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New hadrosauroid material from the Upper Cretaceous Majiacun Formation of Hubei Province, central China

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Abstract　The Xichuan Basin is situated along the northwestern border between Henan and Hubei provinces in central China, and includes a thick accumulation of Upper Cretaceous sediments. Here we report and describe some indeterminate hadrosauroid material on the genus level, which was retrieved from the middle Majiacun Formation (Upper Cretaceous) in the southwestern area of the Xichuan Basin, northwest Hubei. The hadrosauroid remains occur with scattered dinosaur eggs at the same horizon. The majority of the bones may come from the late nestling and early juvenile stages. This condition could be best explained by the geographic segregation of the nestlings and early juveniles from the herd consisting of older individuals, as reported in some hadrosaurids. A minimum of two hadrosauroid taxa are identified through direct morphological comparisons: one may represent a relatively derived non-hadrosaurid hadrosauroid, and the other probably pertains to Hadrosaurinae. Considering the younger age of North American hadrosaurines, the presence of hadrosaurine material within the middle Santonian middle portion of the Majiacun Formation provides new evidence for the Asian origins of both Hadrosaurinae and Hadrosauridae.

Key words　northwest Hubei, Late Cretaceous, middle Santonian, Majiacun Formation, Lijiagou bonebed, hadrosauroid

1　Introduction

Hadrosauroidea is one of the most anatomically derived and ecologically diverse herbivorous clades within the Dinosauria (Brett-Surman, 1979; Sereno, 1999; Norman, 2004). It could be defined as the least inclusive clade containing *Equijubus normani* and *Parasaurolophus walkeri* (You et al., 2003; Xing et al., 2014). Abundant material of Hadrosauroidea is known from all continents except Africa and Oceania (Case et al., 2000; Lund and Gates, 2006), and is restricted to the interval from the Aptian to the end of the Maastrichtian. During the Late Cretaceous, Hadrosauridae diverged from basal members

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of Hadrosauroidea, and progressively dominated coeval terrestrial ecosystems, presumably because of its acquisition of the complex dental structure, duck-billed rostrum, bipedal locomotion, and relatively large body size (Horner et al., 2004; Prieto-Márquez, 2010; Erickson et al., 2012). Hadrosauridae contains two major clades: Hadrosaurinae (including the flat-headed and solid-crested hadrosaurids) and Lambeosaurinae (including the hollow-crested hadrosaurids), the remains of which were mainly collected from the Campanian and Maastrichtian of Asia and North America (Forster, 1997; Horner et al., 2004; Godefroit et al., 2008). Successive discoveries and re-evaluations of hadrosauroid specimens can help clarify the evolutionary and paleobiogeographic histories of ornithopod dinosaurs before the Cretaceous–Paleogene mass extinction. However, the scarcity of pre-Campanian hadrosaurids in the fossil record has led to poor agreement on the early evolution of Hadrosauridae, especially the origins of both this group and Hadrosaurinae.

The Xichuan Basin is located on the northwest border between Henan and Hubei provinces in central China (Fig. 1). This basin is famous for its well-developed Late Cretaceous continental deposits (~1600 m thick red beds) and rich record of contemporary fossil reptiles (Zhou and Han, 1985; Li, 2001; Wang et al., 2008). Paleomagnetic data indicate that the episodic fault-belt uplift and subsequent sedimentation into the lowlands resulted in deposition of the Upper Cretaceous of the Xichuan Basin (Lin et al., 2001). The Upper Cretaceous of the Xichuan Basin mainly occurs in subsurface and outcrops along the Danjiang River. It comprises, in ascending order, the Gaogou, Majiacun, and Sigou formations, all of which have yielded numerous dinosaur eggs (Xi and Pei, 1997; Zhao and Zhao, 1998; Wang et al., 2008). All outcrops of these three formations in the Xichuan Basin are restricted to a narrow, belt-shaped zone that extends from northwest Hubei Province to southwest Henan Province. In fact, the Gaogou, Majiacun, and Sigou formations are well exposed in the uplifted areas along the edges of the Xichuan Basin and the adjacent Xixia Basin that is located in southwest Henan Province (Wang et al., 2008). Within these two basins, the Majiacun Formation is so far the only Upper Cretaceous unit where dinosaur bones have been retrieved (Xing et al., 2014). This formation ranges in age from the late Coniacian to the end of the Santonian, based on the preliminary study of its fossil invertebrates and palynomorphs (Wang et al., 2008). The vast majority of dinosaur remains come from the middle Majiacun Formation (Li, 2001; Xing et al., 2014). This stratigraphic interval consists of complexly interbedded brick-red muddy siltstone or mudstone with calcareous nodules and grey-green fine-grained or medium-grained sandstone (Xi and Pei, 1997; Li, 2001), suggesting a combination of floodplain and point bar deposits that is characteristic of a seasonally wet and dry climate. Although the dinosaur material of the Majiacun Formation in the Xixia Basin has been well documented and described (Wang et al., 2008; Hone et al., 2010; Xu et al., 2010; Xing et al., 2014), the equivalent in the Xichuan Basin requires sufficient collection and research.

Zhou and Han (1985) first reported a few isolated hadrosauroid vertebrae retrieved from the Majiacun Formation of the Xichuan Basin, southwestern Henan. During the 1990s, the regional geological survey of Hubei Province recovered hundreds of dinosaur elements from a rich bonebed within the middle Majiacun Formation of the Xichuan Basin, northwest Hubei (Li, 2001). This new fossil locality is very close to Lijiagou Village, about 4 km east of Meipu Town, northeast Yunxian County (Fig. 1). The dinosaur bonebed contains a poorly sorted mixture of disarticulated non-adult sauropod and hadrosauroid elements, and has yielded scattered dinosaur eggs and fragmentary eggshells (Li, 2001). Its sediments are grey and brick-red, organic-rich muddy siltstone with a considerable number of calcareous nodules. In 2011, an expedition team organized by the Long Hao Institute of Geology and Paleontology carried out a systematic excavation of the Lijiagou bonebed. Most of the newly collected dinosaur elements come from the preadult sauropods and hadrosauroids, but a few adult-sized bones of hadrosauroid origin were also found. In this paper, we describe the available hadrosauroid specimens recovered from the Majiacun Formation at the Lijiagou locality, and discuss their potential systematic status, and the relevant ethological, biostratigraphic, and biogeographic significance.

