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Systematic Palaeontology (Vertebrate Palaeontology)

A new primitive hadrosauroid dinosaur from the Early Cretaceous of Inner Mongolia (P.R. China)

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Abstract

The right dentary of a new hadrosauroid dinosaur, *Penelopognathus weishampeli*, has been discovered in the Bayan Gobi Formation (Albian, Lower Cretaceous) of Inner Mongolia (P.R. China). This new taxon is characterised by its elongated, straight dental ramus, whose lateral side is pierced by about 20 irregularly distributed foramina. Its dentary teeth appear more primitive than those of *Probactrosaurus*, but more advanced than those of *Altirhinus*, both also from the Lower Cretaceous of the Gobi area. Non-hadrosaurid Hadrosauroidea were already well diversified in eastern Asia by Early Cretaceous time, suggesting an Asian origin for the hadrosauroid clade. ***To cite this article: P. Godefroit et al., C. R. Palevol 4 (2005)***.

Résumé

Un nouveau dinosaure hadrosauroïde primitif du Crétacé inférieur de Mongolie intérieure (R.P. de Chine). Le dentaire droit d'un nouveau dinosaure hadrosauroïde, *Penelopognathus weishampeli*, a été découvert dans la formation Bayan Gobi (Albien, Crétacé inférieur) de Mongolie intérieure (R.P. de Chine). Ce nouveau taxon est caractérisé par sa branche dentaire allongée et droite, dont la face latérale est percée par une vingtaine de petits foramens. Les dents de la mâchoire inférieure apparaissent plus primitives que celles de *Probactrosaurus*, mais plus évoluées que celles d'*Altirhinus*, tous deux également du Crétacé inférieur de la région du Gobi. Au cours du Crétacé inférieur, les Hadrosauroidea non-hadrosauridés étaient déjà bien diversifiés en Asie orientale, ce qui suggère une origine asiatique pour le clade des dinosaures hadrosauroïdes. ***Pour citer cet article : P. Godefroit et al., C. R. Palevol 4 (2005)***.

Keywords: Hadrosauroidea; Early Cretaceous; Inner Mongolia; Palaeogeography

Mots clés : Hadrosauroidea ; Crétacé inférieur ; Mongolie intérieure ; Paléogéographie

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Introduction

Les Hadrosauroidea sont définis comme les dinosaures plus proches de *Parasaurolophus* que d'*Iguanodon* [21]. Leurs représentants les plus évolués, les hadrosauridés, étaient les herbivores dominants dans de nombreux écosystèmes terrestres à la fin du Crétacé. Mais le clade des hadrosauroïdes comprend également des formes moins dérivées, qui ont évolué en Laurasie dès la seconde moitié du Crétacé inférieur (Fig. 1).

Nous décrivons dans cet article le dentaire droit d'un dinosaure hadrosauroïde découvert dans la formation de Bayan Gobi (Albien, Crétacé inférieur), à proximité du village de Qiriga (Mongolie intérieure, Chine ; Fig. 2). Bien qu'il soit très fragmentaire, ce fossile suggère que la biodiversité des hadrosauroïdes primitifs était très importante en Asie à la fin du Crétacé inférieur et que cette région a donc joué un rôle très important dans la diversification initiale des hadrosauroïdes.

Paléontologie systématique

Dinosauria Owen 1842
Ornithopoda Marsh 1881
Hadrosauroidea (Cope, 1869)
Penelopognathus weishampeli gen. et sp. nov.

Étymologie. *Penelopognathus* signifie « mâchoire du canard sauvage »; *weishampeli*, baptisé en l'honneur de D.B. Weishampel.

Holotype. IMM 2002-BYGB-1, un dentaire droit conservé au musée de Mongolie intérieure (Hohhot, Chine).

Localité et horizon. Alentours du village de Qiriga (Mongolie intérieure, Chine; Fig. 2). formation de Bayan Gobi (Albien, Crétacé inférieur).

Diagnose. Hadrosauroidea non-hadrosauridé, caractérisé par la branche horizontale du dentaire allongée (rapport « longueur / hauteur à mi-longueur » = 4,6), avec un bord ventral droit et une face latérale percée par une vingtaine de foramens irrégulièrement distribués.

Description et comparaisons (Fig. 3)

IMM 2002-BYGB-1 présente plusieurs caractères autapomorphiques qui permettent de le distinguer des autres hadrosauroïdes décrits à ce jour : la branche horizontale du dentaire est très allongée, avec un bord ventral droit. Sa face latérale est percée d'une vingtaine de foramens lâchement distribués. Ces caractères, qui n'ont été observés chez aucun des hadrosauroïdes primitifs décrits à ce jour, permettent d'ériger un nouveau taxon : *Penelopognathus weishampeli*.

