

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/324488089>

# A large-sized basal ankylopollexian from East Asia, shedding light on early biogeographic history of Iguanodontia

Article in Science Bulletin · April 2018

DOI: 10.1016/j.scib.2018.03.016

CITATIONS

0

READS

332

10 authors, including:



Xing Xu

Chinese Academy of Sciences

295 PUBLICATIONS 8,475 CITATIONS

[SEE PROFILE](#)



Hai Xing

Beijing Museum of Natural History

16 PUBLICATIONS 46 CITATIONS

[SEE PROFILE](#)



Contents lists available at ScienceDirect

Science Bulletin

journal homepage: [www.elsevier.com/locate/scib](http://www.elsevier.com/locate/scib)

## Article

# A large-sized basal ankylopollexian from East Asia, shedding light on early biogeographic history of Iguanodontia

Xing Xu <sup>a,\*</sup>, Qingwei Tan <sup>b</sup>, Yilong Gao <sup>c</sup>, Zhiqiang Bao <sup>c</sup>, Zhigang Yin <sup>c</sup>, Bin Guo <sup>c</sup>, Junyou Wang <sup>d</sup>, Lin Tan <sup>b</sup>, Yuguang Zhang <sup>e</sup>, Hai Xing <sup>e,\*</sup>

<sup>a</sup> Key Laboratory of Evolutionary Systematics of Vertebrates, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China

<sup>b</sup> Long Hao Institute of Geology and Paleontology, Hohhot 010010, China

<sup>c</sup> Bureau of Land and Resources of Bayannur, Bayannur 015000, China

<sup>d</sup> Inner Mongolia Museum of Natural History, Hohhot 010020, China

<sup>e</sup> Beijing Museum of Natural History, Beijing Academy of Science and Technology, Beijing 100050, China

## ARTICLE INFO

## Article history:

Received 2 March 2018

Received in revised form 21 March 2018

Accepted 21 March 2018

Available online xxxxx

## Keywords:

Non-hadrosauriform ankylopollexian

Lower Cretaceous

Bayingebi Formation

Inner Mongolia

Intercontinental dispersal

## ABSTRACT

A presumably mostly quadrupedal ankylopollexian iguanodontian, *Bayannurosaurus perfectus* gen. et sp. nov., is reported here, and is represented by an excellently well-preserved skeleton from the Lower Cretaceous Bayingebi Formation of Inner Mongolia, China. The diagnosis of the taxon includes several autapomorphies, notably a dorsally directed, strap-like posterodorsal process of the jugal and a horizontally oriented preacetabular process of the ilium. The nearly complete caudal series retains eight posterior-most caudals with procoelous, trapezoidal centra in dorsal view, and the last three caudals are fully fused. The discovery of *B. perfectus* opens a critical new window on the early evolution and intercontinental dispersal of Iguanodontia. The skeleton displays a transitional morphology between non-hadrosauriform ankylopollexians and Hadrosauriformes. A phylogenetic analysis indicates that *Bayannurosaurus* is positioned higher on the tree than *Hypselospinus*, but below *Ouranosaurus* just outside of Hadrosauriformes. The tree topology of Iguanodontia with temporal and spatial constraints reveals a possible biogeographic scenario supported by the statistical dispersal-vicariance analysis: around the J/K boundary, non-hadrosauriform ankylopollexians experienced multiple dispersal events from Europe to Asia, accompanying the coeval fall of the global sea level.

© 2018 Science China Press. Published by Elsevier B.V. and Science China Press. All rights reserved.

## 1. Introduction

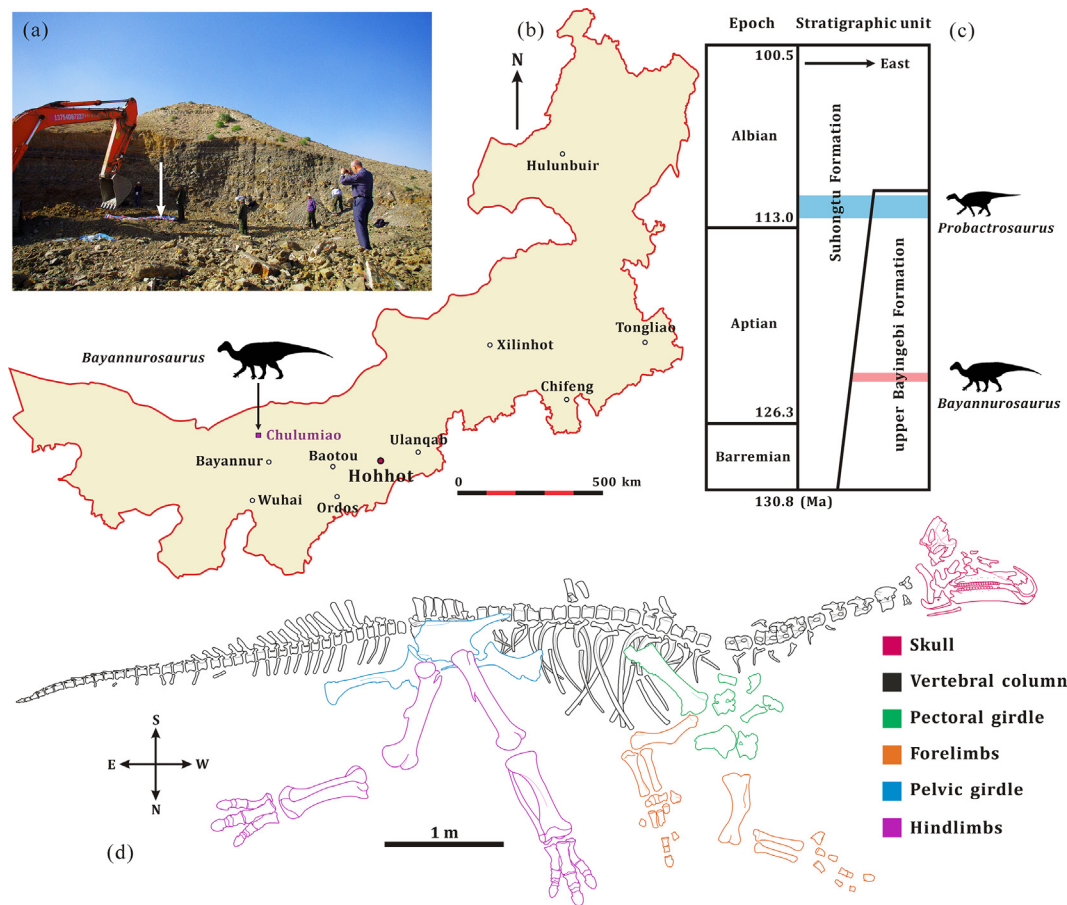
Iguanodontia is among the first-discovered dinosaurian groups in the world [1,2]. Due to the presence of copious, globally distributed remains that extend from the Middle Jurassic to the latest Cretaceous, the group has become one of the best studied ornithischian clades, particularly concerning its taxonomical diversity, ontogeny, geographic dispersal, and social behavior [3–7]. Ankylopollexia is a relatively derived iguanodontian subgroup containing animals of large body size (e.g. *Iguanodon* with an estimated body length of 10 m). Members of this clade display a suite of highly modified features for more efficient herbivory and locomotion [8,9]. These features presumably enabled the evolutionary success of the lineage during the Late Cretaceous, when the well documented hadrosauroids flourished in Asia and North America [10]. Recent discoveries and reviews have enhanced knowledge