Institutional abbreviations AMNH, American Museum of Natural History, New York, USA; CEUM, College of Eastern Utah Prehistoric Museum, Price, USA; CMN, Canadian Museum of Nature, Ottawa, Canada; HGM, Hubei Geological Museum, Wuhan, China; IRSNB, Institut royal des Sciences naturelles de Belgique, Brussels, Belgium; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing,

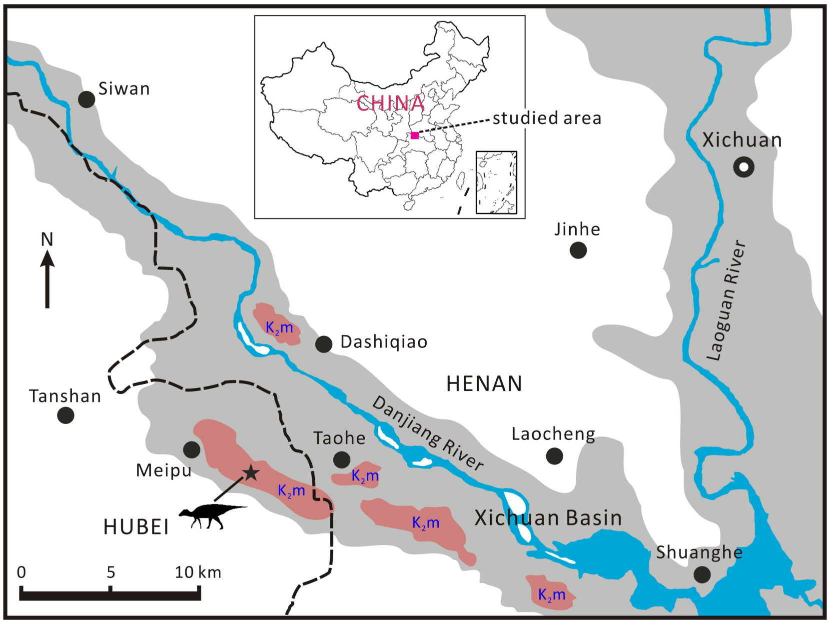

Fig. 1 Geographical map of the Xichuan Basin on the northwest border between Henan and Hubei provinces, which shows the locality of the dinosaur bonebed near Lijiagou Village (the black five-pointed star) (modified from Li, 2001)

The red regions represent the exposed areas of the Upper Cretaceous Majiacun Formation (K_2m) in the Xichuan Basin

China; LACM, Natural History Museum of Los Angeles, Los Angeles, USA; LPM, Liaoning Paleontological Museum, Beipiao, China; MOR, Museum of the Rockies, Bozeman, USA; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; ROM, Royal Ontario Museum, Toronto, Canada; SXMG, Shanxi Museum of Geology, Taiyuan, China; YDENGP, Yunxian Dinosaur Eggs National Geological Park, Yunxian, China; YPM, Yale Peabody Museum of Natural History, New Haven, USA; ZIN, Zoological Institute, Russian Academy of Sciences, St Petersburg, Russia.

2 Material and methods

Although 442 dinosaur specimens have been collected from the bonebed at the Lijiagou locality, about 50% are osteologically or taxonomically indeterminate owing to abrasion and breakage. The number of identifiable specimens is 238, consisting of 195 sauropod specimens (82%), 36 hadrosauroid specimens (15%), and 7 theropod specimens (3%). The majority of the hadrosauroid specimens are assignable to extremely small, preadult individuals, with the exception of a partial left tibia and an ungual of pedal digit IV, probably of adult origin. Ontogenetic stages of the preadult hadrosauroid specimens were determined using the standard of Horner et al. (2000), where six gradational growth stages (i.e. early and late nestlings, early and late juveniles, subadult, and adult) of the hadrosaurine *Maiasaura peeblesorum* were established based on different histological features and corresponding linear measurements of long bones among individuals. Comparisons of linear measurements between the non-adult hadrosauroid bones at the Lijiagou locality and the equivalent elements in the suggested preadult stages of some hadrosauroids indicate that the former material may come from the late nestling and early juvenile individuals (Table 1).

The following is a description of the available hadrosauroid bones recovered from the Lijiagou locality. In order to better appraise their systematic status, detailed morphological comparisons of these bones are made with the homologous elements of other hadrosauriforms, based on direct examination and relevant literature. Given that osteological features of animals may dramatically change through ontogeny (Gould, 1977), the preadult elements are preferentially compared with the counterparts of known hadrosauriforms at the same or adjacent growth stage. Most of the Lijiagou hadrosauroid specimens housed at the HGM are now reconstructed with plaster and mounted for display. It is therefore difficult to properly figure these specimens.

Definitions of the relevant high-level taxonomic units, including Hadrosauriformes, Hadrosauroidea, and Hadrosauridae, follow Xing et al. (2014), which is mainly derived from Sereno (1998). The term “basal hadrosauroids” here refers to all non-hadrosaurid hadrosauroids.

Table 1 Comparisons of linear measurements between non-adult hadrosauroid specimens at the Lijiagou locality and preadult material of some hadrosauroids (mm)

Linear measurement	Non-adult hadrosauroid specimens at the Lijiagou locality	Reference material in preadult forms of some hadrosauroids		
1. length of humerus	YDENGP H001 126.0	*Maiasaura peeblesorum* (LN) YPM PU22400 78.0	*M. peeblesorum* (EJ) YPM PU23444 109.0	*H. stebingeri* (EJ) MOR 548 115.0
2. height of proximal end of scapula	YDENGP H002 43.0 HGM 0018 45.0	*M. peeblesorum* (LN) YPM PU22400 28.5	*H. stebingeri* (EJ) MOR 548 59.0	*B. johnsoni* (EJ)* AMNH 6577 56.0
3. length of femur	HGM 0023 305.0	*Bactrosaurus johnsoni* (LN)* AMNH 6577 145.0	*M. peeblesorum* (LN) YPM PU22400 120.5	*Gryposaurus notabilis* (LJ) CMN 8784 500.0
4. length of proximal end of fibula	YDENGP H003 28.0	*M. peeblesorum* (LN) YPM PU22400 20.0	*H. stebingeri* (EJ) MOR 548 36.0	*G. notabilis* (LJ) CMN 8784 82.0
5. length of ischial shaft	HGM 0062 202.0	*Hypacrosaurus stebingeri* (EJ) MOR 548 180.0	*Procheneosaurus convincens (L*J) PIN 2230 245.0	
6. length and height of centrum in middle dorsals	YDENGP H012 30.0×50.0	*M. peeblesorum* (LN) YPM PU22400 15.0×24.0	*H. stebingeri* (EJ) MOR 548 28.5×48.0	*P. convincens* (LJ) PIN 2230 43.0×69.0
7. length and height of centrum in middle region of anterior caudals	YDENGP H014 32.0×53.0	*M. peeblesorum* (LN) YPM PU22400 12.0×18.0	*M. peeblesorum* (EJ) YPM PU23444 15.0×23.0	*G. notabilis* (LJ) CMN 8784 40.0×58.0
8. length and height of centrum in anterior region of middle caudals	YDENGP H025 24.0×24.0	*M. peeblesorum* (LN) YPM PU22400 8.0×9.0	*Tetragonosaurus praeceps* (LJ) AMNH 5340 35.0×35.5	

Abbreviations: LN. late nestling; EJ. early juvenile; LJ. late juvenile. *AMNH 6577 contains elements from two or more non-adult individuals of *Bactrosaurus johnsoni.*

3 Systematic paleontology

Dinosauria Owen, 1842

Ornithischia Seeley, 1887

Ornithopoda Marsh, 1881

Iguanodontia Dollo, 1888

Ankylopollexia Sereno, 1986

Hadrosauriformes Sereno, 1997

Hadrosauroidea indet. Cope, 1870

(Fig. 2; Li, 2001: figs. 2–4)

Material HGM 0006, three fragments of a preadult right maxilla; HGM 0018, a nearly complete, preadult left scapula; HGM 0023, a complete, preadult right femur; YDENGP H001, a nearly complete, preadult left humerus; YDENGP H003, the proximal two-thirds of a preadult left fibula; YDENGP H005, the proximal end of an adult left tibia.

