauroids and hadrosaurids. Furthermore, some measurement attributes in osteology are applied to the quantitative analysis of Zhanghenglong. For these attributes, the partition of the dataset on most hadrosaur species resulting from model-based cluster analysis almost matches taxonomic separation between basal hadrosauroids and hadrosaurids. Data of Zhanghenglong on selected measurement attributes straddle the two combinations of intervals of partitioned datasets respectively related to basal hadrosauroids and hadrosaurids. This condition is similar to mosaic evolution of morphological characters present in the specimens of the taxon. The phylogenetic analysis of Hadrosauroidae recovers a clade composed of Zhanghenglong, Nanyangosaurus, and Hadrosauridae with an unresolved polytomy.

Conclusions/Significance: Zhanghenglong is probably a relatively derived non-hadrosaurid hadrosauroid, based on the inferences made from the morphological comparisons, quantitative evaluation of measurements, and cladistic analysis. In combination with information on the stratigraphy, phylogeny and biogeography, the material of Zhanghenglong provides direct evidence for the hypothesis that hadrosaurids might have originated in Asia.

Introduction

Hadrosauridae is a diverse and highly specialized clade of herbivorous dinosaurs whose remains have been found in the late Early and Late Cretaceous (Aptian to late Maastrichtian) of Europe, Asia, the Americas, and Antarctica [1–3]. It is amongst the most morphologically derived groups within Ornithischia, consisting of the most recent common ancestor of Equornithidae and Parasaurolophus walkeri plus all its descendants [1]. Since the middle of the 20th century, the group has been recognized as a substantial component of the terrestrial vertebrate faunas of the Late Cretaceous [2,4–6]. The known fossil record of hadrosaurids is one of the richest and best preserved nonrenewable resources of the Dinosauria, and includes dozens of articulated skeletons in addition to multi-individual bonebed assemblages, eggs and embryonic material, soft-tissue impressions, and footprints [4,7–10].

Definitions of relevant taxa are described as follows. Hadrosauriformes is the least inclusive clade containing Iguanodon bernissartensis and Parasaurolophus walkeri [11]. Hadrosauroidea is
the least inclusive taxon containing Equijubus normani and Parasaurolophus walkeri, which follows the phylogenetic topology argued by You et al. [1]. This clade has a series of unambiguous synapomorphies, including the elongate anteroventral corner of the lacrimal, the elevated, subrectangular jugal sutural surface of the maxilla that closely abuts the lacrimal sutural surface of the bone, and the moderately expanded transversely oral margin of the rostrum that is greater than 1.5 times as wide as the maximum constriction of the snout. Hadrosauridae is the monophyletic group consisting of Saurolophus osborni, Parasaurolophus walkeri, their most recent common ancestor, and all other descendants [11].

Given the close affinities of Hadrosaurus foulii with non-lambeosaurine hadrosauroids (see below), Hadrosauridae could be traditionally divided into two major clades: Hadrosaurinae (the flat-headed or solid-crested hadrosauroids) and Lambeosaurinae (the hollow-crested hadrosauroids) [2].

Basal hadrosauroids, or non-hadrosaurid hadrosauroids, display a series of plesiomorphic features, such as a poorly defined posterior margin of the circummaxillary fossa, a relatively low maxillary body with a posteriorly offset dorsal ramus, a nearly vertical or posteriorly inclined coronoid process just concealed entirely by the posterior region of the dental matrix in medial view, and one or two active teeth per dentary alveolar position [1,3,12]. Over the last century and the beginning of the present one, numerous valuable discoveries of basal hadrosauroids in Asia have filled the gap in our understanding of the early evolution of the clade, particularly regarding significant morphological changes that took place from basal hadrosauriforms to more derived hadrosaurs last during the Late Cretaceous [2]. The first Asian basal hadrosaurid species to be erected and described was Tanius sinensis from the Jiangjunding Formation of the Wangshi Group, China [13]. Subsequently, Gilmore [14] briefly described another two basal hadrosauroids, “Mandschureosaurus” mongoliensis and Bactrosaurus johnsoni, from the middle to late Campanian Iren Dabasu Formation of Inner Mongolia, north China, based upon a large number of disarticulated cranial and postcranial bones [15]. Considering Mandschureosaurus as a nomen dubium, Brett-Surman [16] removed this original genus name, and then extended a new genus Gilmoreosaurus to the firstly named hadrosaurid species in Gilmore’s paper [14], with the new combination G. mongoliensis. In 1966, Probactrosaurus gobiensis was established and preliminarily described by Rozhdestvensky on the basis of three partial skeletons and numerous other bones recovered from the Bayingobi Formation in the Maortu area of Inner Mongolia [17]. After this work, Norman [12] further conducted an overall osteological re-evaluation of the taxon, which drew support from the cladistic analysis. Based on a partial postcranial skeleton recovered from the early Late Cretaceous Xiaguan Formation in the Xiuqiao-Gaoqiu Basin of southwest Henan Province, Xu et al. [18] named and thoroughly described Nanyangosaurus zhangi that possibly represents another basal hadrosaurid. However, the phylogenetic position of the taxon is unresolved and controversial all the while. More recently, three primitive non-hadrosaurid hadrosauroids have been found in succession from the late Early Cretaceous (Aptian-Albian) middle grey member of the Xinminbao Formation in the Mazongshan area of Gansu Province [19]: Equijubus normani [1], Jintasaurus meniscus [20], and Xueulong yueluni [21]. The discoveries of these species in East Asia indicate that the ancestral area of Hadrosauridae is very likely located in Asia [1,21]. Sues and Averianov [22] revised the systematics and paleobiogeography of Hadrosauridae, and reported a new basal hadrosaurid taxon Leunosaurus transoxiana from the Turonian deposits of Central Asia, which has a close affinity with B. johnsoni. Furthermore, two additional basal hadrosaurid taxa, Shuangmiaosaurus gilmorei [23] and Nanningosaurus dushiensis [24], are known from the Upper Cretaceous of northeast and southwest China, respectively. Some basal hadrosauriforms outside of Hadrosauridae have also been reported in Asia, including Altitiansaurus karzanoi [25] and Jinzhousaurus yangi [26].

Apart from Asia, basal hadrosauroids are explicitly recorded in Europe (†Telmatosaurus transsylvanicus [27] and †Tethysaurus insularis [28]) and North America (e.g., †Bolimantosaurus [29] and †Prohadosaurus hydei [30]). The fossil record of Europe and North America substantially expands the biodiversity, stratigraphic presence, and paleogeographic distribution of non-hadrosaurid hadrosauroids. Although the known record of basal hadrosauroids has provided a wealth of information on the morphology and diversity of this paraphyletic group, whose phylogenetic interrelationships are becoming better understood, broad consensus on the evolutionary history and systematic positions of derived basal hadrosauroids remains elusive. A major cause of this lack of consensus is the fact that some relatively derived basal hadrosauroids are known only from partial or fragmentary remains, so that a large amount of character information is missing from the fossil record.

The southwestern part of Henan Province in central China contains many down-faulted basins or depressions in which Upper Cretaceous continental sediments are widely distributed, including the Xixia, Xiaguan-Gaoqiu, and Xichuan Basins [31] (Fig. 1A). The Majiacun Formation is a major dinosaur-bearing lithostratigraphic unit that is exposed in the uplifted areas along the edges of the Xixia Basin and the neighboring Xichuan Basin; the formation is bounded above and below by its conformable contacts with the overlying Sigou Formation and the underlying Gaogou Formation, respectively [31,32].

This paper describes a new basal hadrosaurid genus and species from the Upper Cretaceous Majiacun Formation, based on some disarticulated bones collected from Zhoujiagou Village in the Xixia Basin of southwest Henan Province, China (Fig. 1A). The quarry site is located approximately 0.4 km southeast of the centre of the village. According to palynological and stratigraphic data obtained from the recent regional geological survey of Henan Province, the outcrop in Zhoujiagou Village is generally equivalent to most of the middle portion (Unit 2) of the Majiacun Formation plus the upper part of the lower portion (Unit 1) of the formation [31] (Fig. 1B). Unit 2 could be interpreted as a combination of floodplain and point bar deposits, clearly differing from the coarse-grained channel-lag sediments in Unit 1. The layer from which the hadrosaur material was recovered is embedded within Unit 2 of the Majiacun Formation. It consists of a mixture of light purple and red muddy siltstone or mudstone and calcareous nodules that represents well-developed palaeosols, as is characteristic of the fine-grained member of typical hadrosaurid formations. Hadrosaurus foulkii, †B. johnsoni, Jinzhou-
and hadrosaurids, and helps to test the potential dispersal patterns that have been previously suggested for basal hadrosauroids. Attention is also paid to the statistical partitions of osteological measurements; the dataset of each measurement attribute is the collection of the corresponding values for most species within Hadrosauridae and several close relatives of this group. The statistical analysis is enormously enlightened by Prieto-Márquez’s work [3].

Institutional Abbreviations: AEHM, Amur Natural History Museum, Blagoveschensk, Russia; AMNH, American Museum of Natural History, New York, USA; CCMGE, Chernyshev’s Central Museum of Geological Exploration, Saint Petersburg, Russia; CEUM, College of Eastern Utah Prehistoric Museum, Price, USA; CMN, Canadian Museum of Nature, Ottawa, Canada; FGGUB, Facultatea de Geologie si Geofizica, Universitatea Bucuresti, Bucharest, Romania; FMNH, The Field Museum, Chicago, USA; GMV, Geological Museum of China, Beijing, China; GSGM, Gansu Geological Museum, Lanzhou, China; IVP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; LPM, Liaoning Paleontological Museum, Beipiao, China; MOR, Museum of the Rockies, Bozeman, USA; MPZ, Museo Paleontologico de la Universidad de Zaragoza, Zaragoza, Spain; NMMNH, New Mexico Museum of Natural History and Science, Albuquerque, USA; PIN, Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; PMU, Museum of Evolution, Uppsala University, Uppsala, Sweden; RAM, Raymond M. Alf Museum, Claremont, USA; ROM, Royal Ontario Museum, Toronto, Canada; SBDE, Sino-Belgian Dinosaur Expedition; SC, Italian State collections; SMU, Shuler Museum of Paleontology, Southern Methodist University, Dallas, USA; TMP, Royal Tyrrell Museum of Paleontology, Drumheller, Canada; USNM, United States National Museum, Smithsonian Institution, Washington, DC, USA; XMDFEC, Xixia Museum of Dinosaur Fossil Eggs of China, Xixia, China.