of the early evolution of Ankylopollexia in Europe and North America [11,12]. However, comparable material in Asia, notably that of non-hadrosauriform ankylopollexians, is scarce and fragmentary. This hinders attempts to comprehensively elucidate the evolutionary history and related issues of the global iguanodontians.

During the summer of 2013, the Long Hao Institute of Geology and Paleontology, together with the Institute of Vertebrate Paleontology and Paleoanthropology of the Chinese Academy of Sciences, conducted a joint paleontological expedition at the Chulumiao locality, Urad Rear Banner, Bayannur, western Inner Mongolia, China. As a result of sustained excavations, the expedition collected an excellently well-preserved iguanodontian skeleton (~9 m) from the upper half of the Lower Cretaceous Bayingebi Formation (Fig. 1). Here we name and briefly describe a new non-hadrosauriform iguanodontian on the basis of this exquisite specimen, infer the gait of the taxon by means of comparisons of long bone measurements among ornithopods, and discuss the phylogenetic interrelationships among non-hadrosaurid iguanodontians. The discovery of this taxon is also very helpful in shedding light

\* Corresponding authors.

E-mail addresses: [xu.xing@ivpp.ac.cn](mailto:xu.xing@ivpp.ac.cn) (X. Xu), [xinghai@bmnh.org.cn](mailto:xinghai@bmnh.org.cn) (H. Xing).



**Fig. 1.** Locality and horizon of the holotype (IMMNH PV00001) of *Bayannurosaurus perfectus* gen. et sp. nov.. (a) Fossil site at the quarry indicated by a white arrow. (b) Chulumiao locality in southwestern Inner Mongolia (China), where the holotype of *B. perfectus* was collected. (c) Stratigraphic distribution of *B. perfectus* within the upper Bayingebi Formation. (d) Holotype of *B. perfectus* originally exposed at the quarry.

on the process of intercontinental dispersal of Iguanodontia around the Jurassic–Cretaceous boundary.

## 2. Systematic palaeontology

Ornithischia Seeley, 1887.

Ornithopoda Marsh, 1881.

Iguanodontia Dollo, 1888 *sensu* Sereno, 1998.

Ankylopollexia Sereno, 1986 *sensu* Sereno, 1998.

*Bayannurosaurus perfectus* gen. et sp. nov.

### 2.1. Etymology

‘Bayannur’, the name of the general geographic area where the fossil was retrieved; ‘saurus’, based on the Greek word ‘sauros’ for lizard. ‘perfectus’, in reference to the perfect preservation of the skeleton designated as the holotypic specimen.

### 2.2. Holotype

IMMNH PV00001 (housed at the Inner Mongolia Museum of Natural History, Hohhot, Inner Mongolia), a nearly complete, semi-articulated skeleton, including the entire caudal series.

### 2.3. Locality and horizon

Chulumiao, ~7 km north of Chaogewenduer Town, Urad Rear Banner, Bayannur, Inner Mongolia (Fig. 1b); middle part of the

upper half of the Bayingebi Formation (Fig. 1c); Early Cretaceous (early Aptian) [13,14].

### 2.4. Diagnosis

Large non-hadrosauriform iguanodontian (~9 m long in presumable adults) with the following unique combination of features (\*probable autapomorphies): denticulate anteromedial premaxillary oral margin with a shallow peripheral groove; occlusal margin of the premaxilla strongly ventrally offset; small, semicircular depression of the maxilla (indicative of the antorbital fossa), located a short distance from the maxillary ventral margin; markedly bifurcated anterior maxilla with an elevated anterodorsal process; elongate jugal contact surface of the maxilla entirely separated from the thickened ascending process; jugal bearing a relatively robust, slightly anteriorly curved postorbital process and a dorsally directed, strap-like posterodorsal process; posterior neck of the jugal slightly dorsoventrally deeper than the anterior neck; supraoccipital excluded from the foramen magnum; posteriorly inclined coronoid process with a finger-shaped, anteroposteriorly narrow apex; tooth crowns with multiple weak mesiodistal wrinkles; labial surface of the maxillary crown with a prominent primary ridge and 1–2 parallel accessory ridges; each alveolus of the middle dentary holding one replacement tooth and one functional tooth; each dentary crown with a distally offset, weakly developed primary ridge; average height/width ratio of ~1.85 for inactive crowns of the middle dentary; deeply opisthocelous cervical centra; amphiplatyan centra along the dorsal series;

posterior-most caudals with procoelous centra showing trapezoidal dorsal outlines; dorsal and ventral margins of the scapular blade that strongly diverge distally; deltopectoral crest anteriorly directed; carpals fused together to form a massive block; large, subconical ungual of manual digit I with a length/width ratio close to 1.0; iliac preacetabular process horizontally oriented; postacetabular process of the ilium having a strongly convex dorsal margin; distal blade of the pubis mediolaterally thin and deeply expanded dorsoventrally; ischial shaft straight; distal condyles of the femur strongly anteroposteriorly expanded; hoof-like unguals of manual and pedal digits III.

### 3. Description and comparisons

IMMNH PV00001 presumably comes from an adult individual, as indicated by its large size, highly co-ossified skull roof and neurocranium, and closed neurocentral sutures of the cervical series. A concise osteological description is provided here for this specimen (Figs. 1–3; see [Supplementary Material I](#) for additional figures).