Locality and horizon Lijiagou Village, approximately 4 km east of Meipu Town, northeast Yunxian County, Hubei Province (Fig. 1). The horizon occurs in the middle of the Majiacun Formation, with an estimated age of the middle Santonian.

Hadrosauroidea Cope, 1870

Hadrosaurinae indet. Cope, 1870

(Fig. 3; Li, 2001: fig.5)

Material HGM 0062, a preadult right ischium missing the pubic peduncle; YDENGP H002, the proximal end of a preadult right scapula; YDENGP H006, a nearly complete, adult left ungual of pedal digit IV.

Locality and horizon Lijiagou Village, approximately 4 km east of Meipu Town, northeast Yunxian County, Hubei Province (Fig. 1). The horizon occurs in the middle of the Majiacun Formation, with an estimated age of the middle Santonian.

4 Description and comparisons

This section is composed of the osteological descriptions of an indeterminate basal hadrosauroid, an indeterminate hadrosaurine, and some other indeterminate material whose characters and configurations are common among hadrosauroids. Here we emphasize features of systematic and phylogenetic significance, and features that exhibit ontogenetic variability in the Lijiagou hadrosauroid specimens.

4.1 Indeterminate basal hadrosauroid

Maxilla (HGM 0006) Three fragments represent the middle and posterior portions of a preadult right maxilla, which are poorly preserved in the Lijiagou bonebed (Li, 2001: fig. 2). Although incomplete, the lateral outline of the element appears triangular and dorsoventrally short. Just above the straight, tooth-bearing base, the lateral side of the maxillary middle portion is pierced by four scattered small foramina that are roughly aligned anteroposteriorly. This is very common among most non-hadrosaurid hadrosauriforms, such as *Equijubus normani* (IVPP V 12534), *Bactrosaurus johnsoni* [e.g., AMNH 6553 and AMNH 6389 (a juvenile)], and *Gilmoreosaurus mongoliensis* (AMNH FARB 30653). However, in all hadrosaurids that involve their non-adult specimens, the maxillary foramina are relatively large and closely arranged, and occur along the ventral margin of the sutural surface for the jugal (Evans, 2010). The sutural surface for the jugal in HGM 0006 is incomplete dorsally owing to the missing of the dorsal ramus. Its ventral half is dorsolaterally-facing and strongly inclined posteriorly. As in basal hadrosauroids and some basal lambeosaurines (Prieto-Márquez and Wagner, 2009; Xing et al., 2014), the ventral extremity of the jugal sutural facet is dorsally displaced from the anterior end of the ectopterygoid ridge by a short distance. For example, this condition is observed in both juvenile and adult stages of *Eolambia caroljonesa*, including

CEUM 35492 (a juvenile) and CEUM 9758. By contrast, it is never documented in known preadult forms of hadrosaurids, where the ventral extremity of the jugal sutural facet overlaps the anterior end of the ectopterygoid ridge (Horner and Currie, 1994).

In lateral view, the ectopterygoid shelf is gently oblique anterodorsally, forming a 16° angle with the ventral margin of the bone. This character is typical of relatively derived non-hadrosaurid hadrosauroids, including *Shuangmiaosaurus gilmorei* (LPM 0165), but differs from the nearly horizontal condition seen in hadrosaurids such as *Hypacrosaurus altispinus* [e.g., CMN 2247 (?an early juvenile) and ROM 702]. The medial surface of the maxilla bears numerous special foramina arranged in a dorsally convex row. These foramina strictly correspond to the maxillary alveoli. Ventrally, the grinding surface of the tooth battery is medioventrally directed and slightly concave. Each alveolus contains one or two active teeth. The crown of each tooth is labially ornamented with a straight, longitudinally oriented carina. The average mesiodistal length of the tooth crown in the center of the tooth battery is about 5 mm. This dimension is slightly less than the equivalent measurement in the late juvenile form of *H. altispinus* (CMN 2246, 7 mm) and *Gryposaurus notabilis* (CMN 8784, 6 mm).

Scapula (HGM 0018) Although this element comes from a preadult individual, it bears a series of features that are mostly unchanged through ontogeny in basal hadrosauroids: the dorsal edge of the scapular blade is unbent; the dorsal and ventral margins of the scapula strongly diverge from each other towards the distal end of the bone; the anteriormost end of the acromion process is more robust than the rest of this structure; the scapular neck is markedly constricted relative to the proximal expansion of the element (Li, 2001: fig. 4). In accord with *Bactrosaurus* (e.g., AMNH 6553) and *Gilmoreosaurus* (e.g., AMNH FARB 30725), the anterior half of the acromion process slightly curves anterodorsally and becomes progressively wider anteriorly. A weakly developed, wide arcuate eminence forms the deltoid ridge along the lateral side of the proximal half of the scapula, similar to the condition seen in juvenile specimens of *Bactrosaurus johnsoni* (e.g., AMNH 6577). In contrast, the adult *B. johnsoni* possesses a prominent deltoid ridge (Prieto-Márquez, 2011), revealing a notable ontogenetic change in the pectoral girdle of the taxon.

Humerus (YDENGP H001) The humerus is relatively long and slender, in stark contrast to the robust morphology seen in hadrosaurids such as *Maiasaura pebblesorum* [e.g., YPM PU23444 (an early juvenile) and MOR 758]. It is bowed laterally in anterior or posterior view, with a transversely narrow deltopectoral crest (Fig. 2A, B). Proximally, there is a posteriorly directed humeral head between the external and internal tuberosities. All the three protuberances are incompletely preserved. Immediately ventral to the external tuberosity, a weakly developed deltopectoral crest slightly projects anterolaterally and moderately extends longitudinally along the proximal half of the humeral shaft. The laterodistal corner of the deltopectoral crest is shallowly arcuate and located dorsal to the mid-shaft of the bone. This condition differs significantly from the deeply arcuate or angular laterodistal corner of the deltopectoral crest near the humeral mid-shaft observed in hadrosaurids, including their known preadult forms (Brett-Surman and Wagner, 2007). Below the distal constriction of the humerus, the radial and ulnar condyles are separated by a shallow, triangular groove. The radial condyle is more laterally positioned and larger than the ulnar condyle (Fig. 2A, B).