Methods

The necessary permits for the described field studies were obtained from the Department of Land and Resources of Henan Province (Zhengzhou, China), XMDFEC (Xixia, China), and IVPP (Beijing, China). Permission was also granted to the authors for accessing the collection of fossils at the XMDFEC (Xixia, China), in order to examine the hadrosauroid material collected from the fieldwork and housed at the museum. In addition, the individual in this manuscript has given written informed consent (as outlined in PLOS consent form) to publish these case details.

Nomenclatural Acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new names contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix “http://zoobank.org/”. The LSID for this publication is: urn:lsid:zoobank.org:pub:AC2A0339-382D-483D-874E-DB3188DEBE90. The electronic edition of this work was published in a journal with an ISSN, and has been archived and is available from the following digital repositories: PubMed Central, LOCKSS.

Material

All available material assigned to the new basal hadrosauroid taxon described in this paper was collected from three plaster field
New Basal Hadrosauroid from China

Osteological Comparisons and Cladistic Analysis

All known fossils of the new taxon are stored at the XMDFEC. The osteological description of the fossil material is conducted on the basis of detailed qualitative observations supplemented by relevant linear measurements. Comparative information on osteological features in other iguanodontian dinosaurs was obtained from direct observations and the literature. The phylogenetic position of the new taxon was inferred via the maximum parsimony analysis using the tree bisection reconnection (TBR) algorithm in the program TNT [33]. To assess the stability of the major clades within the Hadrosauridae that were found to include the new taxon described in this paper, bootstrap and Bremer decay values were calculated using the option “Resampling” with 1000 replicates and the script “BREMER.-RUN”, respectively.

Model-based Clustering

Model-based cluster analysis (MCA) is a comprehensive mathematical method for partitioning a dataset using the expectation-maximization (EM) algorithm, with the initial classification obtained from agglomerative hierarchical clustering and direct comparisons of potential partition models based on values of the Bayesian Information Criterion (BIC) [36,37]. Prieto-Márquez [3] used MCA, as implemented in the package Mclust of the statistical program R, to divide each of three morphology-based datasets into several discrete intervals with an optimal number of clusters. After this clustering, the intervals of the one-dimensional dataset were objectively transformed into independent but associated character states used for phylogenetic analysis [3]. We follow Prieto-Márquez’s application of MCA to evaluate the taxonomic status of the new hadrosauroid. Measurements derived from phylogenetic characters include linear measurement ratios and angles. The one-dimensional database of each measurement attribute is constituted by the measured values for most available hadrosaurid species and some iguanodontians outside of Hadrosauridae. However, the data of the new taxon are not allowed to participate in MCA. Prior to the application of MCA, the sample mean was used to represent the multiple values obtained from more than one specimens of a certain species. For some attributes referring to almost all hadrosaurid taxa except the newly erected one, the partition of the dataset implemented using MCA is generally aligned with the taxonomic separation between basal hadrosaurids and more derived hadrosaurids. These attributes are very significant for the validation of the new taxon probably representing a basal hadrosaurid dinosaur. They could therefore be selected for the quantitative analysis of the relevant data of this taxon. When the data of the new taxon lie in the intervals of selected measurement attributes, the total distribution of the data could test the potential taxonomic status of the taxon deduced from morphological comparisons among all hadrosaurid taxa to some extent.

Results

Systematic Paleontology

Dinosauria Owen, 1842 [38]
Ornithischia Seeley, 1887 [39]
Ornithopoda Marsh, 1881 [40]
Iguanodontia Dollo, 1880 [41] sensu Sereno, 1998 [11]
Ankylopollexia Sereno, 1986 [42] sensu Sereno, 1998 [11]
Styracosterna Sereno, 1986 [42] sensu Sereno, 1998 [11]
Hadrosauriformes Sereno, 1997 [43] sensu Sereno, 1998 [11]
Hadrosauridea Cope, 1870 [44] sensu You et al., 2003 [1]
Zhanghenglong gen. nov
urn:lsid:zoobank.org:act:0ADAC26E-2FFB-4276-8E93-E0FBF034D97A
Type species. Zhanghenglong yanghengensis sp. nov.
New Basal Hadrosauroid from China

Etymology. “Zhangheng” is derived from the full name of Mr. Zhang Heng, a famous Chinese astronomer, mathematician, inventor, poet, and statesman who lived during the Eastern Han Dynasty (AD 25–220) of China. The figure was born in the outskirts of Nanyang in southwestern Henan Province, quite close to the Xixia Basin. The word “long” is the direct transliteration of the Mandarin Chinese word that means dragon.

Diagnosis. As for the type and only species, Zhanghenglong yangchengensis sp. nov.

Holotype. XMDFEC V0013, an incomplete, disarticulated cranium, including the nearly complete right maxilla, as well as the partial right jugal and dentary.

Paratype. XMDFEC V0014, a partial, disarticulated postcranial skeleton, including five anterior-middle dorsal vertebrae (some of which lack the dorsal portion of the neural spine), fragments of the dorsal ribs, and the nearly complete right scapula and ulna.

Etymology. The specific name is derived from a large administrative region called Yangcheng that was established in the Spring and Autumn period (BC 770–403) of the Eastern Zhou Dynasty of China. This ancient administrative region included what is now southwestern Henan Province.

Locality and horizon. Zhoujiajou Village, about 5 km northeast of Sanlimiao Village where the Xixia Dinosaur Relics Park is located, Xixia Basin, Xixia County, Henan Province (Fig. 1A). The quarry probably occurs in the middle of the middle member (Unit 2) of the Majiacun Formation (Fig. 1B), and is thought to be the middle Santonian in age [31].

Diagnosis. Medium-sized hadrosauroid sauropod characterized by the following autapomorphies: strongly deflected posteroventrally posterior third of the maxilla relative to the anterior two thirds of the same element, and crowns of dentary teeth with both median and distally offset primary ridges. Also diagnosed by a unique combination of the following features: five teeth with both median and distally offset primary ridges. Also characterized by the following autapomorphies: strongly deflected posteroventrally posterior third of the maxilla relative to the anterior two thirds of the same element, and crowns of dentary teeth with both median and distally offset primary ridges. Also diagnosed by a unique combination of the following features: five teeth with both median and distally offset primary ridges.

Osteological Description

The material of *Zhanghenglong yangchengensis* consists of the holotype (XMDFEC V0013) and the paratype (XMDFEC V0014). Partial measurements of these specimens with relevant data comparisons are shown in the online documents (see Supporting Information S1). Reconstructions of the skull and skeleton of the new genus and species are proposed in Fig. 2.

Maxilla (XMDFEC V0013). The maxilla is asymmetrically subtriangular in lateral view, with the dorsal ramus moderately offset towards the posterior end of the bone (Fig. 3A, B). Although the tip of the dorsal ramus is broken away, it is clear that the maxilla is dorsoventrally high, the length of the bone measuring about 2.5 times the estimated height. Anterior to the large anterior foramen, the anteroventral process is slightly pendent. The edentulous anterior end of the anteroventral process is significantly shorter than that in some other non-hadrosaurid hadrosaurids, such as *Shuangmiaosaurus gilmorei* (LPM 0165). The lateral part of the anteroventrally inclined dorsal surface of the anteroventral process extends anteriorly from the large anterior foramen, and would have been exposed in the articulated skull, whereas the medial part forms most of the anterior portion of the articular surface for the premaxilla (Fig. 3C, D). As in other non-hadrosaurid hadrosauriforms such as *Jinzhouaurus yangi* (IVPP V12691), the large anterior foramen is elliptical and laterally exposed; it is located within the anterior half of the anterodorsal surface of the maxilla and just lateral to the articular surface for the premaxilla [3,26]. In contrast, the foramen is limited to the posterior half of the anterodorsal surface of the maxilla in hadrosaurids. For example, in lambeosaurines such as *Hypacrosaurus altispinus* (e.g., ROM 702) and *Parasaurolophus tubicen* (e.g., NMMNH P-25100), the large anterior foramen is displaced posterodorsally relative to its position in basal hadrosaurids, lying just anterior to the articular surface for the jugal, and is obscured by the premaxilla in lateral view. In *Zhanghenglong*, the dorsolateral edge of the anteroventral process is moderately inclined in lateral view, forming a 32° angle with the anterior third of the ventral margin of the maxilla. Dorsally, the articular surface for the posteroventral process of the premaxilla forms a subtriangular trough between the prominent lateral edge of the dorsal surface of the maxilla and an anteroposteriorly oriented ridge separating the premaxillary and vomerine facets (Fig. 3C). This trough gradually becomes dorsoventrally shallower and mediolaterally narrower as it extends posteriad towards the articular surface for the lacrimal.