#### 3.1. Cranium

The skull is anteroposteriorly long and dorsoventrally low in lateral view, measuring ~80 cm in total length. The elongate external naris overhangs the anterior part of the maxilla, in contrast to the small, subcircular external naris restricted to the oral region of the premaxilla in Rhabdodontidae and more basal ornithopods [15]. The premaxillary part of the premaxilla lacks the slightly elevated outer narial fossa seen in hadrosaurines [16]. In the anteromedial oral margin of the premaxilla, two denticulate layers are entirely separated by a shallow, sinuous groove. The dorsoventrally low maxilla is anteriorly bifurcated: the anterodorsal process is unbent and more dorsomedially positioned than the anteroventral one. By contrast, a single wedge-shaped anterior process of the maxilla is present in *Dakotadon*, *Camptosaurus* and most non-ankylopollexian iguanodontians [12]. The elongate, finger-shaped jugal facet of the maxilla is entirely posteroventrally offset from the transversely thick ascending process, as in *Mantellisaurus* and *Iguanodon*. Lateral to the ascending process, a small, semicircular depression represents the antorbital fossa; the distance between the fossa and the maxillary ventral margin is not over 150% the height of the unworn maxillary crown, similar to the condition in *Dryosaurus* and *Camptosaurus*. The jugal has a relatively robust, gently anteriorly curved postorbital process, whereas the process in *Dysalotosaurus* and *Ouranosaurus* is nearly straight. The posterodorsal process of the jugal is strap-like and dorsally directed. In comparison, it is posterodorsally directed in many other ankylopollexians, and is highly reduced in some non-ankylopollexian ornithopods, such as *Tenontosaurus* and *Thescelosaurus* [17,18]. The posterior neck of the jugal is subequal in depth to the anterior neck. The quadrate is mediolaterally expanded along its ventral end, where the medial condyle is nearly flush with the larger, subrectangular lateral condyle. The quadratojugal notch is located well below the dorsoventral midpoint of the quadrate, as in *Levnesovia*. The quadrate process of the pterygoid is strongly forked: the dorsal ramus is much longer than the ventral ramus; the angle between the two rami is approximately 80°.

The dorsal orbital margin is laterally invaded by the flat frontal. The finger-shaped posterior process of the postorbital possesses a short, gradually tapered posteroventral corner, and does not reach the central region of the squamosal above the quadrate cotylus. In posterior view, the medial rami of the paired squamosals are widely separated by the parietal, as in other non-hadrosauriform iguanodontians [4]. The sagittal crest splits into two posterolateral ridges along the posterior third of the parietal, without any emi-

nence in between. This is more similar to the condition in other non-hadrosaurid ornithopods and some basal hadrosaurids (e.g. *Xuwulong*, *Eolambia* and *Sirindhorna*). In dorsal view, the supratemporal fenestra is subovate and anterolaterally-posteromedially elongate. The supraoccipital has an anteriorly tilted posterior surface lacking a median nuchal crest [19,20], and is excluded from the dorsal border of the foramen magnum, unlike the opposite condition in *Camptosaurus* and most non-ankylopollexian ornithopods [21]. The foramen magnum is nearly as deep as the central plate of the paired exoccipitals. The occipital condyle is strongly deflected ventrally, forming an angle of ~75° with the posterior portion of the skull roof, as in other basal iguanodontians. The basiptyergoid processes of the basisphenoid are lateroventrally and slightly posteriorly directed. The mediolateral constriction of the basioccipital between the spheno-occipital tubercles and the occipital condyle is much shorter than that of *Proa* and *Ouranosaurus*.

#### 3.2. Lower jaw

The prementary is broadly bowed in dorsal view, with some small, triangular denticles along the dorsal surface of the antero-medial region. Just below the dorsoventrally compressed, tongue-like dorsal median process, the bilobate ventral median process of the bone projects posteroventrally and progressively expands transversely towards its extremities. The anterior third of the dentary is slightly anteroventrally deflected, as in many other non-hadrosaurid styracosternans. Posterior to the prementary contact surface, the edentulous region of the dentary is ~8% as long as the dental battery, as in *Lanzhousaurus* and *Hypselospinus* [12,22], but is proportionately much shorter than in hadrosaurids [23]. The coronoid process is slightly posteriorly inclined relative to the dorsal edge of the dentary ramus, contrasting with the nearly vertical process in most non-hadrosaurid hadrosaurids such as *Altirhinus* and *Equijubus*. The apex of the coronoid process is anteroposteriorly narrow and finger-shaped. The angular was laterally exposed when in articulation, and has an oblique lateroventral suture with the overlying surangular. The surangular foramen occurs along the anterior region of the laterodorsal flange, as in *Ouranosaurus* and *Probactrosaurus* [24]. The mediolaterally thin prearticular protrudes anteriorly to produce a tapering process along its ventral border. Ceratobranchial II is nearly straight and rod-like, and is marked by numerous longitudinal striations. The broadly arched ceratobranchial I has an enlarged, suboval anterior tip.

#### 3.3. Dentition

The maxillary and dentary dental batteries contain 20 and 18 alveoli, respectively. Among the maxillary and dentary teeth, the apical half of the crown bears numerous elongate, lingulate marginal denticles, similar to the condition in all non-hadrosaurid iguanodontians and some basal hadrosaurids (e.g. *Tethyshadros*) [25]. Each denticle consists of multiple extremely small, loosely arranged knobs. Interestingly, the center of each denticle in a few functional teeth developed a flat, subcircular wear surface probably via attrition; moving apically, this surface gradually increases in size. There are a suite of subhorizontal mesiodistal wrinkles connecting the primary ridge with the marginal denticles in most maxillary and dentary crowns, as in *Mantellisaurus* and *Sirindhorna*. The labial side of the maxillary crown is ornamented with a prominent primary ridge and 1–2 slightly short, parallel accessory ridges, in striking contrast to at least 10 evenly-spaced accessory ridges with no primary ridge in Rhabdodontidae [15]. The largest dentary tooth has a crown measuring 52 mm high and 28 mm wide. The dentary tooth crowns are mesiodistally broad and shield-like, and bear a distally offset primary ridge, a shorter, less developed