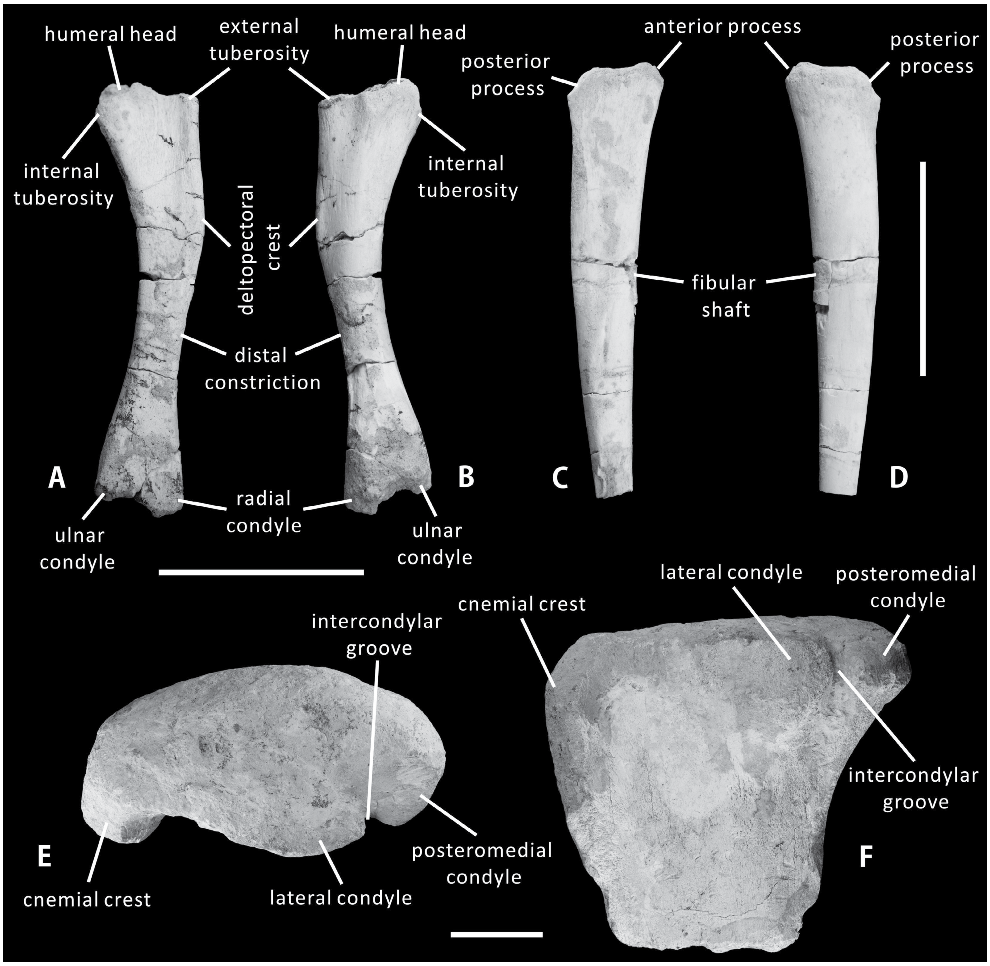

Fig. 2 Specimens of an indeterminate basal hadrosauroid recovered from the Lijiagou locality
A–B. left humerus (YDENGP H001) in anterior (A) and posterior (B) views;
C–D. left fibula (YDENGP H003) in medial (C) and lateral (D) views;
E–F. left tibia (YDENGP H005) in proximal (E) and lateral (F) views. Scale bars=6 cm

Femur (HGM 0023) As in basal hadrosauroids like *Probactrosaurus gobiensis* (e.g., PIN 2232/39-1) and *Bactrosaurus johnsoni* [e.g., AMNH 6577 (?an early juvenile)], the femur is slightly curved medially. At the saddle-like proximal end of the element, the femoral head is separated from the greater trochanter by a distinct neck. The lesser trochanter forms a mediolaterally compressed, finger-shaped prominence located anterolateral to the greater trochanter (Li, 2001: fig. 3). The cleft between the two trochanters is narrow but conspicuous. The fourth trochanter extends proximodistally along the posterior side of the middle of the shaft, adjacent to the medial surface of the bone. It is subtriangular in medial view, with a pointed posterior extremity slightly offset distally. This is similar to the condition in some basal hadrosauroids such as *Eolambia* [CEUM 34252 (a juvenile)] and *Gilmoreosaurus* (AMNH FARB 30741), but contrasts with that in many non-hadrosauroid iguanodontians such as *Mantellisaurus* (IRSNB 1551), where the triangular fourth trochanter is strongly pendant and asymmetrical (Norman, 1986; McDonald et al., 2012). Distally, the intercondylar extensor groove is partially enclosed by the posteriorly projecting lateral and medial condyles, which is also observed in some basal hadrosauroids, including *Yunganglong* (SXMG V00001) and *Levnesovia* (ZIN PH 1388/16).

Fibula (YDENGP H003) As is typical for neornithischians, the fibula is a slender, mediolaterally compressed bone, whose proximal half becomes progressively narrower towards the midpoint of the shaft (Fig. 2C, D). The distal third of the fibula is not preserved in YDENGP H003. The lateral surface of the proximal third of the fibula is slightly convex, whereas the medial surface is gently concave to fit into the anteroposteriorly wide articular facet of the tibia between the cnemial crest and the lateral condyle. The anterior region of the proximal fibula exhibits an anteriorly directed, subtrapezoidal anterior process, the anterodorsal edge of which is straight and strongly sloping anteroventrally. This process bears a distinct resemblance to the equivalent structure in *Gilmoreosaurus mongoliensis* (e.g., AMNH FARB 30748). In contrast, the rounded anterior process of the proximal fibula with a broadly arched anterodorsal edge is common among all other hadrosauroids that include their known preadult forms, such as *Maiasaura pebblesorum* [e.g., YPM PU22400 (a late nestling) and ROM 44770], *Probactrosaurus gobiensis* (PIN 2232/10), and *Magnapaulia laticaudus* (LACM 20874). The posterior process of the fibular proximal end in YDENGP H003 is too damaged to discern details of its morphology. Similar to the condition in basal hadrosauroids, the posteromedial side of the mid-shaft slightly twists medially so that the mid-shaft shows a mediolaterally narrow, subtriangular profile in cross section.

Tibia (YDENGP H005) This specimen only preserves the proximal end of an adult-sized left tibia, which has a heavily eroded cnemial crest and lateral condyle (Fig. 2E, F). As in other hadrosauroids, the proximal region of this element is strongly expanded anteroposteriorly relative to the main shaft, with a laterally hooked cnemial crest gradually tapering distally (Norman, 2002; Godefroit et al., 2004). Posterior to the cnemial crest are two bulbous condyles that would have contacted the distal end of the femur: the lateral and posteromedial condyles both project posterolaterally, and are separated by an anteroposteriorly narrow and mediolaterally deep intercondylar groove. In proximal view, the lateral condyle is skewed posteriorly, and is more robust than the posteromedial condyle (Fig. 2E). This condition is also seen in some non-hadrosaurid hadrosauroids, including *Bactrosaurus johnsoni* [e.g., AMNH 6577 (a juvenile) and AMNH 6553] and *Gilmoreosaurus mongoliensis* (AMNH FARB 30742), but is in contrast to more derived hadrosaurids, in which the lateral condyle of the tibia is either slightly smaller than or as large as the posteromedial condyle. The preserved part of the shaft is oval in cross section, the long axis of which is anteroposteriorly oriented.