Medial to the anteroventral process, the anterodorsal process of the maxilla is medially offset from the anterior third of the main part of the bone, showing the shape of a small, triangular, anteriorly directed prong. In dorsal view, it forms a 22° angle with the maxillary body, in contrast to the relatively low angle of 10° seen in *Gilmoreosaurus mongoliensis* (AMNH FARB 30653). The anterodorsal process projects anteroidally, and is slightly shorter than the more laterally positioned anterodorsal process, as in *Bactrosaurus johnsoni* (AMNH 6553) and *Protohadros byrdi* (SMU 74582). The condition contrasts with an elongate, raised anterodorsal process of the maxilla observed in hadrosaurines [3,45]. The ridge separating the premaxillary and vomerine facets extends anteriorly onto the anterodorsal process, so that the lateral part of the process contacts the premaxilla whereas the medial part meets the vomer (Fig. 3C, D). It represents the prominent, narrow, somewhat dorsally projecting lateral edge of the articular surface for the vomer. The dorsal margin of the ridge is weakly convex and slightly inclined anteriodially. It is angled more gently than the dorsolateral margin of the anterodorsal process. The part of the anterodorsal process contacting the vomer forms a thin, medially projecting shelf, below which perches the anterior portion of the medial wall of the maxilla that covers the anterior region of the dental battery.

The articular surface for the jugal is relatively low dorsoventrally along the lateral side of the dorsal ramus, a short distance above the anterior end of the ectopterygoid ridge. By contrast, the corresponding articular surface in hadrosaurids other than *Pararhabdodon isenensis* and *Tsintaosaurus spinorhinus* is dorsoventrally...
deep and in contact, at its ventral extremity, with the anterior end of the ectopterygoid ridge [46,47]. Although the dorsal ramus is not intact in the holotype of *Zhanghenglong*, this structure is sufficiently well preserved to confirm that the articular facet for the jugal has a subrectangular outline in lateral view as in other basal hadrosauroids. The jugal articular surface of the maxilla is composed of the dorsal portion on the lateral side of the dorsal ramus and the ventral portion located anterodorsal to the ectopterygoid shelf. The dorsal portion of this surface faces laterally, whereas the ventral portion faces dorsolaterally. The surface tapers anteriorly to a peak at the level of its dorsoventral midpoint, suggesting that the anterior process of the jugal would have tapered in a similar way, and is separated by an anteroventrally directed ridge from the articular surface for the lacrimal. The posteroventral corner of the articular surface for the jugal forms a posterolaterally directed prominence, which is preserved in contact with a small fragment that may represent part of the jugal. Above the prominence, the posterior margin of the articular surface for the jugal is built up into a slight, lateroventrally oriented ridge. The maxilla meets the lacrimal laterally and dorsally, and forms the articular surface for the latter that occupies the anterodorsal region of the lateral side of the dorsal ramus, as well as a stretch of the mediolaterally narrow dorsal side between the posterior end of the articular surface for the premaxilla and the anterodorsal apex of the dorsal ramus. It is more likely that the jugal did not strongly interfere with the laterally visible maxilla-lacrimal joint in the fully articulated skull. The articular surface for the lacrimal abuts the more posteroventrally positioned articular surface for the jugal along the lateral side of the dorsal ramus, as in many basal hadrosauroids. By contrast, in some basal hadrosauriforms such as *Altirhinus kurzanoi* (e.g., PIN 3386/7), the finger-shaped articular facet for the jugal is strongly offset posteroventrally from the dorsal ramus, where the articular facet for the lacrimal occurs.

A large, oval foramen is situated anterodorsal to the ectopterygoid ridge and just below the anteroventral margin of the articular surface for the jugal. The condition is apparently more similar to hadrosaurs, in which the posteriormost one or two maxillary foramina are enlarged and adjacent to the ventral extremity of the articular facet for the jugal when a series of maxillary foramina with the total number less than seven are arranged in an anterodorsally oriented row and dorsally positioned. In *Zhanghenglong*, four small additional foramina are also laterally visible, forming an irregular horizontal row near the
ventral margin of the lateral side of the maxilla; the first two of these small foramina are positioned far anterior to the others. Typical basal hadrosauroids resemble Zhanghenglong in having a ventrally positioned, nearly horizontally aligned row of small, irregularly spaced foramina. Therefore, Zhanghenglong shows similarities to both hadrosaurids and typical basal hadrosauroids in the configuration of the foramina on the lateral surface of the maxilla. This condition in Zhanghenglong could be interpreted as an intermediate stage. The total count of five foramina on the lateral surface of the maxilla of Zhanghenglong is unusually low for other basal hadrosauroids with the exception of Telmatosaurus transsylvaniaicus (FGGUB R1010, three or four maxillary foramina) [27] and Tethyshadros insularis (SC 57021, three maxillary foramina) [28].

As in other hadrosaurids, the posterior third of the maxilla bears the palatine and pterygoid processes medially, the ectopterygoid ridge laterally, and the ectopterygoid shelf in between. Interestingly, the part of the maxilla is strongly deflected posteroventrally, forming an angle of 43° with the anterior two thirds of the bone. This feature is comparable to, although not as same as, the strongly curved ventrally posterior half of the maxilla seen in Shuangmiaosaurus gilmorei [23]. However, the possibility that this downturning of the maxilla in Zhanghenglong is the result of distortion cannot be excluded. Posteroventral to the articular surface for the jugal, the ectopterygoid shelf is transversely broad and flat, and extends laterally to form a prominent lip-shaped ectopterygoid ridge. The ectopterygoid ridge is very robust and straight along its entire length; it is approximately 36% as long as the maxillary body. Such a ridge bears a distinct resemblance to the equivalent structure in hadrosaurids such as Edmontosaurus regalis (e.g., CMN 2289) and Tsintaosaurus spinorhinus (e.g., IVPP V725). In contrast, the slightly shorter ectopterygoid ridge is weakly developed anteriorly but becomes dorsoventrally thick posteroventrally in basal hadrosauroids [3], such as Lennesovia transoxiana (CCMGE 579/12457). In lateral view, the ectopterygoid shelf and ridge are moderately inclined posteroventrally even relative to the posterior portion of the maxilla, being deflected downwards at an angle of 16° rather than nearly horizontal as in most hadrosaurids [3,48]. The palatine and pterygoid processes are too eroded to provide detailed morphological information. They protrude dorsally from the medial margin of the ectopterygoid shelf, and respectively form an anterior contact with the palatine and a posterior contact with the pterygoid.

The medial surface of the maxilla is perfectly flat, and is pierced by a dorsally convex row of round nutrient foramina that are typical of hadrosaurids (Fig. 3B). The nutrient foramina are limited to the dorsal half of the maxilla. The number of nutrient foramina is consistent with that of maxillary tooth positions. The dental battery of the maxilla includes a minimum of 27 tooth positions. As preserved, the occlusal surface is dorsally convex because of the downward curvature of the posterior third of the maxilla, and is also inclined to face ventromedially.

**Jugal (XMDFEC V0013).** The jugal is a triradiate bone that contributes to the ventral margins of the orbit and the infratemporal fenestra (Fig. 4A, B). As seen in other iguanodontians, it consists of the anterior process, ascending postorbital process, and posterior process, as well as two dorsoventrally constricted necks [2,49]. This element is mediolaterally compressed and laterally convex from its anterior contact with the
As in basal hadrosaurids such as *Equijubus normani* (IVPP V12534) and *Xiaosuolong yuelunai* (GSGM-F00001), the anterior process is slightly expanded dorsoventrally relative to the anterior neck. It is too damaged to be confidently reconstructed, but probably tapered anteriorly. The posterodorsal margin of the anterior process is sufficiently high to indicate that the process does not strongly expand dorsally. By contrast, in most hadrosaurids such as *Prosaurolophus maximus* (e.g., TMP 84.1.1) and *Corythosaurus casuarius* (e.g., ROM 1933), the anterior process of the jugal is comparatively high relative to the anterior neck of the bone due to a pronounced, strongly recurved, subtriangular dorsal expansion of the process. The lateral side of the anterior process is relatively flat, whereas the medial side bears a markedly concave, medioventrally directed articular facet for the maxilla. This concave facet is ornamented with numerous faint striations that radiate anterodorsally and anteriorly from its posterior margin. The medial face of the anterior process is bounded posteriorly by a crescent-shaped articular facet for the palatine (Fig. 4B). A similar feature is present in all hadrosaurids, in which a dorsoventrally elongate, arched articular surface for the palatine occurs along the posterodorsal edge of the medial side of the jugal anterior process [49,50]. However, the condition observed in *Zhanghenglong* strongly contrasts with that in most non-hadrosaurid iguanodontians, in which a dorsoventrally narrow, strip-like facet for articulation with the palatine is situated on the dorsal border of the medial face of the anterior process [51,52]. Anterodorsal to the palatine articular surface of the jugal, the dorsal edge of the anterior process forms a narrow carina for contact with the lacrimal. However, only the posteriormost part of the carina remains intact. This configuration is slightly protuberant dorsally so as to meet the posteroverentral sulcus of the lacrimal. The articular facet for the maxilla is proportionally higher, with a relatively wide angle of 65° between its posterodorsal and posteroverentral borders, than the anteroposteriorly elongate but dorsoventrally narrow equivalent facet seen in *Bactrosaurus johnsoni* (e.g., SBDE 95E5/7) and *Tianjinia xingyiensis* (PMU R240). In dorsal view, the anterior process abruptly becomes mediolaterally narrow posteriorly from the posterior margin of the articular surface for the maxilla to contact the anterior neck.