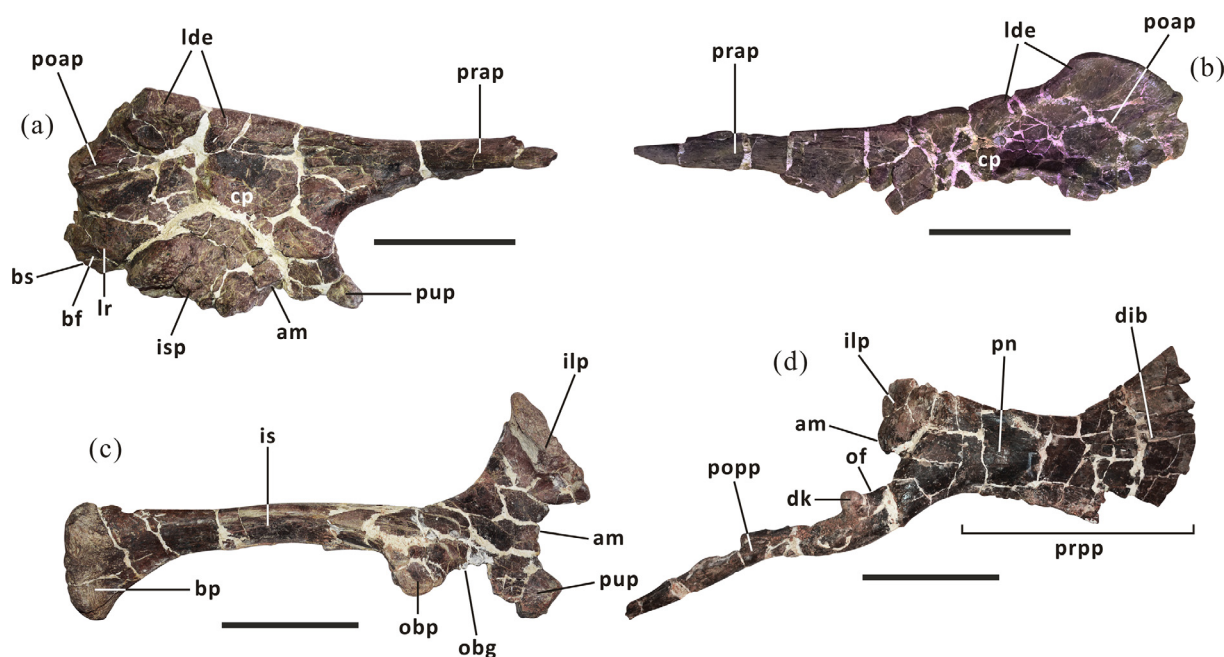
**Fig. 2.** Skull elements of *Bayannurosaurus perfectus* gen. et sp. nov. (holotype: IMMNH PV00001), most of which are incomplete. Fused skull roof and neurocranium in (a) dorsal and (b) posteroventral views; right premaxilla in (c) lateral view; articulated right pterygoid and quadrate in (d) posteromedial view; articulated right maxilla and ectopterygoid in (e) lateral view; right jugal in (f) medial view; right ceratobranchial II in (g) lateral view; right ceratobranchial I in (h) lateral view; predentary in (i) posterior view; articulated left surangular and angular in (j) lateral view; right prearticular in (k) lateral view; right dentary in (l) medial view; left maxillary teeth in (m) labial view; right dentary teeth in (n) lingual view. Scale bars: 10 cm (a–l) and 2 cm (m–n). See supplementary material I for anatomical abbreviations.

secondary ridge, and 1–2 truncated, relatively faint accessory ridges on their lingual surfaces. The primary ridges of the dentary crowns are mesiodistally narrower and labiolingually lower than those of the maxillary crowns. Each alveolus in the middle dental battery of the dentary holds one replacement tooth and one functional tooth.

### 3.4. Postcranium

Twenty-eight presacral vertebrae are preserved, and a few more may be missing. Among these vertebrae are 11 cervicals and 17 dorsals. The neural spine of the axis is dorsoventrally tall and anteroposteriorly expanded. The centra of the cervicals are deeply opisthocoealous, unlike the nearly amphiplatyan centra in

*Tenontosaurus*. As in *Lanzhousaurus*, *Uteodon* and most non-styracosternan ornithomorphs [26,27], the centra are amphiplatyan throughout the entire dorsal series. The sacrum consists of six sacral vertebrae. The caudal series comprises 39 vertebrae, the centra of which gradually decrease in depth moving posteriorly (see [Supplementary Material II](#) for measurements). The anterior caudals have relatively tall neural spines that are slightly longer than the corresponding chevrons. In the last nine caudals, the centra shift from being slightly amphicoelous to modestly procoelous, and are trapezoidal in dorsal view, with the anterior end mediolaterally wider than the posterior one. The amphiplaty/ slight amphicoelous for most of the caudal series may indicate that the tail of this animal has relatively high flexibility but appears to be not quite stable in locomotion [28]. Compared to some non-ankylopollexian iguan-



**Fig. 3.** Selected elements of the pelvic girdle of *Bayannurosaurus perfectus* gen. et sp. nov. (holotype: IMMNH PV00001). Partial right ilium in (a) lateral view; partial left ilium in (b) lateral view; nearly complete right ischium in (c) lateral view; partial left pubis in (d) medial view. Scale bars: 20 cm (a–d). See supplementary material I for anatomical abbreviations.

odontians such as *Valdosaurus*, proportionally dorsoventrally taller centra and larger prezygapophyseal angles of posterior caudals in *Bayannurosaurus* may suggest greater dorsoventral stiffness for sustained terrestrial locomotion; however, owing to the possession of relatively lower centra and smaller prezygapophyseal angles, the intervertebral joints of posterior caudals of *Bayannurosaurus* are possibly less stiff dorsoventrally as compared with those of some hadrosauroids (e.g. *Olorotitan*) [29]. The last three caudals lack any evidence of bony neural spines and zygapophyses, and are fused together to form a pygostyle-like structure that tapers posteriorly, similar to the condition in *Iguanodon* and several non-avian theropods [30,31]. This structure may be ascribed to intraspecific variation throughout ontogeny.

The posterolateral process of the sternum appears to be slightly shorter than the anteromedial plate. The dorsal and ventral borders of the scapular blade strongly diverge distally from each other, as in many basal iguanodontians such as *Rhabdodon*. The posterovertral corner of the coracoid adjacent to the glenoid is pointed and ventrally projecting.

The humerus is ~142% as long as the ulna. The deltopectoral crest is anteriorly directed and broadly arcuate, as in many non-hadrosauriform iguanodontians. The carpals are fused together to form a massive block. Metacarpals II–IV are appressed in situ. The ungual of manual digit I is enlarged and subconical, being as long as it is wide. The ungual of manual digit III is flattened and hoof-like, contrasting with the sharply pointed ungual in *Camptosaurus* and most non-ankylopollexian ornithomorphs [32].