4.2 Indeterminate hadrosaurine

Scapula (YDENGP H002) A partial preadult scapula is available for the indeterminate hadrosaurine recovered from the Lijiagou locality, preserving only the proximal region (Fig. 3A–C). The scapular proximal constriction is modest; the ratio between the depth of the scapular neck and the maximum height of the scapular proximal end is 0.56. This condition is also observed in the nestling and juvenile forms of some hadrosaurids, such as *Maiasaura pebblesorum* (e.g., YPM PU22400) and *Hypacrosaurus stebingeri* (MOR 548). By contrast, the strong constriction of the scapular neck is only known from non-hadrosaurid hadrosauriforms, including their known preadult stages (Prieto-Márquez, 2011). The dorsal margin of the scapular proximal end bears a straight, stout acromion process that protrudes laterally, but the anteriormost end of this process is missing (Fig. 3A, B). In fact, the unbent acromion process is typical of hadrosaurines, and appears invariant through ontogeny in these taxa. This contrasts with the recurved acromion process seen in lambeosaurines and most basal hadrosauroids. In lateral view, the deltoid ridge is confluent with the more proximally positioned acromion process, and dorsally delimits a deep, triangular fossa on the lateral surface of the scapular proximal end, which may represent the attachment area for the supracoracoideus muscle (Norman, 1986; Dilkes 2000). Posteroventral to the coracoid facet, the shallowly concave glenoid cavity faces anteroventrally and is supported by a triangular, ventrolaterally directed buttress. This cavity is crescent-shaped in proximal view, and is transversely narrower than the coracoid facet (Fig. 3C). As in other hadrosauroids, the lateral side of the proximal scapula is strongly concave, whereas the medial side is prominently convex.

Ischium (HGM 0062) This element is composed of a dorsoventrally expanded proximal plate that borders the acetabulum, and an elongate, rod-shaped distal shaft (Li, 2001: fig. 5). Unfortunately, the pubic peduncle is not preserved in the proximal plate of HGM 0062. The iliac peduncle is anterodorsally directed and subrectangular in lateral view. It is mediolaterally compressed at its ventral base, and gradually widens mediolaterally towards its articular facet. Proximally, the subovate articular facet of the iliac peduncle is greatly expanded transversely and strongly everted. It is approximately twice as long as wide. As in hadrosaurines such as *Edmontosaurus regalis* (e.g., CMN 2289) and *Brachylophosaurus canadensis* (e.g., MOR 794), the posterodorsal corner of the iliac peduncle does not moderately or strongly curve posteriorly. Beneath the iliac peduncle, the ventral enclosure of the obturator notch cannot be discerned because the obturator process is not intact. The distal shaft is straight and lunate in cross section. It extends posteriorly and terminates in a rounded point, as in all hadrosaurines (Horner et al., 2004). A low, anteroposteriorly prolonged eminence occurs along the dorsoventrally convex lateral side of the proximal region of the distal shaft. It gradually diminishes in prominence posteriorly, and eventually merges with the lateroventral edge of the distal shaft at the anterior quarter of the latter.

Pedal phalanx (YDENGP H006) Only one pedal element pertaining to hadrosauroids

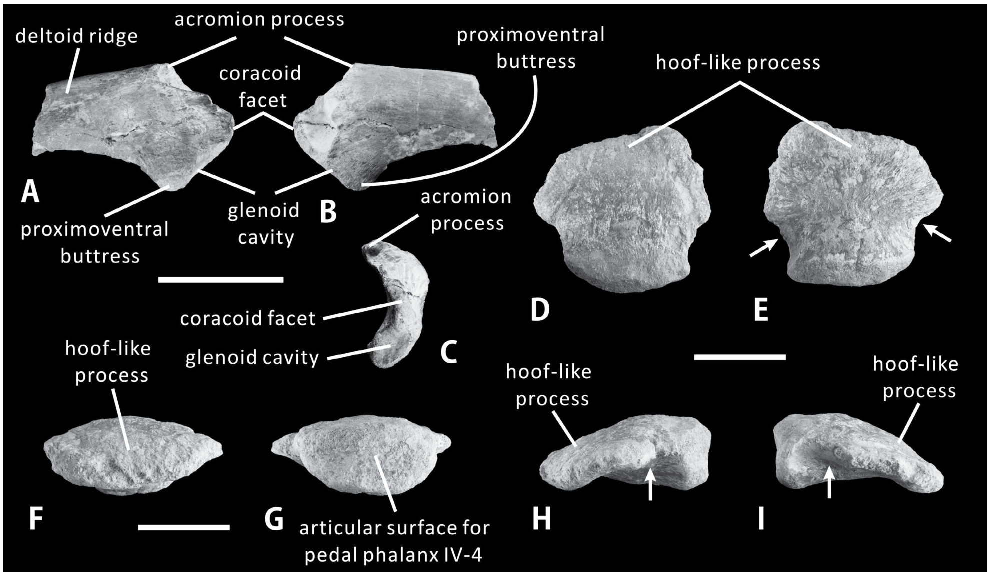

Fig. 3 Specimens of an indeterminate hadrosaurine recovered from the Lijiagou locality
A–C. right scapula (YDENGP H002) in lateral (A), medial (B), and proximal (C) views;
D–I. left ungual of pedal digit IV (YDENGP H006) in dorsal (D), plantar (E), distal (F), proximal (G), lateral (H), and medial (I) views. Scale bars=4 cm
The arrows indicate large neurovascular foramina along the lateral or medial surface of the ungual

was retrieved from the Lijiagou bonebed, namely an adult-sized ungual of pedal digit IV (Fig. 3D–I). This bone exhibits hoof-like dorsal and plantar contours, owing to the presence of a transversely expanded but longitudinally shortened distal region. This closely resembles the condition in hadrosaurids, including *Gryposaurus* (e.g., ROM 764), *Edmontosaurus* (e.g., CMN 8399) and *Corythosaurus* (e.g., AMNH 5240). However, among non-hadrosaurid hadrosauriforms such as *Eolambia* (CEUM 14415), *Probactrosaurus* (e.g., PIN 2232/10), and *Iguanodon* (e.g., IRSNB 1534), the ungual of pedal digit IV possesses a relatively long and slender distal region, and is arrow-shaped in dorsal or plantar view (Norman, 2002).