The anterior neck represents a modest dorsoventrally deep constriction of the jugal, the shallowest region of the neck being about 73% as dorsoventrally deep as the anterior process. The dorsal margin of the anterior neck is slightly concave, forming a bridge from the dorsal carina of the anterior process to the base of the postorbital process. The posterior neck is moderately downturned posteriorly, forming an angle of 143° with the anterior neck, and the posterior neck is also slightly dorsoventrally shallower than the anterior one. The postorbital process projects dorsally, and is gently tilted posteriorly. The dorsal part of this process, which would have contacted the ventral ramus of the postorbital dorsally and laterally, is not preserved. As in other iguanodontians, the postorbital process is very robust at the base, and gradually tapers dorsally. Much of the posterior process of the jugal, including the quadrate jugal flange, is broken away. If intact, the posterior process would have projected posterodorsally and formed the ventral part of the posterior margin of the infratemporal fenestra. The shape of the preserved part of the posterior process suggests that this posterodorsal projection would have been more strongly angled posteriorly than the postorbital process. A small part of the posteroverentral margin of the posterior process is preserved. It is very likely that this margin is only very shallowly concave, as in other basal hadrosaurids such as *Bactrosaurus johnsoni* (e.g., AMNH 6396) and *Plesiadapis hyrbi* (SMU 74582). The condition differs significantly from the deep concavity along the posteroverentral margin of the jugal posterior process observed in *Gephyrosaurus monumentensis* (e.g., RAM 6797) and *Kritosaurus navajovius* (e.g., AMNH 5799). The ventral half of the infratemporal fenestra, bounded by the postorbital process, posterior process, and posterior neck of the jugal, clearly has a deep, somewhat U-shaped outline in lateral view. The anteroposterior width of the infratemporal fenestra is slightly less than that of the orbit, which is judged from the lateral profile of the bone. Unlike other basal hadrosaurids such as *Tethyshadros insularis* (SC 57021) and *Eolambia caroljonesa* (e.g., CEUM 52204), the ventral edge of the jugal bears a strong embayment whose depth is equal to about 60% of the minimum height of the posterior neck (Fig. 4A, B).

**Dentary (XMDFEC V0013).** The massive right dentary is well preserved and undistorted in XMDFEC V0013. This bone consists of an elongate dentary ramus, a slightly eroded tooth battery, and a nearly vertical coronoid process lacking the dorsal apex (Fig. 5A, B). There are 26 vertical tooth families visible medially along the long axis of the tooth battery. A series of nutrient foramina, located at half height of the medial side of the dentary ramus, are arranged in a slightly convex ventrally row. Each alveolar position strictly corresponds to one of these
Accessory nutrient foramina at the base of the tooth battery (Fig. 5B). The occlusal surface of the dentary is difficult to thoroughly reconstruct because the teeth are not complete anteriorly. However, it is clearly directed dorsolaterally, and may have had a dorsally convex curvature matching the ventrally concave curvature of the occlusal surface of the maxilla. In contrast, the nearly straight, dorsolaterally-facing occlusal surface of the dentary tooth row is very common among most other iguanodontians such as *Jinzhouaurus yangi* (IVPP V12691) and *Parasaurolophus walkeri* (ROM 768).

Anterior to the first tooth lies a particularly short edentulous region that is the diastema, whose length (42 mm) is only about 17% of the entire length of the tooth battery (247 mm). The diastema gently deflects anteroventrally at a low angle relative to the horizontal posterior part of the dentary ramus. The anterior end of the bone curves lingually and also twists progressively so that the outer surface of the anteriormost part of the dentary is ventrally directed, forming a symphysial process that would have contacted the predentary anterodorsally and the contralateral dentary along the sagittal plane. The contact between the symphysial processes of the two dentaries would have represented the posterior part of the mandibular symphysis, and would have appeared ventrally convex in anterior view if the paired dentaries were placed in articulation with the predentary removed. The articular surface for the predentary, located just anteromedially to the diastema, occurs along the anterior margin of the symphysial process. As in other basal hadrosaurids, the posteroventral part of the articular border for the predentary forms a rather steep slope in lateral or medial view, as it sharply descends towards the slightly dorsomedially concave platform of the symphysial process [3].

The angle between this steep slope and the ventral margin of the posterior portion of the dentary ramus is about 70°. The symphysial process is clearly wider mediolaterally than the main body of the dentary ramus, with the ratio of 1.52 between the mediolateral breadth of the former and that of the latter. In dorsal view, the medial margin of the symphysial process slightly diverges from the lateral side of the dentary at a relatively low angle of approximately 13° (Fig. 5C). The anteromedial corner of the symphysial process bears an oval, anteroventrally-facing fossa for articulation with the ventral median process of the predentary [2]. Specifically, the anterior region of the dentary ramus is not strongly deflected anteroventrally, resembling the plesiomorphic condition present in non-hadrosaurid hadrosauriforms such as *Probactrosaurus gobiensis* (PIN 2232/42-1) [12], *Jinzhouaurus yangi* (IVPP V12691) [26], and *Gilmoreosaurus mongoliensis* (AMNH FARB 30654) [39].

The main body of the dentary ramus is pierced laterally by a number of irregularly distributed small foramina of variable size (Fig. 5A). Its lateral surface is gently convex dorsoventrally, and bears numerous anteroposteriorly directed striations. Medially, the Meckelian groove is situated at the posteroventral corner of the dentary ramus, wedging anteriorly along the ventromedial border of the posterior part of the bone. The groove tapers anteriorly and terminates near the anteroposterior midpoint of the ventromedial margin of the dentary ramus (Fig. 5B). The posterior region of the Meckelian groove represents the relatively deep anterior portion of the mandibular adductor fossa. Dorsal to the posterior region of the Meckelian groove and posterior to the tooth battery, the lateral surface of the dentary bears a subtriangular articular facet for the splenial. In dorsal view, the long axis of the tooth battery is nearly parallel with the lateral side of the dentary ramus, a feature common among hadrosaurids [3,53]. However, the long axis of the tooth battery and the lateral side of the dentary ramus diverge from each other towards the coronoid process in most basal hadrosaurids, including *Eolambia caroljonesa* [29,54] and *Shuangmiaosaurus gilmorei* [23]. The coronoid process is not intact owing to the lack of the dorsal apex, whereas it exhibits typical morphological features of basal hadrosaurids: the coronoid process is

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**Figure 5. Dentary of *Zhanghenglong yangchengensis*.** Right dentary (XMDFEC V0013, holotype) in lateral (A), medial (B), dorsal (C), and posterior (D) views. doi:10.1371/journal.pone.0098821.g005
nearly perpendicular to the dorsal margin of the dentary rami; a
dorsoventrally elongate, weakly developed ridge occurs on the
medial side of the coronoid process; the posteriormost end of the
dentary tooth row does not exceed the posterior margin of the
coronoid process in median view. The coronoid process is also well
offset laterally from the tooth row, as in other hadrosaurids [2,3,12].
There is a transversely broad and dorsoventrally shallow
cavity between the tooth row and the base of the coronoid
process. In posterior view, the posterior surface of the coronoid
process bears a deep, longitudinally elongate trough that extends
ventrally to the base of the mandibular adductor fossa (Fig. 5D).
The trough probably represented an area of muscle attachment in
the living animal.

**Maxillary teeth (XMDFEC V0013).** The right maxilla of
the holotype retains 27 tooth families, representing the full
complement of tooth positions. Some of the tooth families are
partially preserved. In lateral view, the enameled labial surface of
the crown of each functional tooth is apicobasally elongate,
symmetrical and subtriangular, with mesial and distal margins that
converge dorsally towards the narrowest base of the crown (Fig. 6A).
Unworn replacement teeth are estimated to have measured approximately 35 mm in apicobasal height, although no complete examples are visible along the ventral border of the
maxilla. In the middle part of the tooth row, the maximum
mesiodistal width of each tooth is about 10 mm. The following
features of maxillary teeth observed in XMDFEC V0013 are
typical of most hadrosaurids: the tooth crown is labially
ornamented with one primary ridge and one weaker secondary
ridge; the robust primary ridge is mesiodistally centered and
buccally prominent, extending along the entire apicobasal height
of the crown; adjacent to the primary ridge, a shortened secondary
ridge runs longitudinally throughout the distal half of the labial
side of the crown. By contrast, the primary ridges of the maxillary
teeth are slightly distally offset in *Equijubus normani* [1], *Xiaosaurus
yuehui* [21], and *Fishousaurus yangi* [26]. Interestingly, the median
primary ridges of the maxillary tooth crowns in *Zhanghenglong* are
nearly straight in some teeth but slightly sinuous in others (Fig. 6A).
This condition is very similar to that in some hadrosaurids such as
*Corythosaurus intermedius* (e.g., ROM 776) and *Beaufortosaurus
canaensis* (e.g., CMN 8893). Mammilliform denticles occur along
the mesial and distal margins of the crown (Fig. 6A). These
marginal denticles are well-developed and equal in size. As in
some derived basal hadrosaurids such as *Shuangmiusaurus gilmorei*
(LPM 0165), each alveolus has only one functional tooth for most
of the tooth row, with the sporadic presence of two functional teeth
in the middle of the occlusal surface [14,53]. The worn surface of
each functional tooth is slightly concave ventrally and strongly
oblique laterocentrally in anterior view.