The ilium has an elongate, horizontally oriented preacetabular process. The dorsal margin of the iliac central plate is straight and slightly anteroventrally inclined, as in *Camptosaurus* and Dryosauridae. The postacetabular process of the bone is strongly dorsally convex, and is comparable to that in *Tenontosaurus*. The deep brevis fossa on the ventral surface of the postacetabular process is laterally defined by a ridge. There is an incipiently developed laterodorsal eminence between the dorsal regions of the central plate and postacetabular process. The straight ischial shaft has a boot-like, strongly anteroventrally expanded distal end, and forms an angle of ~135° with the pubic peduncle. A dorsal knob

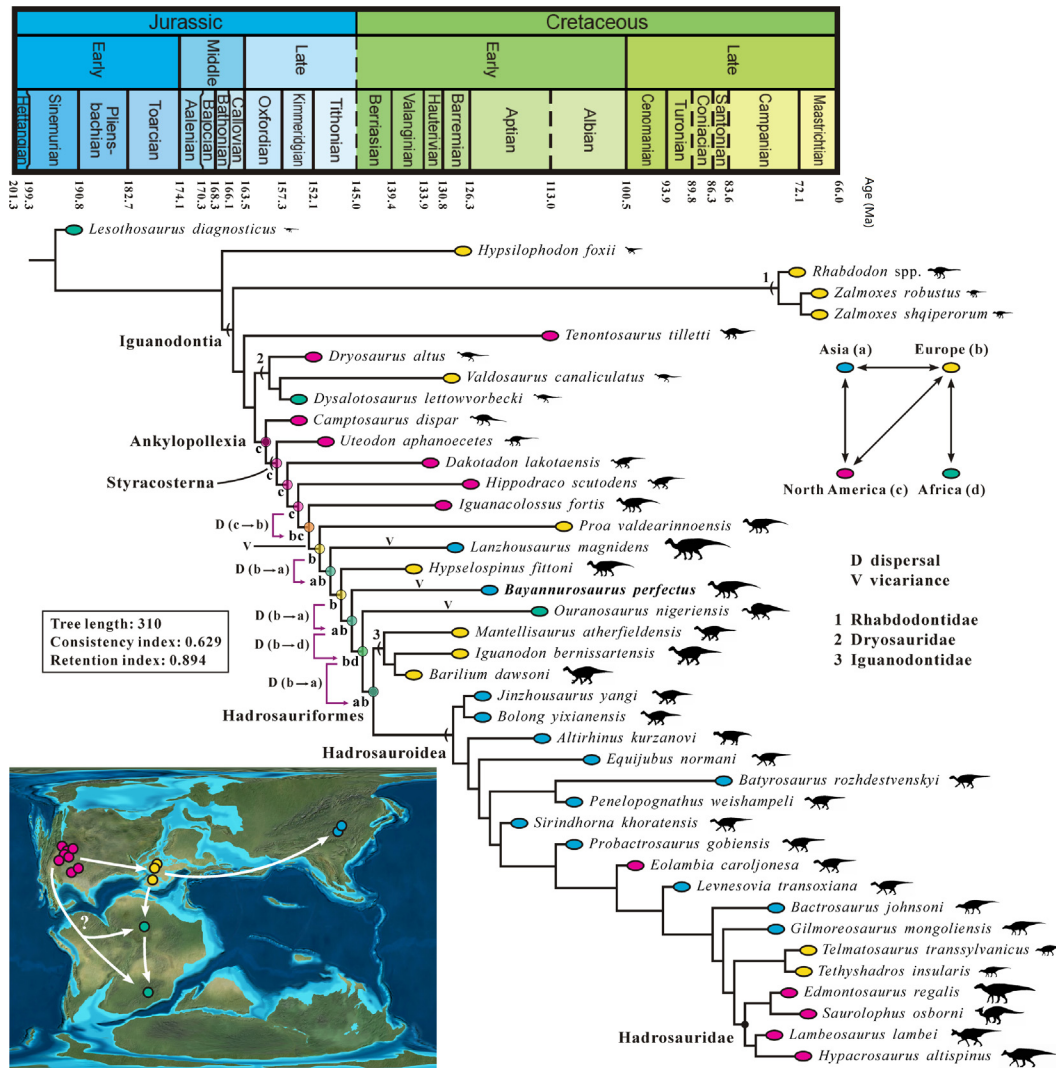
is present along the proximal segment of the postpubic process of the pubis.

The femur has a longitudinal cleft separating the greater and lesser trochanters. The femoral shaft is nearly straight, with a mediolaterally thick, subtriangular fourth trochanter along its middle portion. Two distal tarsals are preserved beneath the massive calcaneum and astragalus; the reniform distal tarsal IV is anteroposteriorly much longer than the round distal tarsal III. Metatarsal I is small and splint-like, showing a sigmoid medial outline. The pedal phalangeal formula is 0-3-4-5-0, as in most ankylopollexians. The unguals of pedal digits II–IV are proximodistally elongate and hoof-like, in contrast to the shortened unguals in many hadrosauroids.

## 4. Discussion

### 4.1. Phylogenetic analysis

To assess the systematic position of *Bayannurosaurus*, we conducted a phylogenetic analysis of Iguanodontia based on an updated data matrix comprising 40 species and 123 unordered characters, with the incorporation of almost all known unquestionable non-hadrosauroid ankylopollexians (see [Supplementary Materials III and IV](#)). The data matrix was mainly modified from McDonald [4] and Norman [12], and was analyzed in the program TNT, using a traditional search under the TBR swapping algorithm with 100 trees saved per replication [33]. The cladistic analysis produced a single most parsimonious tree that provides a new phylogenetic framework for non-hadrosauroid ankylopollexians (Fig. 4). *Bayannurosaurus* is recovered within Ankylopollexia but outside of Hadrosauriformes, and is positioned higher on the tree than *Hypselospinus*, but below *Ouranosaurus*. Our current analysis also posits a sister–taxon relationship between *Ouranosaurus* and Hadrosauriformes. Furthermore, Rhabdodontidae forms the first lineage of Iguanodontia to branch off; Iguanodontidae is constituted by the clade of *Mantellisaurus* + (*Barilium* + *Iguanodon*) endemic to Europe; the clade of *Bolong* + *Jinzhouosaurus* occupies the most basal position of Hadrosauroidea.