The distal region of YDENGP H006 forms an asymmetrical hoof-like process, which is much more expanded mediolaterally than the proximal articular surface (Fig. 3D, E). The dorsal surface of this process bears many small neurovascular foramina along its deeply arcuate anterior margin, and is marked by two prominent anteromedially directed claw grooves (Fig. 3D, F). The ventral side of the hoof-like process is smooth and slightly concave proximodistally; its central region is pierced by five small irregularly shaped nutrient foramina (Fig. 3E). Proximally, the elliptical articular facet for pedal phalanx IV-4 is about twice as wide mediolaterally as tall dorsoventrally (Fig. 3G). In lateral and medial views, the hoof-like process slightly curves ventrally, and becomes progressively narrower dorsoventrally moving anteriorly (Fig. 3H, I). The proximal region of this ungual is strongly constricted transversely relative to the hoof-like process, with the poorly defined laterodorsal and mediodorsal margins that are roughly parallel to each other. This condition is also seen in the hadrosaurid genera

Brachylophosaurus (e.g., MOR 794), *Maiasaura* (e.g., MOR 005), and *Tsintaosaurus* (IVPP V 725), but differs from other known hadrosaurids, in which the proximal region of pedal phalanx IV-5 is distinctly narrow transversely near the hoof-like process, and gradually widens mediolaterally towards its articular facet.

It is noteworthy that YDENGP H006 does not differ markedly from the ungual of pedal digit II seen in Ceratopsidae, such as *Centrosaurus apertus* (AMNH 5351) and *Anchiceratops ornatus* (CMN 8547). Nevertheless, three subtle differences in morphology between these two types could be discerned with confidence: 1) the proximal articular facet of YDENGP H006 is slightly deeper dorsoventrally than that of pedal phalanx II-3 in Ceratopsidae; 2) the laterally and medially flared portions of the hoof-like process in YDENGP H006 is markedly elevated relative to the median base of the process, in contrast to the ungual of pedal digit II in Ceratopsidae, where the transversely flared region of the hoof-like process is generally flush with the base of this element; 3) two large neurovascular foramina are present in the shallow, dorsoventrally oriented lateral and medial sulci between the proximal constriction and hoof-like process of YDENGP H006 respectively (Fig. 3E, H, I), whereas the equivalent foramina are never found in pedal phalanx II-3 of Ceratopsidae.

4.3 Other indeterminate material of hadrosauroids

Some preadult vertebrae found in the Lijiagou bonebed do not differ drastically from the equivalents in hadrosauriforms. However, based on the information derived from osteological comparisons in current research, we argue that all other bones from this bonebed do not explicitly suggest the presence of non-hadrosauroid hadrosauriforms. Additionally, the known stratigraphic age of non-hadrosauroid hadrosauriforms never extends to the Late Cretaceous (Paul, 2008; McDonald, 2012). Thus, the preceding vertebrae recovered from the Lijiagou bonebed are recognized as Hadrosauroidea indet.

Dorsal vertebrae (YDENGP H012–H013) Two preadult middle dorsal vertebrae were collected from the Lijiagou bonebed. Both of them are incomplete and heavily eroded, where the neural spine and most of the paired neural arches are missing from each element (Fig. 4A–F). The centra of these two middle dorsal vertebrae are nearly amphiplatyan in lateral view, as in other known hadrosauroids. They are dorsoventrally taller than mediolaterally wide and anteroposteriorly long. Both the anterior and posterior articular surfaces of each centrum are heart-shaped; the anterior one is slightly shorter dorsoventrally than the posterior one (Fig. 4A–D). The left and right lateral sides of the centrum are laterally bowed along the transverse plane but anteroposteriorly concave. The ventral half of each lateral side is pierced by several small foramina. Between the paired neural arches, the centrum contributes to the ventral limit of the neural canal (Fig. 4A, B, E). In ventral view, the paired lateral surfaces of each centrum gradually converge to form a keel-like ridge along the sagittal plane (Fig. 4F). This sharp ridge is modestly convex dorsally (Fig. 4C, D). Interestingly, a deep, round hole is visible on the anterior surface of YDENGP H012 (Fig. 4A, E). It is inferred to reveal invertebrate scavenging (e.g., the larval borings) that likely resulted in damage of this bone prior to final burial. This taphonomic feature is also known from the Dalton Wells dinosaur bonebeds in Utah (Britt et al., 2009).

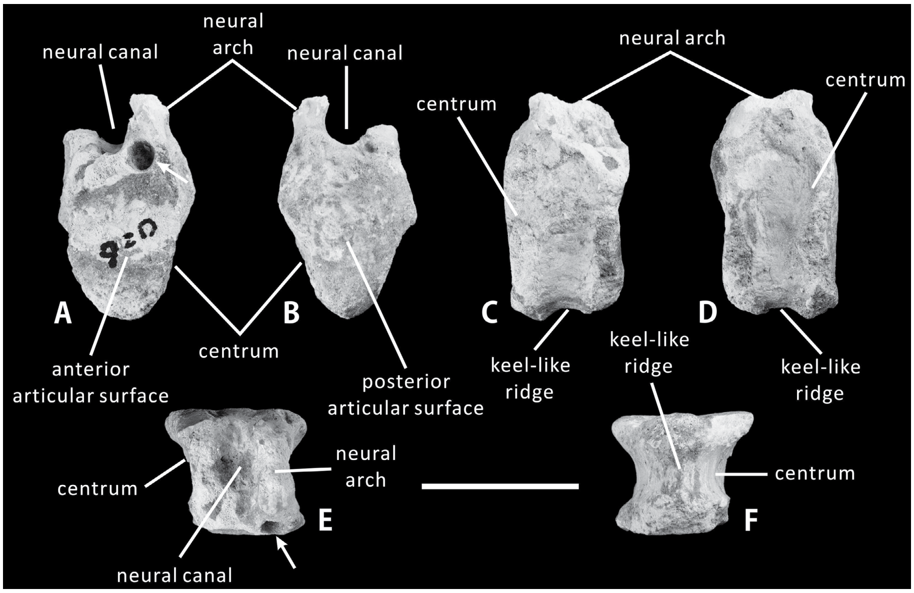

Fig. 4 Indeterminate hadrosauroid dorsal vertebra (YDENGP H012) recovered from the Lijiagou locality
In anterior (A), posterior (B), right lateral (C), left lateral (D), dorsal (E), and ventral (F) views
Scale bar=4 cm. The bioerosive trace produced by invertebrate borings is indicated by the arrow

Caudal vertebrae (YDENGP H014–H027)　During the 2011 field season, we retrieved fourteen hadrosauroid anterior and middle caudal vertebrae at the Lijiagou locality, each of which lacks the neural spine and paired neural arches, and definitely comes from the preadult stages (Fig. 5A–D). All the centra are typically amphiplatyan and subrectangular in lateral view. Ventrally, four lunate facets for articulation with two neighboring chevrons are located at the corners of the subrectangular base of each centrum; the anterior chevron facets are slightly convex and face anteroventrally, whereas the posterior chevron facets are enlarged, more ventrally positioned, and posteroventrally directed. There is no sign of the median keel on the strongly depressed ventral surface of each centrum. A fairly narrow base of the neural canal lies between the sutural surfaces of each centrum for the paired neural arches.

For the vertebrae in the middle region of the anterior caudals (YDENGP H014–H016), the centrum retains circular anterior and posterior articular surfaces; its dorsoventral height is approximately equal to the mediolateral width, but is significantly greater than the anteroposterior length (Fig. 5A).