**Dental battery (XMDFEC V0013).** The dental battery
consists of 26 vertical tooth families. For most of the dental
battery, two or three teeth are arranged dorsoventrally in each
alveolus. There is one exception to the preceding condition: the 14th
and 16th alveoli of the tooth row both bear four teeth, namely
two replacement teeth and two functional teeth. Like the
maxillary dentition, the dental occlusal surface holds one worn
tooth per alveolus in its anterior and posterior regions. Not
surprisingly, the number of functional teeth in each alveolus keeps
one or increases to two along the midsection of the tooth row, as in
other basal hadrosaurids. Significantly, the 17th tooth position of
the dental battery shows three functional teeth that contribute to
the occlusal surface, similar to the condition seen in more derived
hadrosaurids. It also accommodates four teeth. As is common for
all hadrosaurids, the enameled lingual side of each unworn tooth
crown is diamond-shaped and bisected by a conspicuous primary
ridge [2,4]. The primary ridge is very straight, crossing longitudi-
nally the entire crown (Fig. 6B). For about 40% of all dentary
teeth, the primary ridge is located along the midline of the lingual
side of the crown, whereas in other dentary teeth, the primary
ridge is slightly offset distally from the midline of the lingual side
of the crown. The condition in *Zhanghenglong* may represent the
intermediate form of the morphological change in the position of
the primary ridge of the dentary tooth crown from basal
hadrosaurids to more derived hadrosaurids. In most basal
hadrosaurids such as *Bactrosaurus johnsoni* (AMNH 6553) and
*Tethysaurus insularis* (SC 57026), the primary ridge of each dentary
tooth is distally offset from the midline of the corresponding crown
[1–3]. By contrast, in more derived hadrosaurids, most of the
primary ridges of the crowns in the dentary tooth row are
mesiodistally centered [2,3,47]. Although the enamel layer is
incompletely preserved, evidence of faint ridges is apparent on the
mesial half of the lingual side of each tooth crown (Fig. 6B).
For each discernable tooth, one or two dorsoventrally elongate faint
ridges are situated very close to the mesial margin of the crown.
Each faint ridge is much thinner and shorter than the primary
ridge. Owing to the highly eroded condition, no papillae are
identified from the dentary dental battery. In lingual view, the
tooth size progressively increases towards the middle region of the
dental battery. The dentary tooth crowns have an approximate
height/length ratio of 2.36. Similar to the typical growth pattern of
the dentary dentition in iguanodontians, the teeth in the same row
along the long axis of the dental battery progressively approach the
occlusal surface posteriorly, and appear to erupt from back to
front; alternate tooth families in the dental battery are subject to
the same replacement cycle [55]. Each alveolus is defined
anteriorly and posteriorly by two vertical dental laminas.

**Dorsal vertebrae (XMDFEC V0014).** Five anterior-middle
dorsal vertebrae are preserved in the plastron field jackets,
containing the first dorsal vertebra (D1) and the fourth to seventh
dorsal vertebrae (D4–D7). Linear measurements of these bones are
shown in Table 1. D4 possibly underwent slight post-depositional
deformation due to transverse crushing, and the measured height
of its centrum is likely to be greater than the actual dorsoventral
depth of the structure.

As in some iguanodontian taxa in which the cervical and dorsal
series are associated together, D1 shows the intermediate
morphology between posterior cervical vertebrae and typical
anterior dorsal vertebrae. It cannot be markedly differentiated
from posterior cervical vertebrae in the following aspects: the
centrum is strongly opisthocoelous in lateral view, and bears
dorsoventrally short, oval anterior and posterior articular surfaces;
the wide prezygapophysis extends dorsolaterally, and occupies
the medial half of the slightly arched transverse process; the elongate
postzygapophysis moderately arches posterolaterally and dorsally
from the top of the neural arch; the neural spine is relatively short
dorsoventrally (Fig. 7A–C). The vertebra also has some osteolog-
ical features that are common for the dorsal series, such as
the large, dorsomedially-facing articular facet of the prezygapophysis
that is entirely higher than and located dorsolateral to the neural
canal in anterior view, the gently concave parapophysis on the
anterolateral side of the base of the neural arch, and the slightly
shorter anteroposteriorly centrum (Fig. 7A, C). In anterior view,
the centrum of D1 is about 1.6 times as tall as the paired neural
arches; its posterior articular surface is slightly wider transversely
than the anterior one. The lateral side of the centrum has
prominent, broadly arcuate anterior and posterior edges, and is
strongly concave anteroposteriorly in ventral view. The ventral
half of the lateral side of the centrum is pierced by two small, oval
foramina that face laterocentrally. The transversely narrow ventral
side of the centrum is essentially flat, lacking any trace of the keel-like ridge. Dorsal to the centrum, the elliptical neural canal is surrounded predominantly by indistinguishably fused neural arches. The pedicles of paired neural arches gradually narrow dorsoventrally towards the sagittal plane, so that their ventromedial corners are triangular in shape and separated by the slightly concave dorsal surface of the centrum in the middle. Each neural arch measures 31 mm in total length, about half the anteroposterior length of the centrum. Only the right transverse process is accessible in D1. It projects dorsolaterally from the dorsolateral corner of the right neural arch to form the prezygapophysis, and nearly keeps horizontal along its lateral half (Fig. 7A, B). The angle between the long axis of the lateral half of the transverse process and that of the medial prezygapophysis is approximately 140°. The robust diapophysis for articulation with the tuberculum of the dorsal rib is located at the lateral extremity of the elongate transverse process. Dorsally, the paired postzygapophyses approach the relatively high neural spine with a short distance, and widely diverge posteriorly from the dorsoventral midpoint of the latter. Each postzygapophysis has a large, oval articular surface that faces ventrolaterally. The hooked neural spine of D1 is mediolaterally compressed and slightly tilted posterodorsally, which is about 1.2 times longer than the postzygapophysis. In contrast, the neural spine of D1 is proportionally shorter in some basal hadrosauroids such as *Eolambia caroljonesa* (CEUM 52173) and *Bactrosaurus johnsoni* (e.g., SBDE 95E5/15). In lateral view, the neural spine of D1 in *Zhanghenglong* tapers dorsally, and terminates into a blunt point (Fig. 7C).

The other four dorsal vertebrae in the paratype represent an incomplete anterior-middle dorsal series probably referable to D4–D7. The morphological features of these four dorsal vertebrae are very similar but distinct significantly from those of D1 (Fig. 8A–L). The centra are weakly opisthocoelous or nearly amphiplatyan in lateral view. They are anteroposteriorly longer than transversely wide and dorsoventrally high, and remain heart-shaped anteriorly and posteriorly. Similar to the condition observed in D1, two or three special foramina pierce the strongly concave anteroposteriorly lateroventral surface of each centrum. Ventrally, the left and right lateral sides of each centrum gradually converge downwards to form the median keel-shaped prominence. For each one in D4 to D7, vertical neural arches rise dorsally from laterodorsal regions of the centrum and partially enclose the circular neural canal. They are proportionally higher than those of D1. The average dorsoventral height of the paired neural arches in D4 to D7 is approximately 65% the average dorsoventral height of the corresponding centra. The strongly concave parapophysis has migrated dorsally to the dorsolateral side of the neural arch, and is located just below the base of the transverse process. The elongate transverse processes, which no longer bear the prezygapophyses medially, extend posterodorsally and laterally from the neural arch. They are straight and subtriangular in cross-section, and bear relatively blunt distal diapophyses. In lateral view, the base of the transverse process is sandwiched between the reduced prezygapophysis and postzygapophysis. In either one of D4 to D7, the truncated prezygapophyses arise from the anterodorsal region of the fused neural arches, and are placed more medially.

### Table 1. Measurements for the anterior dorsal vertebrae (D1 and D4–D7) of *Zhanghenglong* (in mm).

| Dorsal vertebra (XMDFEC V0014) | D1 (in mm) | D4 (in mm) | D5 (in mm) | D6 (in mm) | D7 (in mm) |
|-------------------------------|------------|------------|------------|------------|------------|
| 1. anteroposterior length of the centrum | 61 90 83 76 78 |
| 2. dorsoventral height of the centrum | 70 71 73 75 74 |
| 3. mediolateral width of the centrum | 78 64 70 72 73 |
| 4. proximodistal length of the transverse process | 85 98 114 95 106 |
| 5. anteroposterior width of the neural spine | 33 53 42 40 45 |
| 6. dorsoventral height of the neural arch | 30 32 36 40 42 |
| 7. anteroposterior length of the neural arch | 27 50 45 43 44 |

The robust diaphysis for articulation with the tuberculum of the dorsal rib is located at the lateral extremity of the elongate transverse process. Dorsally, the paired postzygapophyses approach the relatively high neural spine with a short distance, and widely diverge posteriorly from the dorsoventral midpoint of the latter. Each postzygapophysis has a large, oval articular surface that faces ventrolaterally. The hooked neural spine of D1 is mediolaterally compressed and slightly tilted posterodorsally, which is about 1.2 times longer than the postzygapophysis. In contrast, the neural spine of D1 is proportionally shorter in some basal hadrosauroids such as *Eolambia caroljonesa* (CEUM 52173) and *Bactrosaurus johnsoni* (e.g., SBDE 95E5/15). In lateral view, the neural spine of D1 in *Zhanghenglong* tapers dorsally, and terminates into a blunt point (Fig. 7C).
and anteriorly than those of D1. The elliptical articular facet of each prezygapophysal process is dorsoventrally and mediolaterally directed and steeply inclined dorsolaterally, with its long axis dorsoventrally-ventromedially oriented and slightly deflected posteriorly. As in other hadrosauroid taxa, the anterior margin of the prezygapophysal articular facet is continuous with the anterior lamina of the transverse process. The paired postzygapophyses are slightly longer than the corresponding prezygapophyses; they project posterodorsally from the posteroventral corner of the neural spine. Like D1, the articular surfaces of the postzygapophyses in D4 to D7 are also ventrolaterally-facing and oval in shape. No neural spines are completely preserved in D4–D7. These partial neural spines are strongly canted posteriorly and mediolaterally compressed, showing subrectangular lateral profiles. Significantly, the neural spine of D5 is greatly elongate. It is about 4.3 times as tall as the corresponding centrum (Fig. 8D–F). The dorsoventrally high neural spines of anterior dorsal vertebrae can be also observed in some other iguanodontians, such as Ouranosaurus nigeriensis [51], Saurolophus angustirostris [56], and Tintornasaurus spinorhinus [57]. Except for D1, the preserved anterior-middle dorsal series (D4–D7) reveals the following trends of morphological change in the dorsal series which are very common for other hadrosaurids: the strongly tilted posteriorly neural spine gradually becomes more vertical towards the sacrum; the posteriorly and laterally directed transverse process progressively tends to project laterally towards the sacrum; the neurocentral suture and parapophysis become progressively higher posteriorly, and are accompanied by the elevation of the postzygapophysis; the slightly opisthocoelous centrum is transformed into the amphiplatyan centrum moving posteriorly (Fig. 8A–L) [57,58].