**Fig. 4.** Phylogenetic, temporal and paleogeographical relationships among 38 iguanodontians, showing the systematic position of *Bayannurosaurus perfectus* gen. et sp. nov. and deducing a intercontinental dispersal pattern of non-hadrosauriform iguanodontians around the J/K boundary (paleogeographic map of 140 Ma courtesy of Ron Blakey), based on the SDVA using RASP. The tree topology is based on a single most parsimonious tree resulting from the maximum parsimony analysis of Iguanodontia.

#### 4.2. Character evolution

Multiple characters occurring in *Bayannurosaurus*, such as the denticulate oral margin of the premaxilla and the posterolaterally and ventrally directed basiptyergoid process, demonstrates unequivocally the ankylopollexian affinities of the taxon [4,12]. Of note, *Bayannurosaurus* shares a series of primitive features with many non-hadrosauriform iguanodontians. These features include a small, roughly circular antorbital fossa, a jugal contact surface of the maxilla entirely posteriorly offset from the ascending process, only one replacement tooth per alveolus in the middle dental battery of the dentary, and an anteriorly directed deltopectoral crest of the humerus. This taxon also exhibits some derived features largely typical of hadrosauriforms, including a clearly bifurcate anterior part of the maxilla, a dorsoventrally tall and anteroposteriorly wide neural spine of the axis, a mediolaterally thin, dorsoventrally expanded distal blade of the pubis, and a flattened, hoof-like ungual of manual digit III. Overall, the current osteological comparisons present a combination of plesiomorphic and apomorphic characters of Ankylopollexia in the holotype skeleton of *Bayannurosaurus*, providing key information on the transitional morphology between basal ankylopollexians and more derived hadrosauriforms.

#### 4.3. Locomotion pattern

Maidment and Barrett [9] proposed a scheme to determine the quadrupedal ability of ornithischians using five characters, among which the possession of a femur longer than the tibia and a reduced, non-pendant fourth trochanter appears more closely correlated with quadrupedal locomotion than that of the other three characters. Here we partly adopt this scheme to infer the stance of *Bayannurosaurus*: (1) the ratio between the lengths of the femur and tibia and (2) the development of the fourth trochanter are utilized as two major indicators of locomotion patterns.

Comparisons of limb proportions (i.e. humerus + ulna–femur–tibia ratios) among ornithopods are visualized on a ternary diagram (Fig. 5) using the package ggtern of the software R [34], where the total disparity of character 1 in Ornithopoda is vividly reflected (see the dataset in Supplementary Material V). The data point of *Bayannurosaurus* lies in the plotting area above the blue line. This limited area covers ornithopods having the femur longer than the tibia. *Bayannurosaurus* plots near a cluster of hadrosaurids, because of similar limb proportions. Mature hadrosaurids are currently interpreted as facultatively bipedal (mostly quadrupedal), based on results of biomechanic and morphometric analyses, as well as trackway evidence [35–37]. It is therefore postulated that

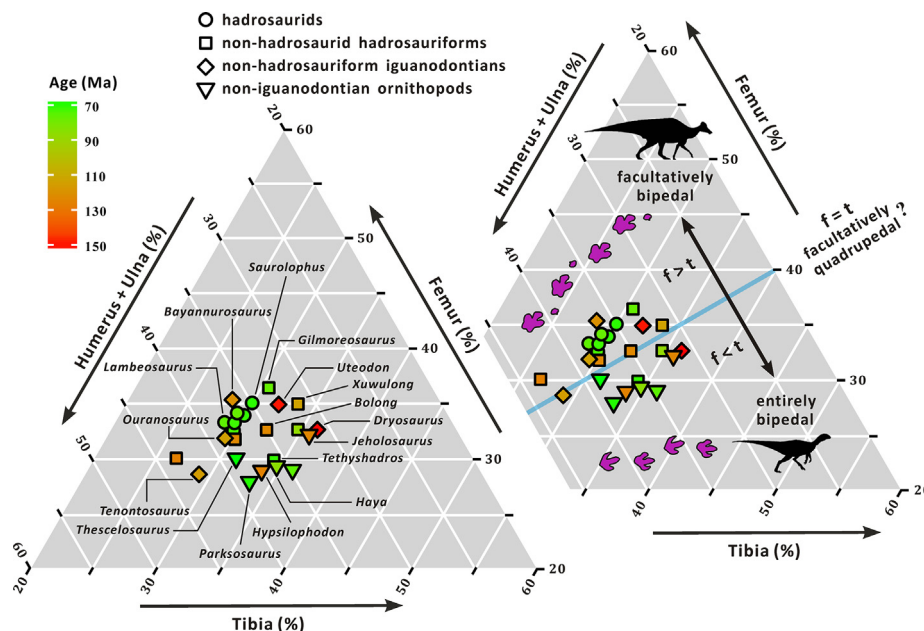


Fig. 5. Ternary morphospace diagrams of length measurements and proportions of selected limb elements (humerus + ulna, femur and tibia) for ornithomorphs.

*Bayannurosaurus* is also a facultative biped. Likewise, the reduced fourth trochanter of the femur is indicative of the long-term quadrupedality for *Bayannurosaurus*; the hoof-like manual unguals and development of the lateral process of the ulna that show potential correlations with quadrupedality are also found in this taxon [9]. In addition, *Tenontosaurus* and *Bolong* almost plot along the blue line that denotes the femur as long as the tibia. This line may be correlated with the facultatively quadrupedal pattern.

#### 4.4. Biogeographic inference

Numerous studies have so far focused on the phylogeny of Iguanodontia [3,4,11,12]. However, reconstruction of biogeographic history of non-hadrosauriform iguanodontians has lagged behind. Our current phylogenetic topology incorporating *Bayannurosaurus*, with temporal and spatial constraints, provides a new hypothesis regarding patterns of intercontinental dispersal of basal iguanodontians. The bulk of the hypothesis resulted from the statistical dispersal–vicariance analysis (SDVA) using the software RASP [38] (see Supplementary Material VI for the result of the SDVA in detail).