Chez *Penelopognathus*, les dents dentaires ressemblent très fort à celles d' *Altirhinus kurzanovi* [15] et de *Probactrosaurus gobiensis* [16], deux hadrosauroïdes primitifs également découverts dans le Crétacé inférieur de la région du Gobi. Des différences notables existent cependant. Ainsi, les dents dentaires de *Penelopognathus* apparaissent plus évoluées que celles d'*Altirhinus* : elles esquissent la miniaturisation et la simplification observées chez les hadrosauridés : rapport longueur/hauteur de la couronne moindre, asymétrie moins prononcée, disparition des petites denticulations sur la lèvre à la base du bord distal de la couronne et facettes de contact avec les dents adjacentes mieux marquées. En revanche, les dents dentaires de *Probactrosaurus* ressemblent plus à celles des hadrosauridés évolués que les dents de *Penelopognathus*, indiquant que la batterie dentaire était plus compacte : couronnes dentaires plus étroites, crête distale moins distincte et n'atteignant jamais le sommet de la couronne, rides accessoires moins distinctes à la base des denticulations mésiales et facettes de contact avec les dents adjacentes mieux marquées. Les dents associées au squelette de « *Probactrosaurus* » *manzongshanensis*, du Crétacé inférieur de la province de Gansu [11], ressemblent quant à elles très fort à celles d'*Altirhinus* [16].

D'autres hadrosauroïdes primitifs ont récemment été décrits en Asie, dans le Crétacé inférieur ou à la base du Crétacé supérieur. Tous montrent des différences notables avec *Penelopognathus*. Chez *Jingzhousaurus yangi* (Fm Yixian, province du Liaoning, Chine [25]) et surtout chez *Fukuisaurus tetoriensis* (Fm Kitadani, préfecture de Fukui, Japon [10]), la branche horizontale du dentaire est courte et particulièrement robuste. Cette branche est également très robuste et les dents présentent de nombreux traits primitifs chez *Equijibus normani* (groupe de Xinminhao, province de Gansu, Chine [29]). La branche horizontale du dentaire est très allongée chez *Shiangmiaosaurus gilmorei* (Fm Sunjiawan, province du Liaoning, Chine), mais, contrairement à ce qui est observé chez *Penelopognathus*, son bord ventral est concave et le processus coronoïde est très incliné vers l'arrière [28].

Chez *Protohadros byrdi*, du Cénomanien du Texas, la branche horizontale du dentaire est nettement plus robuste que chez *Penelopognathus* et sa partie antérieure est élevée et infléchie vers le bas [5]. Chez *Bactrosaurus johnsoni*, *Gilmoreosaurus mongoliensis* (Maastrichtien inférieur de Mongolie intérieure, Chine [24]) et *Telmatosaurus transsylvanicus* (Maastrichtien inférieur de Roumanie [26]), la morphologie des dents dentaires est simplifiée et commence à ressembler très fort à celle des hadrosauridés évolués : la crête distale tend à disparaître, la crête mésiale n'atteint jamais le sommet de la couronne, les crénulations marginales sont atténuées et ne présentent plus la complexité observée chez les formes plus primitives dont *Penelopognathus* ; enfin, la lèvre à la base du bord distal est très peu développée. Cette simplification des couronnes dentaires se poursuit chez les hadrosauridés typiques ; en outre, le processus coronoïde est incliné vers l'avant et un diastème est développé entre le point antérieur de la batterie dentaire et la surface articulaire pour le prédentaire.