Scapula (XMDFEC V0014). The scapula is a proximodistally elongate, blade-like bone that is slightly convex laterally so as to follow the general contour of the lateral side of the rib cage (Fig. 9A, B). The proximal end of the scapula is more expanded mediolaterally and dorsoventrally than the distal blade of the bone, and bears the coracoid facet and glenoid cavity along its anterior margin. The anteriorly-facing coracoid facet is rugose, gently concave and oval in shape. The facet is transversely wider and proximodistally shallower than the glenoid cavity, and is located just anterodorsal and slightly medial to the latter. The lunate glenoid cavity forms a relatively deep embayment that is moderately concave anteroventrally. It is supported ventrally by a stout proximoventral buttress. The enclosed rim of the glenoid cavity is considerably thinner than that of the coracoid facet. The glenoid cavity is 110% as dorsoventrally tall as the coracoid facet; in lateral view, these two articular surfaces meet at an angle of 145°. As in some basal hadrosaurid species such as Tianus sinensis (PMU R241) and Bactrosaurus johnsoni (e.g., AMNH 6553), the rod-shaped acromion process is anteroposteriorly directed and slightly recurved, where it slightly extends laterally from the proximoventral border of the scapula (Fig. 9C); the anterior end of the acromion process is very robust and oriented anterodorsally (Fig. 9A). However, in hadrosaurines, the acromion process is unbent and relatively slender along its entire length [47,59]. The proximal region of the scapula is broadly U-shaped in anterior view (Fig. 9C). Between the acromion process and the proximoventral buttress is a deep, subtriangular depression on the lateral surface of the proximal region of the bone. This depression may have served as the attachment area of the supracoracoideus muscle [60]. The medial surface of the proximal end of the scapula is strongly convex dorsoventrally and marked by fine anteroposteriorly oriented striations.

Figure 7. First dorsal vertebra of Zhanghenglong yangchengensis. D1 (XMDFEC V0014, paratype) in anterior (A), posterior (B), and right lateral (C) views. doi:10.1371/journal.pone.0098821.g007
of the scapula is bounded by nearly parallel dorsal and ventral borders in all lambeosaurine species except *Arenysaurus ardevoli* (MPZ 2008/333a–b), *Tsintaosaurus spinorhinus* (IVPP V725), and *Parasaurolophus cyrtocristatus* (FMNH P27935).

**Ulna (XMDFEC V0014).** The ulna, which is one of the longest components of the forelimb, does not differ markedly from that seen in other hadrosauroids. The proximal end of the ulna is much more expanded mediolaterally than the distal end of the element. It consists of two pronounced processes and one subconical olecranon (Fig. 9D, E). Just below the olecranon, these two subtriangular processes, together with the proximal fourth of the shaft, partially enclose a mediolaterally wide and anteroposteriorly shallow concavity for reception of the proximoposterior portion of the radius (Fig. 9D). The larger medial process is anteromedially directed, whereas the weakly developed lateral process protrudes anterolaterally. The mediolateral width of the medial process is 55% greater than that of the lateral process. The stout olecranon projects dorsally from the proximoposterior region of the ulna. It is mediolaterally broad and anteroposteriorly constricted, and exhibits an elliptical outline in proximal view. The diaphysis of the ulna is straight in both anterior and posterior views, with a slightly sigmoid lateral or medial profile. The proximal end of the bone has a V-shaped cross-section that opens anteriorly. However, the distal outline of the element is subtriangular and medially tapering. Situated posterior to and partially shrouded by the medial process, a wedge-shaped, proximodistally directed groove occurs along the proximal half of the medial side of the ulnar shaft (Fig. 9E). This distinct groove

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**Figure 8. Anterior-middle dorsal vertebrae of *Zhanghenglong yangchengensis*.** Four dorsal vertebrae probably representing D4–D7 orderly (XMDFEC V0014, paratype) in anterior (A, D, G, J), posterior (B, E, H, K), and left lateral (C, F, I, L) views.

doi:10.1371/journal.pone.0098821.g008
becomes progressively narrower and shallower towards the mid-shaft, and possibly serves as the attachment area of the pronator quadratus muscle. A shallowly concave, triangular facet for articulation with the posterodistal region of the radius is present on the anteromedial surface of the distal third of the ulna (Fig. 9D). The bone has a smooth and convex distal surface that contacts the carpus. Compared to *Gilmoreosaurus mongoliensis* [53], the ulna of *Zhanghenglong* is relatively slender, with the proximodistal length/mediolateral width at mid-shaft ratio of 8.60.

**Discussion**

**Confirmation of the Taxonomic Status in Light of Morphology**

*Zhanghenglong yangchengensis* exhibits a series of plesiomorphic features typical of non-hadrosaurid hadrosauroids, including a large anterior foramen limited to the anterior half of the anterodorsal surface of the maxilla, a truncated and relatively low anterodorsal process of the maxilla, less than 30 tooth positions in the maxillary dental battery, a slightly expanded dorsoventrally anterior process of the jugal relative to the anterior neck of the bone, a nearly vertical coronoid process of the dentary, the dentary with less than 30 alveoli, the posterior terminus of the dentary tooth row overlapping the posterior margin of the coronoid process in medial view, one or two functional teeth in each alveolus of the dentary, and a strongly dorsoventrally-constricted scapular neck [1–3,12,53,54]. Therefore, most of the material available for this genus and species unambiguously pertains to a non-hadrosaurid hadrosauroid.

*Zhanghenglong yangchengensis* also possesses some features rarely reported in basal hadrosauroids but observed in more derived hadrosaurids: the maxillary body is dorsoventrally tall; the elongate ectopterygoid ridge of the maxilla is straight and well-developed along its entire length; a lunate articular facet for the palatine occurs along the posterior border of the medial side of the jugal anterior process; the ventral edge of the jugal is strongly concave, forming a dorsoventrally deep embayment; the long axis of the dentary tooth row runs parallel with the lateral side of the dentary ramus; the median primary ridge of each maxillary tooth crown is either straight or slightly sinuous; the dentary shows a maximum of 4 teeth for each alveolus; the dorsal margin of the scapular blade is slightly convex [2,3,9,47]. This taxon displays a unique combination of plesiomorphic and derived hadrosaurid features, revealing morphological transitions and the mosaic pattern of trait evolution from basal hadrosauroids to more derived hadrosaurids.

Among the diagnostic characters of *Zhanghenglong yangchengensis*, a couple of transitional features between basal hadrosauroids and more derived hadrosaurids are particularly significant, including five maxillary foramina consisting of four small scattered ones arranged anteroposteriorly in a row and a large one close to the ventral extremity of the articular surface for the jugal, as well as dentary tooth crowns ornamented with both median and distally offset primary ridges. For the feature of the maxilla, it is not only reminiscent of basal hadrosauroids in which the maxillary foramina are ventrally positioned and anteroposteriorly aligned discontinuously on the lateral side of the element (Fig. 10A–C), but also apparently similar to hadrosaurids in which the posteriormost one or two of the dorsally positioned, closely aligned anterodor-
sally maxillary foramina are enlarged and located directly beneath the articular surface for the jugal (Fig. 10D–F). This configuration resembles the condition seen in *Trachyrhinos insularis* (SC 57021) and *Telmatosaurus transoxianus* (FGGU/B R1010). The other feature may represent the intermediate condition between the plesiomorphic and derived characters of hadrosaurids with regard to the position of the primary ridge of the dentary tooth crown. In most basal hadrosaurids, the primary ridge of each tooth in the dentary dental battery is located distal to the midline of the lingual side of the crown (Fig. 11A–C). Nevertheless, the median primary ridge for all or most of the teeth in the dentary dental battery is definitely characteristic of more derived hadrosaurids (Fig. 11D–F). These two conditions define two different character states used in some phylogenetic analyses of Hadrosauridae (e.g., character 39 in [1], character 6 in [3], and character 7 in [59]).

In summary, *Zhanghenglong yangchengensis* is probably a non-hadrosaurid hadrosaurid based on a series of plesiomorphic features present in this taxon. The new genus and species significantly differs from other known members of Hadrosauridae in having two distinct autapomorphies and a unique combination of features. Despite the confluence of some plesiomorphic features typical of non-hadrosaurid hadrosaurids, *Zhanghenglong* possesses some derived characters seen in hadrosaurids, as well as two transitional features that are intermediate between the corresponding plesiomorphic and derived characters of hadrosaurids. *Z. yangchengensis* may therefore represent a relatively derived non-hadrosaurid hadrosaurid, and is thought to be one of the closest relatives to Hadrosauridae.

**Statistical Examination using the MCA Method**

To test the potential taxonomic status of *Zhanghenglong yangchengensis*, a quantitative analysis of one-dimensional measurement data of the taxon was carried out by means of measurement attributes (MA) selected from phylogenetic characters of hadrosaurids via MCA (see Supporting Information S2). Approximately 21% of the phylogenetic characters coded here (73 characters in Supporting Information S3) could be confidently considered to be the measurement attributes for MCA. The dataset of each measurement attribute consists of the values of almost all hadrosaurid species except *Z. yangchengensis*, as well as those of three iguanodontians closely related to Hadrosaurinae (Iguanodon bernissartensis, Mantellisaurus alikeri, and Ouranosaurus nigeriensis). Given that *Z. yangchengensis* is inferred to be a derived non-hadrosaurid hadrosaurid, we have chosen some particular measurement attributes for quantitative testing. For each one of these attributes, the subsets yielded by the partition of the database using MCA reveal a distinct quantitative disparity between basal hadrosaurids and more derived hadrosaurids. Some of the selected measurement attributes are available for *Z. yangchengensis*; they are referable to the following phylogenetic characters in Supporting Information S3: the ratio between the maximum dorsoventral height and anteroposterior length of the maxilla (character 111; MA1), ratio between the anteroposterior length of the ectopterygoid shelf and that of the maxillary tooth row (character 112; MA2), angle between the ectopterygoid ridge and the ventral margin of the posterior portion of the maxilla (character 113; MA3), ratio between the anteroposterior length of the edentulous region and that of the tooth row of the dentary (character 38; MA4), angle between the mediolateral border of the dentary symphysial process and the lateral surface of the dentary ramus (character 44; MA5), and ratio between the dorsoventral depth of the scapular neck and the maximum dorsoventral height of the scapular proximal end (character 261; MA6) (Fig. 12A–L).