Given the basal positions of many North American species (e.g. *Dryosaurus altus*, *Tenontosaurus tilletti* and *Uteodon aphanocetes*) in Iguanodontia, we speculate that the extensive radiation of this clade might have first occurred in North America. Ankylopollexia is hypothesized to have originated in North America, as suggested by the SDVA (Fig. 4). This evolutionary event probably occurred no later than the early period of the Late Jurassic considering that the oldest two of the five North American species showing the most basal placement of Ankylopollexia are of Kimmeridgian and Tithonian age. Owing to the alternate occurrences of multiple European and Asian ankylopollexians (e.g. *Hypselospinus* and *Bayannurosaurus*) in the slightly more highly nested positions of the tree topology and the Early Cretaceous age (early Valanginian–early Albian) of these taxa, basal ankylopollexians are inferred to have immigrated to West Europe from North America prior to the Valanginian, and to have subsequently repeatedly dispersed into East Asia from West Europe via the east–west-oriented, elongate Tethyan archipelago around the Jurassic–Cretaceous boundary (Fig. 4), probably associated with the coeval global marine regression [39]. The biogeographic reconstruction using RASP indicates that two inde-

pendent dispersal events of non-hadrosauriform ankylopollexians from Europe to Asia and later vicariance would have led to allopatric speciation of *Lanzhousaurus magnidens* and *Bayannurosaurus perfectus* in Asia, in a similar manner to the formation of the ancestral taxon of Hadrosauroida in Asia. There are several other interpretations of the intercontinental dispersal of non-hadrosauriform ankylopollexians within Laurasia; however, the currently proposed “North America–Europe–Asia” model seems more logical based on available data and the result of the biogeographic analysis (Fig. 4). Moreover, the presence of non-hadrosauriform iguanodontians in the Upper Jurassic and Lower Cretaceous of Africa (e.g. *Ouranosaurus*) strongly indicates a land connection between Laurasia and Gondwana, as argued by Galton [40]. The related dispersal route from North America to Africa appears to go through either South America or West Europe (Fig. 4). Because basal iguanodontian material in Central and South America is extremely rare, West Europe is regarded herein as the most authentic transit area of the pre-Late Cretaceous iguanodontian dispersal from Laurasia to Gondwana. This possibility is also firmly corroborated by the SDVA.

Overall, West Europe might have played an important role in pushing the intercontinental dispersal of non-hadrosauriform iguanodontians forward around the Jurassic–Cretaceous boundary; in this period, non-hadrosauriform ankylopollexians possibly experienced multiple dispersal events from Europe to Asia, following the fall of the global sea level. New fossil finds from the uppermost Jurassic and lowermost Cretaceous of Asia, Europe and Africa will help clarify the biogeographic history of non-hadrosauriform iguanodontians.

#### Conflict of interest

The authors declare that they have no conflict of interest.

#### Acknowledgements

We thank the field crew for fossil collection, J.P. Jiao, T.Z. Liu, B.P. Zhou and K.X. Hui for major preparation, R.M. Dai, W.J. Zhao and W.P. Xie for coordinating the study, H.L. Zang for photography, Y. Kobayashi for discussions and sharing unpublished data, R. Blakely for providing paleogeographical maps, J. Mallon for revising the early draft, and three anonymous referees for their constructive



comments. This work was supported by the Beijing Natural Science Foundation (5174032), the National Natural Science Foundation of China (41688103, 41120124002, 91514302 and 41602006), the Strategic Priority Research Program of the Chinese Academy of Sciences (XDB18030504), the Youth Backbone Training Plan (201601), Overseas Talents Attracting Program (OTP-2018-001) and Innovative Team Program (IG201705N) of the Beijing Academy of Science and Technology, the Beijing Millions of Talents Project in the New Century and the Department of Land and Resources of Inner Mongolia.

### Author contributions

X. Xu and Q.W. Tan designed the project. X. Xu, Q.W. Tan, Y.L. Gao, Z.Q. Bao, Z.G. Yin, B. Guo and L. Tan collected the specimen and field data. X. Xu, Q.W. Tan, J.Y. Wang, Y.G. Zhang and H. Xing conducted anatomic experiments and statistical analyses. X. Xu and H. Xing wrote the manuscript. All authors prepared figures.

### Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.scib.2018.03.016>.