Paléogéographie des Hadrosauroidea primitifs

Les hadrosauroïdes sont issus d'un stock de dinosaures Styracosterna primitifs (dinosaures plus proches de *Parasaurolophus* que de *Camptosaurus* [21]), groupe qui avait une distribution cosmopolite au cours du Crétacé inférieur. Les plus anciens hadrosauroïdes ont été découverts en Asie et datent du Barrémien : il s'agit de *Jingzhousaurus yangi* (province du Liaoning, Chine [17,25] et de *Probactrosaurus gobiensis* (Mongolie intérieure, Chine [24]). Les hadrosauroïdes se sont rapidement diversifiés en Asie orientale: « *Probactrosaurus* » *mazongshanensis* et *Equijibus normani* (Barrémien –Albien du Gansu, Chine [11,29]), *Penelopognathus weishampeli* (Albien de Mongolie intérieure, Chine), *Altirhinus kurzanovi* (Albien supérieur de la R. P. Mongolie [6]), *Fukuisaurus tetoriensis* (Aptien–Albien de la préfecture de Fukui, Japon [10]), et *Nanyangosaurus zhugeii* (?Albien du Henan, Chine [27]). En dehors de l'Asie, les hadrosauroïdes du Crétacé inférieur sont représentés en Afrique par *Ouranosaurus nigeriensis*, de l'Aptien supérieur du Niger [22] et par du matériel morphologiquement ou stratigraphiquement ambigu d'Asie centrale [13], d'Europe [12] et d'Amérique du Nord [1,5]. Quoi qu'il en soit, on retrouve des hadrosauroïdes primitifs en Asie [28] et en Amérique du Nord [5,9] au début du Crétacé supérieur. Les hadrosauroïdes primitifs vont progressivement se faire remplacer par les hadrosauridés au cours du Crétacé supérieur. Ils subsisteront cependant jusqu'au Maastrichtien inférieur dans des endroits isolés, où ils n'ont pas dû affronter la concurrence des hadrosauridés : *Telmatosaurus*, de la formation de Sanpetru, en Roumanie [26], ainsi que *Bactrosaurus* et *Gilmoreosaurus*, de la formation d'Iren Dabasu, en Mongolie intérieure (Chine) [4,24].

1. Introduction

Hadrosauroidea, or 'duck-billed' dinosaurs, can be defined as those dinosaurs more closely related to *Parasaurolophus* than to *Iguanodon* [21]. Their advanced representatives, Hadrosauridae (*Parasaurolophus*, *Saurolophus*, their most recent common ancestor and all descendants [21]), were the primary constituents of many terrestrial vertebrate faunas during the closing stages of the Cretaceous. Besides typical latest Cretaceous hadrosaurids, the hadrosauroid clade includes a number of less derived forms that evolved in Laurasia from the late Early Cretaceous until the Maastrichtian (Fig. 1). Until recently, the fossil record of Early Cretaceous basal hadrosauroids remained very scarce. However, in the last few years, new taxa have been discovered in northern China [10,11,25,27–29] and older known forms from the Gobi area have recently been re-described as well [2,15,16].

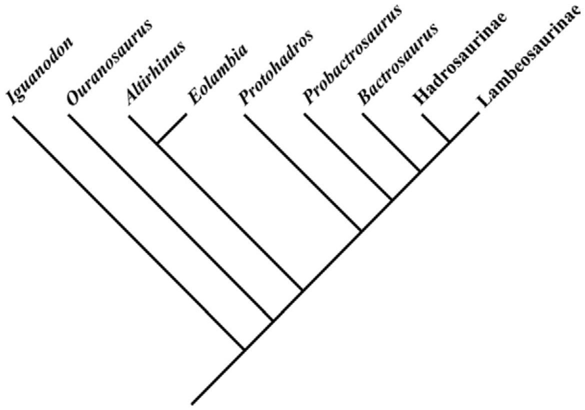

Fig. 1. Phylogenetic relationships within hadrosauroid dinosaurs, modified from Norman [17].

Fig. 1. Relations phylogénétiques au sein des dinosaures hadrosauroïdes, modifiées d'après Norman [17].

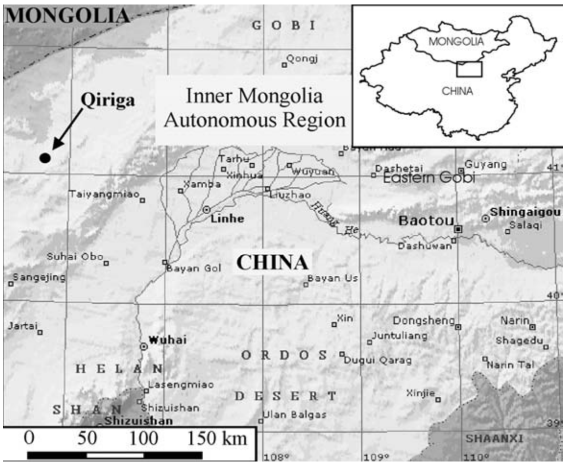

Fig. 2. Generalised map showing the location of Qiriga (Inner Mongolia, P.R. China), the type locality of *Penelopognathus weishampeli*.

Fig. 2. Carte générale montrant l'emplacement de Qiriga (Mongolie intérieure, R. P. Chine), la localité-type de *Penelopognathus weishampeli*.