Four vertebrae (YDENGP H017–H020) display the general morphology of those in the posterior region of the anterior caudals among hadrosauriforms. Each centrum is characterized by hexagonal anterior and posterior articular surfaces, somewhat anteroposteriorly concave lateral sides, and markedly defined edges (Fig. 5B). It is slightly taller dorsoventrally and wider mediolaterally than long anteroposteriorly. The lateral edges of the subrectangular ventral surface of each centrum are moderately convex dorsally.

The morphology of the middle caudal vertebrae (YDENGP H021–H027) is quite similar to that of the vertebrae in the posterior region of the anterior caudals (Fig. 5C, D). However, the centra of the former elements are proportionally longer than those of the latter elements. The three dimensions of each centrum in the middle caudals are generally equal to one another.

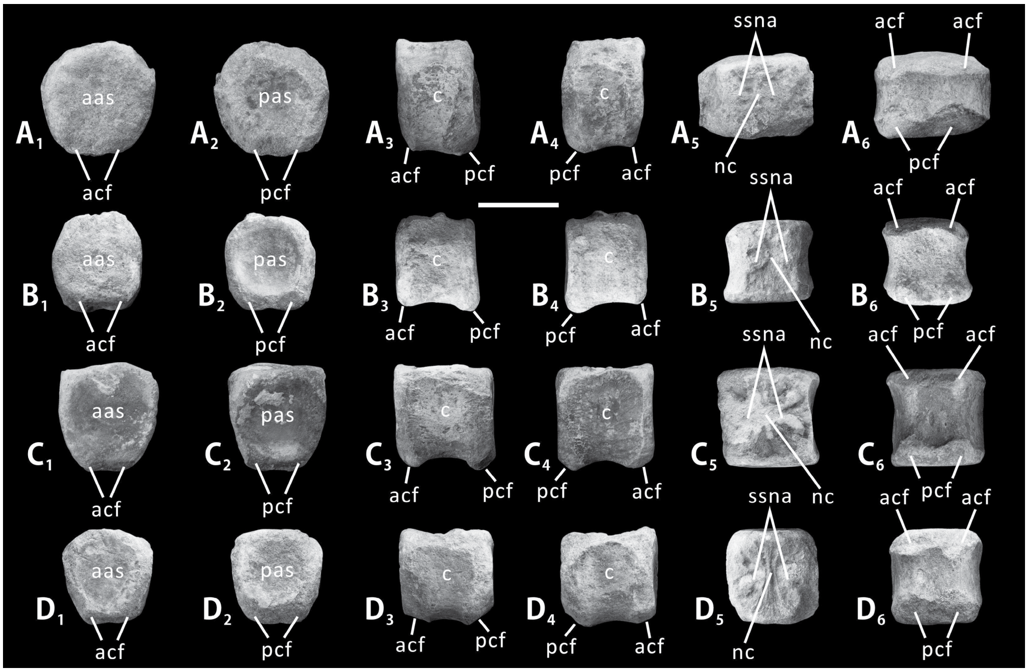

Fig. 5 Indeterminate hadrosauroid caudal vertebrae recovered from the Lijiagou locality
A. vertebra in the middle region of the anterior caudals (YDENGP H015), B. vertebra in the posterior region of the anterior caudals (YDENGP H019), C. vertebra in the anterior region of the middle caudals (YDENGP H025), D. vertebra in the middle region of the middle caudals (YDENGP H027), in anterior (A$_1$–D$_1$), posterior (A$_2$–D$_2$), left lateral ((A$_3$–D$_3$), right lateral (A$_4$–D$_4$), dorsal ((A$_5$–D$_5$), and ventral (A$_6$–D$_6$) views
Scale bar=2 cm
Abbreviations: aas. anterior articular surface 前关节面; acf. anterior chevron facet 前脉弧面; c. centrum 椎体; nc. neural canal 椎管; pas. posterior articular surface 后关节面; pcf. posterior chevron facet 后脉弧面; ssna. sutural surface for the neural arch 椎弓缝合面

5 Discussion

5.1 Systematic status

At least two hadrosauroid taxa are known from the Lijiagou bonebed within the middle part of the Upper Cretaceous Majiacun Formation: a basal taxon and a more derived one. These two taxa cannot be confidently identified to the genus level, because of a lack of diagnostic characters and the dominance of preadult specimens in the Lijiagou hadrosauroid material.

The basal taxon shows close hadrosauroid affinities, as indicated by a series of plesiomorphic features seen in non-hadrosaurid hadrosauroids. These features are unchanged throughout ontogeny, and include: ventrally positioned, anteroposteriorly aligned dispersedly small foramina on the lateral surface of the maxilla, a straight dorsal edge of the scapular blade, a transversely narrow deltopectoral crest of the humerus with a shallowly arcuate laterodistal corner, a slightly curved medially femoral shaft, and a slight medial twist of the posteromedial surface of the fibular mid-shaft. Furthermore, this taxon shares three characters with the relatively derived non-hadrosaurid hadrosauroids, especially the genera *Gilmoreosaurus* and *Bactrosaurus*: an ectopterygoid shelf that is slightly inclined anterodorsally, a gently recurved anterior half of the acromion process, and a robust lateral condyle of the tibia relative to the posteromedial condyle. Therefore, the basal taxon described here may represent a relatively derived non-hadrosaurid hadrosauroid that is closely related to the genera *Gilmoreosaurus* and *Bactrosaurus*. Notably, Xing et al. (2014) reported two non-hadrosaurid hadrosauroids from the Zhoujiagou bonebed of the adjacent Xixia Basin, which also occur in the middle Majiacun Formation. One taxon appears *Gilmoreosaurus*-like, and the other is *Zhanghenglong yangchengensis*, a basal hadrosauroid closely related to Hadrosauridae. It is possible that the indeterminate basal hadrosauroid from the Lijiagou bonebed and the *Gilmoreosaurus*-like taxon from the Zhoujiagou bonebed represent the same genus and species. However, this hypothesis requires further testing via the discovery of adult cranial material for the indeterminate basal hadrosauroid at the Lijiagou locality.

The other taxon from the Lijiagou bonebed appears to be more derived than the indeterminate basal hadrosauroid, and exhibits a combination of features typical of hadrosaurines: a straight acromion process of the scapula, a weakly developed posterodorsal corner of the iliac peduncle of the ischium, a rounded terminus of the rod-shaped ischial shaft, and a hoof-shaped ungual of pedal digit IV that is mediolaterally expanded in its distal region. Although the first three characters are from the preadult specimens, they are relatively invariant through ontogeny in hadrosaurines. Thus, the more derived taxon from the Lijiagou bonebed is very likely to be of hadrosaurine origin. Significantly, this indeterminate hadrosaurine possesses a strongly constricted transversely proximal region of pedal phalanx IV-5, in which the laterodorsal and mediodorsal margins are roughly parallel to each other. Within Hadrosaurinae, this configuration is only seen in *Brachylophosaurus* and *Maiasaura* of the tribe Brachylophosaurini (Gates et al., 2011). Therefore, the possibility that the indeterminate hadrosaurine at the Lijiagou locality represents an Asian member of Brachylophosaurini cannot be ruled out.