### References

- Mantell G. Notice on the *Iguanodon*, a newly discovered fossil reptile, from the sandstone of the Tilgate Forest, in Sussex. *Philos Trans R Soc Lond* 1825;115:179–86.
- Dollo L. *Iguanodontidae* et *Camptonotidae*. *C R Acad Sci* 1888;106:775–7.
- Norman DB. Basal iguanodontia. In: Weishampel DB, Dodson P, Osmólska H, editors. *The Dinosauria*. Berkeley: University of California Press; 2004. p. 413–37.
- McDonald AT. Phylogeny of basal iguanodonts (Dinosauria: Ornithischia): an update. *PLoS One* 2012;7:e36745.
- Hübner TR. Bone histology in *Dysalotosaurus lettowvorbecki* (Ornithischia: Iguanodontia) – variation, growth, and implications. *PLoS One* 2012;7:e29958.
- Horner JR, Makela R. Nest of juveniles provides evidence of family structure among dinosaurs. *Nature* 1979;282:296–8.
- Prieto-Márquez A. Global historical biogeography of hadrosaurid dinosaurs. *Zool J Linn Soc* 2010;159:503–25.
- Norman DB, Weishampel DB. Ornithopod feeding mechanisms: their bearing on the evolution of herbivory. *Am Nat* 1985;126:151–64.
- Maidment SCR, Barrett PM. Osteological correlates for quadrupedality in ornithischian dinosaurs. *Acta Palaeontol Pol* 2014;59:53–70.
- Sues H-D, Averianov A. A new basal hadrosauroid dinosaur from the Late Cretaceous of Uzbekistan and the early radiation of duck-billed dinosaurs. *Proc R Soc Lond B* 2009;276:2549–55.
- Boyd CA, Pagnac DC. Insight on the anatomy, systematic relationships, and age of the Early Cretaceous ankylopollexian dinosaur *Dakotadon lakotaensis*. *PeerJ* 2015;3:e1263.
- Norman DB. On the history, osteology, and systematic position of the Wealden (Hastings group) dinosaur *Hypselospinus fittoni* (Iguanodontia: Styracosterna). *Zool J Linn Soc* 2015;173:92–189.
- Wu RG, Zhou WP, Xu Z, et al. Discussion on the chronology of Suhongtu Formation in Bayingebi Basin. *Uranium Geol* 2010;26:152–7.
- Li S, Zheng DR, Zhang Q, et al. Discovery of the Jehol Biota from the Celaomiao region and discussion of the Lower Cretaceous of the Bayingebi Basin, northwestern China. *Palaeoworld* 2016;25:76–83.
- Weishampel DB, Jianu C-M, Csiki Z, et al. Osteology and phylogeny of *Zalmoxes* (n.g.), an unusual euornithopod dinosaur from the latest Cretaceous of Romania. *J Syst Palaeont* 2003;1:65–123.
- Xing H, Mallon JC, Currie ML. Supplementary cranial description of the types of *Edmontosaurus regalis* (Ornithischia: Hadrosauridae), with comments on the phylogenetics and biogeography of Hadrosaurinae. *PLoS One* 2017;12:e0175253.
- Thomas DA. The cranial anatomy of *Tenontosaurus tilletti* Ostrom, 1970 (Dinosauria, Ornithopoda). *Palaeontol Electronica* 2015;18.2(37A):1–98.
- Boyd CA. The cranial anatomy of the neornithischian dinosaur *Thescelosaurus neglectus*. *PeerJ* 2014;2:e669.
- Galton PM. The cranial anatomy of *Dryosaurus*, a hypsilophodontid dinosaur from the Upper Jurassic of North America and East Africa, with a review of the hypsilophodontids from the Upper Jurassic of North America. *Geol Palaeontol* 1983;17:207–43.
- Carpenter K, Lamanna MC. The braincase assigned to the ornithopod dinosaur *Uteodon* McDonald, 2011, reassigned to *Dryosaurus* Marsh, 1894: implications for iguanodontian morphology and taxonomy. *Ann Carnegie Mus* 2015;83:149–65.
- Brown CM, Boyd CA, Russell AP. A new basal ornithopod dinosaur (Frenchman Formation, Saskatchewan, Canada), and implications for late Maastrichtian ornithischian diversity in North America. *Zool J Linn Soc* 2011;163:1157–98.
- You HL, Ji Q, Li DQ. *Lanzhousaurus magnidens* gen. et sp. nov. from Gansu Province, China: the largest-toothed herbivorous dinosaur in the world. *Geol Bull China* 2005;24:785–94.
- Prieto-Márquez A. Global phylogeny of hadrosauridae (Dinosauria: Ornithopoda) using parsimony and Bayesian methods. *Zool J Linn Soc* 2010;159:435–502.
- Norman DB. On Asian ornithopods (Dinosauria: Ornithischia). 4. *Proctosaurus* Rozhdestvensky, 1966. *Zool J Linn Soc* 2002;136:113–44.
- Dalla Vecchia FM. *Tethyshadros insularis*, a new hadrosauroid dinosaur (Ornithischia) from the Upper Cretaceous of Italy. *J Vertebr Paleontol* 2009;29:1100–16.
- Carpenter K, Wilson Y. A new species of *Camptosaurus* (Ornithopoda: Dinosauria) from the Morrison Formation (Upper Jurassic) of Dinosaur National Monument, Utah, and a biomechanical analysis of its forelimb. *Ann Carnegie Mus* 2008;76:227–63.
- Bulter RJ, Jin LY, Chen J, et al. The postcranial osteology and phylogenetic position of the small ornithischian dinosaur *Changchunsaurus parvus* from the Quantou Formation (Cretaceous: Aptian–Cenomanian) of Jilin Province, north-eastern China. *Palaeontology* 2011;54:667–83.
- Fronimos JA, Wilson JA. Concavo-convex intercentral joints stabilize the vertebral column in sauropod dinosaurs and crocodylians. *Ameghiniana* 2017;54:151–76.
- Molnar JL, Pierce SE, Bhullar B-AS, et al. Morphological and functional changes in the vertebral column with increasing aquatic adaptation in crocodylomorphs. *R Soc Open Sci* 2015;2:150439.
- Barsbold R, Osmólska H, Watabe M, et al. A new oviraptorosaur (Dinosauria, Theropoda) from Mongolia: the first dinosaur with a pygostyle. *Acta Palaeontol Pol* 2000;45:97–106.
- Xu X, Cheng Y, Wang XL, et al. Pygostyle-like structure from *Beipiaosaurus* (Theropoda, Therizinosauridae) from the Lower Cretaceous Yixian Formation of Liaoning, China. *Acta Geol Sin* 2003;77:294–8.
- Gilmore CW. Osteology of the Jurassic reptile *Camptosaurus*, with a revision of the species of the genus, and descriptions of two new species. *Proc US Natl Mus* 1909;36:197–332.
- Goloboff P, Farris FC, Nixon KC. TNT, a free program for phylogenetic analysis. *Cladistics* 2008;24:774–86.
- Hamilton N. ggtern: an extension to 'ggplot2', for the creation of ternary diagrams. R package (version 2.1.5); 2016. <https://cran.r-project.org/package=ggtern>.
- Dilkes DW. An ontogenetic perspective on locomotion in the Late Cretaceous dinosaur *Maiaosaurus peeblesorum* (Ornithischia: Hadrosauridae). *Can J Earth Sci* 2001;38:1205–27.
- Currie PJ, Nodon GC, Lockley MG. Dinosaur footprints with skin impressions from the Cretaceous of Alberta and Colorado. *Can J Earth Sci* 1991;28:102–15.
- Díaz-Martínez I, Pereda-Suberbiola X, Pérez-Lorente F, et al. Ichnotaxonomic review of large ornithopod dinosaur tracks: temporal and geographic implications. *PLoS One* 2015;10:e0115477.
- Yu Y, Harris AJ, Blair C, et al. RASP (Reconstruct Ancestral State in Phylogenies): a tool for historical biogeography. *Mol Phylogenet Evol* 2015;87:46–9.
- Miller KG, Komazin MA, Browning JV, et al. The phanerozoic record of global sea-level change. *Science* 2005;310:1293–8.
- Galton PM. The ornithopod dinosaur *Dryosaurus* and a Laurasia-Gondwanaland connection in the Upper Jurassic. *Nature* 1977;268:230–2.



Xing Xu is currently a research scientist at the Institute of Vertebrate Paleontology and Paleoanthropology of the Chinese Academy of Sciences, and focuses on morphology, ontogeny, evolution and biostratigraphy of Archosauria. He has named many dinosaurs, such as *Yinlong*, *Guanlong* and *Gigantoraptor*.



Hai Xing is a research scientist at the Beijing Museum of Natural History. He majors in the study of vertebrate paleontology, notably morphology and phylogeny of ornithischian dinosaurs.