Here we describe the dentary of a hadrosauroid dinosaur discovered in the late Early Cretaceous of Inner Mongolia. This specimen was discovered in the vicinity of Qiriga Village (Urad Houqi Banner, Bayan Nor League, Inner Mongolia, P. R. China; Fig. 2). The type locality is situated in exposures of the Bayan Gobi Formation. This formation had already yielded an abundant vertebrate fauna in the Alxa Desert area, including champsosaurs, trionychids and larger freshwater turtles, mammals, psittacosaurid dinosaurs and the therizinosaurid dinosaur *Alxasaurus elesitaiensis* [20]. Such a fauna suggests an Albian age [8,20].

Although it is very fragmentary, this fossil suggests that the biodiversity of basal hadrosauroids was very important in Asia by late Early Cretaceous times and, consequently, that this area was an important place in the early diversification of duck-billed dinosaurs.

2. Systematic palaeontology

Dinosauria Owen 1842
Ornithopoda Marsh 1881
Hadrosauroidea (Cope, 1869)
Penelopognathus weishampeli gen. et sp. nov.

Etymology. *Penelops*: Greek for 'wild duck'; Penelope is also the name of Odysseus' wife, forced to fend off suitors while her husband is away fighting at Troy. *Gnathos*: Greek for 'jaw'. *weishampeli*: in honour of D.B. Weishampel, for his important contribution in the knowledge of duck-billed dinosaurs.

Holotype. IMM 2002-BYGB-1, a right dentary housed in the Inner Mongolia Museum (Hohhot, Inner Mongolia, P.R. China).

Locality and horizon. Vicinity of Qiriga village (Urad Houqi Banner, Bayan Nor League, Inner Mongolia, P. R. China). Bayan Gobi Formation (Albian, Lower Cretaceous).

Diagnosis. Non-hadrosaurid Hadrosauroidea characterised by an elongated dental ramus (ratio 'length /height at mid-length' = 4.6), with a straight ventral margin, and whose lateral side is perforated by about 20 irregularly distributed foramina.

Description (Fig. 3). The dentary ramus appears, in lateral view, proportionally elongated and low. It is nearly perfectly straight, with sub-parallel ventral and dorsal margins and a ventral margin that is not distinctly deflected downwardly. It terminates rostrally at a scalloped and ovate predentary attachment region and symphysis. The sutural surface for the predentary forms an edentulous, concave, and slotted area that sweeps upwards to merge with the dorsal alveolar border. There is no diastema between the caudal point of the predentary sutural surface and the rostral point of the alveolar area. Although it is incompletely preserved, the symphysis appears quite short and is very slightly ventrally positioned. The lateral surface of the dentary is hemicylindrical. Its dorsal half is pierced by about 20 irregularly distributed foramina. The coronoid process is elevated and slightly inclined caudally. Its apex is slightly expanded rostrocaudally. Its caudal edge is deeply slotted for attachment of the surangular. The coronoid process is laterally offset from the alveolar border and the labial shelf, or 'cheek recess', is therefore well developed. There is no trace of a facet for the coronoid bone. The dentary teeth fitted into approximately 20 narrow parallel-sided alveolar grooves, visible in medial view. The alveolar groove is particularly low, suggesting that tooth replacement was probably limited. A very thin, medial, alveolar parapet, whose base can be observed in this specimen, concealed the dental battery. Beneath the alveolar trough and the alveolar parapet, a curved groove is pierced by regularly distributed, low, and rectangular foramina, for the neurovascular supply to the dental laminae at the base

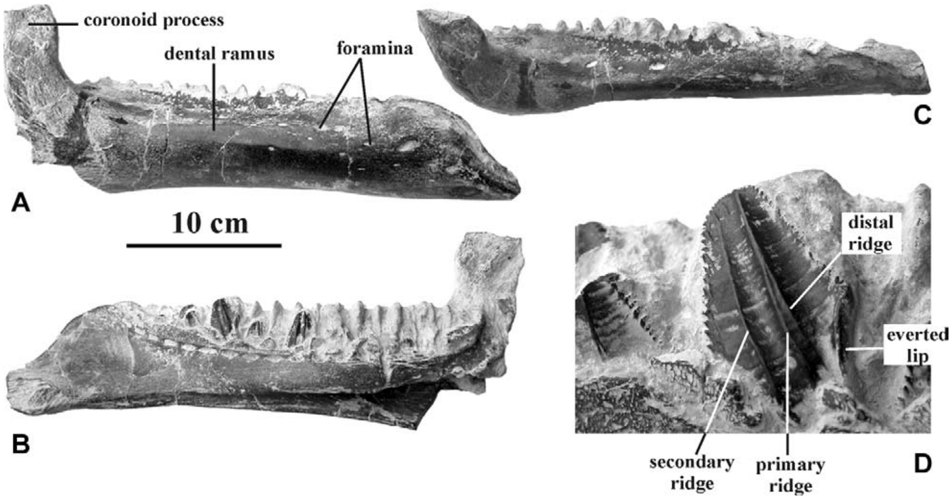

Fig. 3. Holotype right dentary (IMM 2002-BYGB-1) of *Penelopognathus weishampeli* gen. et sp. nov. **A**: lateral view; **B**: medial view; **C**: dorsal view; **D**: detail of dentary teeth.