5.2 Ethological implication

The overwhelming majority (94%) of hadrosauroid elements uncovered in the Lijiagou bonebed are inferred to come from late nestlings and early juveniles (Table 1), similar to the age structure of sauropods at the same horizon. The co-occurrence of these preadult dinosaurs with scattered eggs and eggshell fragments in the Lijiagou bonebed suggests that the habitat of the late nestling and early juvenile dinosaur individuals was not far away from the nests. The dominance of late nestling and early juvenile specimens in the Lijiagou hadrosauroid material supports the hypothesis of Carpenter (1999) that the hadrosaur herd consisting of the late juveniles, subadults, and adults was geographically segregated from the younger individuals that had not reached half of the adult size. This possible life behavior has also been advocated for the hadrosaurids *Amurosaurus riabinini* (Lauters et al., 2008), *Maiasaura peeblesorum* (Horner and Makela, 1979), and *Hypacrosaurus stebingeri* (Horner and Currie, 1994). The presence of a few adult-sized hadrosauroid specimens at the Lijiagou locality may suggest parental care for the non-adult hadrosauroid individuals less than 50% of the adult size.

5.3 Biostratigraphic and biogeographic significance

The geographic origin of Hadrosauridae has been a difficult issue, largely unresolved because of the considerable uncertainty regarding the phylogenetic topology of Hadrosauroidea, especially Hadrosaurinae (Horner et al., 2004; Godefroit et al., 2008; Prieto-Márquez, 2010). Recently, Xing et al. (2014) recovered two Asian basal hadrosauroid genera *Nanyangosaurus* and *Zhanghenglong* as the closest relatives to Hadrosauridae based on the results of cladistic analyses, and therefore argued that Hadrosauridae might have originated in Asia. However, the tree topology of Hadrosaurinae in Xing et al. (2014) provides little help in resolving the issue of the geographic origin of this group, as the North American and Asian origins of Hadrosaurinae are both plausible (Fig. 6). This makes the preceding hypothesis (i.e. the Asian origin of Hadrosauridae) slightly suspicious, although Asia has been broadly recognized as the ancestral area of Lambeosaurinae.

Temporal and stratigraphic calibration of the hadrosauroid cladogram proposed by Xing et al. (2014) indicates a minimum of 1.2 million year ghost lineage at the base of Hadrosaurinae

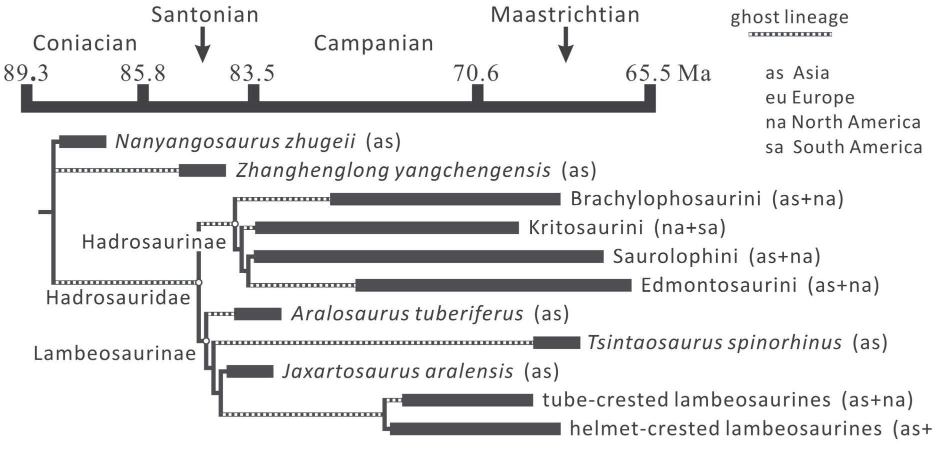

Fig. 6 Simplified cladogram of Hadrosauridae after time-stratigraphic calibration based on the strict consensus tree proposed by Xing et al. (2014)

(Fig. 6). Owing to the absence of a pre-Campanian fossil record of Hadrosaurinae, which is attributable to insufficient sampling, the early diversity of this taxon is severely underestimated, as indicated by the extensive ghost lineages for Kritosaurini and particularly Brachylophosaurini (Fig. 6). The discovery of an indeterminate hadrosaurine from the middle Santonian middle part of the Majiacun Formation nearly fills the pre-Campanian gap of Hadrosaurinae, and shortens the length of the ghost lineage at the base of this clade. In light of this important discovery, Hadrosaurinae is more likely to have originated in Asia than in North America. Consequently, the hypothesis that Hadrosauridae also originated in Asia becomes more plausible.

The Lijiagou locality exhibits the co-occurrence of basal hadrosauroid and hadrosaurid material at the same horizon, which has not been formally documented elsewhere in global Upper Cretaceous terrestrial deposits. This unique fossil assemblage may mirror the regional assemblage dynamics of hadrosauroids during the Santonian interval, in contrast to the great radiation of hadrosaurids and abrupt decline of basal hadrosauroids that took place in Eurasia and the Americas through the Campanian (Campione et al., 2012).

6 Conclusion

Phylogenetically informative features of available hadrosauroid specimens indicate the presence of at least two hadrosauroid taxa in the Lijiagou bonebed, despite the fact that most specimens are of the late nestling and early juvenile stages. Owing to the dominance of preadult material and a lack of diagnostic characters, none of the Lijiagou hadrosauroid specimens could be confidently identified to the genus level. One taxon may represent a relatively derived non-hadrosaurid hadrosauroid, and the other taxon is regarded as pertaining to Hadrosaurinae. The hypothesis that dinosaur nestlings and early juveniles are geographically segregated from the remaining herd is supported by the age structure of the Lijiagou hadrosauroid assemblage. The discovery of hadrosaurine material from the middle Santonian middle portion of the Majiacun Formation fills the pre-Campanian gap of Hadrosaurinae in the fossil record, providing further support for the Asian origins of both this clade and Hadrosauridae.

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湖北上白垩统马家村组的鸭嘴龙超科新材料

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摘要：报道和描述了一些在属级别上不确定的鸭嘴龙超科材料；标本发现于湖北省西北地区与河南交界的淅川盆地西南部的上白垩统马家村组中段。鸭嘴龙超科的骨骼化石和分散的恐龙蛋共存于同一层位，大部分的骨骼化石属于未离巢晚期和幼年早期的个体发育阶段。这一状况可以很好地解释为未离巢和幼年早期阶段的个体与更年老个体所组成的群体之间的地域分隔。通过直接的形态学对比研究，确信可以识别出至少两个鸭嘴龙超科的类群：其中一个类群可能代表了一个相对进步的基干鸭嘴龙类，而另一个类群则很可能归属于鸭嘴龙亚科。鉴于北美鸭嘴龙亚科最早出现的地层时代要更晚，中桑顿期马家村组中段的鸭嘴龙亚科化石材料提供了鸭嘴龙亚科乃至鸭嘴龙科亚洲起源的新证据。

关键词：湖北西北部，晚白垩世，中桑顿期，马家村组，李家沟骨层，鸭嘴龙超科

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