The partitioned datasets of selected measurement attributes provide standards for the quantitative evaluation of one-dimensional measurement data on osteological characters of *Zhanghenglong yangchengensis*. In each standard, the two detached intervals of the database on the corresponding measurement attribute are adequately representative of the distribution ranges of the values of non-hadrosaurid iguanodontians and hadrosaurids, respectively. For MA3, MA4, and MA6, the value of *Z. yangchengensis* falls within the interval representing basal hadrosaurids and some iguanodontians outside of Hadrosauridae. By contrast, for MA1, MA2, and MA5, the value for this species is restricted to the interval that represents hadrosaurids. Consequently, the data of *Z. yangchengensis*

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**Figure 10. Comparison of the foramina on the lateral sides of the maxillae of some hadrosaurid species (all maxillae in lateral view).** (A) *Bactrosaurus johnsonii* (AMNH 6553). (B) *Levensosaurus transoxianus* (CCMGE 579/12457). (C) *Gilmoreosaurus mongoliensis* (AMNH FARB 30653, reversed). (D) *Amurosaurus riabinini* (AEHM 1/12). (E) *Edmontosaurus regalis* (CMN 2289). (F) *Brachylophosaurus canadensis* (MOR 1071-8-15-98-573). Positions of maxillary foramina are indicated by arrows. doi:10.1371/journal.pone.0098821.g010
on selected measurement attributes straddle the two combinations of intervals of partitioned datasets respectively related to basal hadrosauroids and more derived hadrosaurids (Table 2). This condition is apparently similar to the mosaic pattern of trait evolution from basal hadrosauroids to more derived hadrosaurids present in the specimens of the species, and corroborates the preceding inference made from morphology. Based on the result of the quantitative analysis and evidence from morphology, we argue that Z. yangchengensis probably represents a relatively derived non-hadrosaurid hadrosauroid dinosaur closely related to Hadrosauridae.

Phylogenetic Analysis

A comprehensive phylogenetic analysis of Hadrosauroidea was conducted in order to assess the systematic position of Zhangheng-long yangchengensis and construct an overall tree topology on the phylogeny of basal hadrosauroids. The data matrix used in this analysis includes 61 species-level taxonomic units (4 iguanodontians outside of Hadrosauroidea and 57 hadrosauroids) coded across 346 equally-weighted characters (see Supporting Information S3 and Supporting Information S4). These applicable characters consist of 235 cranial and 111 postcranial components. Most of them were culled or modified from some recently published character lists for phylogenetic analyses of Hadrosauroidea, especially You et al. [1], Horner et al. [2], Evans and Reisz [9], Godefroit et al. [61], Prieto-Máquez and Wagner [47], and Xing et al. [59]. 10 new characters explicating in Supporting Information S3 were also added to the data matrix used here. The non-hadrosaurid iguanodontian Ouranosaurus nigeriensis was appointed the single outgroup, due to its strong affinities with Hadrosauroidea. In addition, we have adequately revised the previously published data on the character coding of some hadrosaurid species (including Charonosaurus jiayinensis, Lophorhothon atopus, and Nipponosaurus sachalinensis) because the ascription of the available material for each of these taxa is highly contentious (see Supporting Information S4). The databases of Edentorhamphosaurus and Magnapaulia laticaudus used for the phylogeny were also updated in light of the new morphological information mentioned in relevant literature [54,62]. Finally, Hadrosaurus foulkii is excluded from the data matrix used in this paper because this taxon is considered a nomen dubium that lacks any diagnostic characters [63].

The data matrix of 346 characters and 61 taxa was analyzed using the maximum parsimony method in the program TNT version 1.0 [35]. Prior to the traditional search, 10000 trees were set as maximum trees in memory. A heuristic search with 10000 replicates of Wagner trees using random addition sequences was performed, followed by the TBR branch swapping holding 1000 trees per replicate. The support of clades was evaluated by standard absolute frequencies in 1000 replicates of bootstrap analysis and decay indices of Bremer support (bootstrap and Bremer decay values).

The maximum parsimony analysis resulted in 54 most parsimonious trees (MPTs), with a tree length of 1004 steps, a consistency index (CI) of 0.495 and a retention index (RI) of 0.863. Fig. 13 shows the strict consensus tree derived from the 54 MPTs. The tree topology of the strict consensus indicates that Zhangheng-long yangchengensis, Nanyangosaurus zhugeii, and Hadrosauridae together constitute a monophyletic group with an unresolved polytomy, which is weakly supported by the low bootstrap (21%) and Bremer decay (1) values. This clade is diagnosed by five unambiguous synapomorphies, although only three of these features are currently known from Z. yangchengensis: the median primary ridges available for all or most of the tooth crowns in the dentary dental battery (character 7), the ratio between the vertical distance from the apex of the maxillary dorsal process to the maxillary ventral margin and the anteroposterior length of the maxillary ventral margin greater than 0.35 and up to 0.45 (character 111), and the arcuate dorsal margin of the scapula in lateral view (character 256) (see Supporting Information S5). N. zhugeii and Z. yangchengensis are depicted as having the closest affinities with Hadrosauridae. For the 50% majority rule consensus tree, Z. yangchengensis is positioned as the sister taxon to the clade consisting of N. zhugeii and Hadrosauridae (Fig. 14);
the phylogenetic relationships among the three groups are very similar to but slightly more complicated than those of the strict consensus. In all MPTs and the strict consensus tree, Z. yangchengensis is placed in a relatively derived position within the paraphyletic group that represents basal hadrosauroids. This phylogenetic hypothesis is very consistent with the inferences drawn from the morphological comparisons and quantitative analysis of measurement data.

The tree topology of basal hadrosauroids in the strict consensus is generally identical to that in the 50% majority rule consensus (Figs. 13 and 14). The former is briefly described as follows. Hadrosauroidea is defined as the least inclusive clade containing Equijubus normani and Parasaurolophus walkeri, following You et al. [1]. Xuaculon yueluni is recovered as slightly more derived than E. normani. Eolambia caroljonesa and Protohadros byrdi together form a North American clade of basal hadrosauroids that is more derived than Probactrosaurus gobiensis. These two species are united based on three unequivocal synapomorphies, including the absence of the strongly curved upwards posterior process of the surangular (character 640) and wider infratemporal margin of the jugal relative to the orbital margin of the bone (character 1272). There is a polytomy at the base of Hadrosauroidea which involves Jintasaurus meniscus, the preceding clade consisting of E. caroljonesa and P. byrdi, and the least inclusive clade containing Levnesovia transoxiana and Edmontosaurus regalis. L. transoxiana seems to be more basal than Tanius sinensis and Bactrosaurus johnsoni, although these species share strong similarities in cranial morphology [22]. Gilmoreosaurus mongoliensis occupies a more highly nested position than B. johnsoni. Shuangmiaosaurus gilmorei is recovered as slightly more derived than G. mongoliensis but slightly more basal than Nanningosaurus dashiensis. Similar to the systematic position of Claosaurus agilis presented in the strict consensus tree, N. dashiensis is recovered as a derived non-hadrosaurid hadrosauroid. Telnatossaurus transsylvanicus is found to be the sister taxon of Tethyshadros insularis. These two taxa constitute the single European clade of basal hadrosauroids, which is depicted as slightly more derived than N. dashiensis but slightly more basal than C. agilis. This European clade is diagnosed by the following unambiguous synapomorphies: bamboo leaf-like marginal denticles along the dorsal half of the dentary tooth crown (character 11), saw-toothed marginal denticles along the ventral half of the maxillary tooth crown (character 23), and the angle between the slope of the dentary anterior end which contacts the predentary and the horizontal greater than 130° (character 40). C. agilis, one of the closest relatives to Hadrosauridae, is depicted as more basal than Zhanghenglong yangchengensis, Nanyangosaurus zhugeii, and Hadrosauridae.

For the tree topology of Hadrosaurinae in the strict consensus, our present analysis does not significantly alter the relevant result argued by Xing et al. [59]. There is one exception to the condition: Lophorhothon atopus is placed as the sister group to the clade composed of the genera Prosaurolophus and Saurolophus (Fig. 13), based on the anatomical data of the holotype of this species [64]. The posterior fragments of the paired nasals are well preserved in the holotype of L. atopus. Either of the fragments shows evidence of a dorsoventrally low, strongly invaginated
Table 2. Relevant data of *Zhanghenglong* and detached intervals of the datasets consisting of the values of most hadrosaurids and some basal iguanodontians on selected measurement attributes*.

| Measurement attribute (XMDFEC V0013 and V0014) | Value of *Zhanghenglong* | Interval related to basal hadrosaurids | Interval related to hadrosaurs |
|-----------------------------------------------|--------------------------|--------------------------------------|-------------------------------|
| 1. ratio between maximum dorsoventral height and anteroposterior length of maxilla | 0.37 | up to 0.35 | greater than 0.35 |
| 2. ratio between anteroposterior length of ectopterygoid shelf and that of maxillary tooth row | 0.37 | up to 0.35 | greater than 0.35 |
| 3. angle between ectopterygoid ridge and ventral margin of posterior portion of maxilla | 16° | greater than 10° | up to 10° |
| 4. ratio between anteroposterior length of edentulous region and that of tooth row of dentary | 0.17 | up to 0.20 | greater than 0.20 |
| 5. angle between medial border of dentary symphyseal process and lateral surface of dentary ramus | 13° | greater than 15° | up to 15° |
| 6. ratio between dorsoventral depth of scapular neck and maximum dorsoventral height of scapular proximal end | 0.50 | up to 0.59 | greater than 0.59 |

*the boundary value between the two intervals was estimated to be the average value of the greatest value from the former component with low values and the least value from the latter component with high values. C, the component resulting from MCA of the database consisting of the sample means of all measured taxa.

doi:10.1371/journal.pone.0098821.t002

**circumarial fossa with a thick, right-angled posterodorsal margin (character 163°)**, which is typically seen in the genera *Prosaurlophus* and *Saurolophus*. However, the solid nasal crest of the species is only incipiently developed, compared with that of the genera *Prosaurlophus* (the relatively short, moderately developed nasal crest bounded posteriorly by the underlying frontal buttress) and *Saurolophus* (the elongate, well-developed nasal crest overhanging the occiput). Given the incompletely fused calvarial sutures and relatively small size of the holotype of *L. atopus*, the hypothesis that *L. atopus* may represent the juvenile form of *Prosaurlophus maximus* cannot be rejected.

The strict consensus tree has a large polytomy involving numerous helmet-crested lambeosaurines (Fig. 13). Therefore, the phylogenetic relationships among helmet-crested lambeosaurines are not fully resolved. Within the unresolved polytomy, the monophyly of the genus *Hypacrosaurus* is corroborated again after the work by Evans [48]. In the more complex 50% majority rule analysis, the participation of *H. foulkii* produced 486 MPTs of 1012 steps. This analysis does not significantly alter the phylogenetic position of *Z. yangchengensis* (see Supporting Information S5, Fig. 2). In the strict consensus tree derived from the 486 MPTs, *H. foulkii* is recovered as more basal than *Z. yangchengensis* and *Nanyangosaurus zhugei*.

The material of *Hadrosaurus foulkii* consists of several poorly preserved fragments of the cranium and a partial postcranial skeleton [4,63]. Most of the phylogenetically informative characters of the taxon come from the postcranial elements, including the coracoid, humerus, ilium, and ischium. Except for the wide arcuate laterodistal corner of the deltopectoral crest, the vast majority of the features in *H. foulkii* are typical of *Edmontosaurus* and *Shantungosaurus* (see Supporting Information S4). Prieto-Márquez [65] discussed the wide arcuate laterodistal corner of the deltopectoral crest seen in *H. falkwii* and basal hadrosaurids, and considered it to be plesiomorphic for Hadrosauroida, in comparison with the angular laterodistal corner of the deltopectoral crest common among most hadrosaurids. However, this configuration is also observed in a few humeri from the hadrosaurid genera *Brachylophosaurus* (e.g., CMN 8893), *Shantungosaurus* (e.g., GMV 1780-48), and *Edmontosaurus* (e.g., USNM 2414), which could be interpreted as intraspecific variation. Here we argue that the wide arcuate laterodistal corner of the deltopectoral crest may disturb the accurate character coding of *H. foulkii*, such as the measurement taken for the proximodistal length of the deltopectoral crest in character 269. In fact, the coding of the four characters associated with the laterodistal corner of the deltopectoral crest (characters 267, 269, 271, and 272) plays an important
role in placing \textit{H. foulkii} outside of Hadrosauridae (see Supporting Information S5, Fig. 2). When these four characters are coded as polymorphic for \textit{Brachylophosaurus}, \textit{Shantungosaurus}, and \textit{Edmontosaurus}, the alternate phylogeny indicates that \textit{H. foulkii} is definitely a member of the monophyletic group that consists of all non-lambeosaurine hadrosaurids (Fig. 15; Supporting Information S5, Fig. 3). Therefore, \textit{H. foulkii} is considered here a \textit{nomen dubium} owing to a lack of diagnostic characters, and may represent an enigmatic member of the monophyletic group that consists of all non-lambeosaurine hadrosaurids (i.e. Hadrosaurinae). This is why we adhere to the traditional taxonomy of Hadrosauridae argued by Horner et al. [2], where Hadrosauridae is divided into two major clades: Hadrosaurinae and Lambeosaurinae.

**Biogeographic Implications**

In current iguanodontian research, the issue of the geographic origin of Hadrosauridae has long been debated, and refers to two proposed hypotheses, an Asian or North American origin of Hadrosauridae [66]. Our cladogram indicates that the two Asian basal hadrosauroids \textit{Zhanghenglong yangchengensis} and \textit{Nanyangosaurus zhugeii} represent the closest relatives to Hadrosauridae (Fig. 13). Until now, the first appearance of lambeosaurine species in the stratigraphic record is represented by \textit{Jaxartosaurus aralensis} from the middle Santonian to earliest Campanian Syuk-Syuk Formation [67,68]. The stratigraphic age of the oldest hadrosaurine \textit{Gryposaurus latidens} was estimated to be the late Santonian to early Campanian [49]. Therefore, the most recent common ancestor of
Hadrosauridae is very likely to have split into Lambeosaurinae and Hadrosaurinae no later than the early Santonian. This temporal interval is quite close to the stratigraphic age of *Z. yangchengensis*, which is thought to be the middle Santonian [31,33]. The other basal hadrosauroid closely related to Hadrosauridae, *N. zhugeii*, was recovered from the early to middle Coniacian lower portion of the Xiaguan Formation in the Xiaguan-Gaoqiu Basin of southwestern Henan Province [69]. The stratigraphic age of this species is slightly older than the deadline of the presumptive temporal interval when the split of Hadrosauridae into Hadrosaurinae and Lambeosaurinae occurred. Thus, these two basal hadrosauroids, both from the Upper Cretaceous of southwestern Henan Province, could be considered to be the known closest relatives of Hadrosauridae, supporting the Asian origin hypothesis.

Because most basal lambeosaurines (*Aralosaurus tuberiferus* [70], *Tsintaosaurus spinorhinus* [57], and *Jaxartosaurus aralensis* [71]) are found in Asia, the geographic origin of Lambeosaurinae is probably restricted to this continent. On the other hand, three of the four major groups within Hadrosaurinae have the first divergent Asian species (Fig. 13), including *Wulagasaurus dongi* [61], *Shantungosaurus giganteus* [72], and *Kerberosaurus manakini* [73]. Except for the first divergent Asian species, each of these three groups includes at least three North American species. This phenomenon could be interpreted as the dispersal of Asian hadrosaurine clades to North America for further radiation. However, the possibility that Hadrosaurinae originated in North America and subsequently migrated to Asia cannot be ruled out. Combining the phylogenetic and stratigraphic data on *Zhanghenglong yangchengensis* with the biogeographical inferences on Hadrosaurinae and Lambeosaurinae has yielded support for the hypothesis that Hadrosauridae might have originated in Asia. Although the discovery of *Z. yangchengensis* provides direct evidence for the Asian origin of

![Figure 14. 50% majority rule consensus of 54 most parsimonious trees produced by the maximum parsimony analysis implemented in the software TNT, showing the potential phylogenetic position of Zhanghenglong yangchengensis within Hadrosauridae. Numbers above nodes represent bootstrap values, whereas those beneath nodes represent Bremer decay values. Bootstrap values lower than 20 and Bremer decay values less than 2 are not shown. doi:10.1371/journal.pone.0098821.g014](http://www.plosone.org/doi/10.1371/journal.pone.0098821.g014)
Hadrosauridae, the preceding hypothesis still requires further testing.

**Supporting Information**

Supporting Information S1 Measurements of selected skeletal elements of *Zhanghenglong yangchengensis* and some hadrosaur relatives. (DOC)
Supporting Information S2 Datasets on the selected measurement attributes for model-based clustering. (DOC)

Supporting Information S3 Characters used in the phylogenetic analysis of Hadrosauridea. (DOC)

Supporting Information S4 Character-taxon matrix used in the phylogenetic analysis of Hadrosauridea. (DOC)

Supporting Information S5 Original information in the analytical process of the program TNT, with the strict consensus tree and list of synapomorphies. (DOC)

Acknowledgments

The authors sincerely thank all the colleagues for attending the fieldwork in Henan Province, Lishi Xiang, Sicai He, and Xiaoqing Ding for preparing the specimens, Hailong Zang for taking photographs of the specimens, Diego Pol and Albert Prieto-Márquez for providing guidance on the uses of relevant programs (TNT and R), and Hailu You, Yuanqing Wang, Xiaqiao Wan, Jordan Mallon, Michael Brett-Surman, David Eberth, Nicolas Campione, and Lin Tan for valuable discussions. We are very grateful to the following people providing access to the specimens under their care: Xijin Zhao (deceased), Xiaochun Wu, Xiaolin Wang, Xiujuan Yang, Shuhui Hai, Vladimir Alifanov, Mark Norell, Robert Sullivan, Alexander Averianov, and Xabier Pereda-Suberbiola. Thanks also go to Hans-Dieter Sues and Yuri Bolotisky for sharing the images of Lambeosaurus and Anomoepus, respectively. This paper benefited greatly from the helpful comments of Andrew T. McDonald, Paul Barrett, and the academic editor David Evans.

Author Contributions

Conceived and designed the experiments: DW XX HX. Performed the experiments: HX FH CS. Analyzed the data: HX DW FH CS. Contributed reagents/materials/analysis tools: HX DW FH CS QM YH DWEH FY RD XX. Wrote the paper: HX DW.

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