Fig. 3. Dentaire droit holotype (IMM 2002-BYGB-1) de *Penelopognathus weishampeli* gen. et sp. nov. **A** : vue latérale ; **B** : vue médiale ; **C** : vue dorsale ; **D** : détail des dents.

of the alveoli. Each foramen strictly corresponds to one alveolar slot. In caudal view, the base of the dentary is excavated by the large adductor fossa, which extends horizontally at the base of the medial side towards the level of the symphysis as a deep mandibular groove.

Six dentary teeth are preserved in the dental battery. The collection also comprises five isolated dentary teeth. It is therefore impossible to estimate the number of teeth per tooth family. The enamel is restricted to the lingual side of the crown and to the marginal denticles. The labial side of the crown and the root are composed of dentine, smeared with rough areas of cementum. In mesial and distal views, the tooth is arched outwardly. Two pairs of vertical facets mark the mesial and distal sides of the root and of the base of the crown. These facets represent the contact areas with adjacent teeth within the dental battery. The enamelled lingual side of the crown is asymmetrically diamond-shaped. Although the proportions of the crown are variable within the dental battery, the height/width ratio of the crown is lower than 2. A prominent primary ridge runs the entire height of the crown, dividing the crown surface into two unequal halves. A less prominent secondary ridge, parallel to the primary ridge, bisects the larger mesial half of the crown and always reaches the upper part of the mesial margin. The distal half of the crown also bears a vertical ridge. On several teeth, this distal ridge reaches the apex of the crown; on other teeth, it fuses with the primary ridge before reaching the upper part of the distal margin. The upper part of the mesial margin is strongly curved and forms a shoulder-like structure before merging with the apex of the crown. On the upper part of the edge of the crown, the denticulations form simple tongue-shaped structures. The structure of the marginal denticulations becomes more elaborated further down the sides of the crown. The edge becomes thickened and each of the denticulations forms a curved and crenulated ledge, with additional mammillations, which wrap around the edge of the crown. On the mesial half of the crown, a variable number of subsidiary ridges are extensions of the bases of the marginal denticles. Marginal denticulations are not developed on the edges along the lower part of the crown. At this level, the mesial edge is only slightly thickened. On the other hand, the distal edge forms an everted, oblique lip, as if the edge of the crown had been pinched inward. The base of the enamelled surface is slightly abraded, which corresponds to the contact area with a tooth from the next generation. There is no developed wear facet on the preserved teeth.

***Measurements*.** Length of the dentary (from the rostralmost point of the dentary to a line tangent to the caudal point of the coronoid process, taken parallel to the upper margin of the dentary): 300 mm; height of the dentary ramus (taken at mid point of the dentary length): 65 mm.

3. Comparisons

In the general distribution of morphologic features, the dentary teeth of IMM 2002-BYGB-1 closely resemble those described in *Altirhinus kurzanovi* [15] and *Probactrosaurus gobiensis* [16], also from the Early Cretaceous of the Gobi area. However, a closer look reveals interesting differences. The enamelled crown of *Altirhinus* is more mesiodistally expanded than in IMM 2002-BYGB-1. It would suggest that the dentary teeth in IMM 2002-BYGB-1 begin to exhibit the miniaturisation of the individual crowns seen in more derived hadrosauroids. The primary ridge on the lingual side of the dentary crowns is more distinctly offset distally in *Altirhinus* than in IMM 2002-BYGB-1. In *Altirhinus*, the rolled edge at the base of the distal margin of the crown bears tiny, but distinct denticulations [15]; this character is also described in *Iguanodon* [14]. The vertical facets on the lateral sides of the crown appear less clearly marked in *Altirhinus* than in IMM 2002-BYGB-1, suggesting a less compact dental battery.

On the other hand, dentary teeth of *Probactrosaurus* more closely resemble those of typical hadrosaurids. The crown is proportionally narrower than in IMM 2002-BYGB-1, with a height/width ratio between 2.1 and 2.3. The distal vertical ridge is usually less distinct and never reaches the apex of the crown. Subsidiary ridges at the base of the mesial denticulations are also far less distinct. The structure and organisation of the contact facets on the root and the notch at the base of the enamelled surface closely resemble the condition observed in hadrosaurids [16], indicating that the dental battery as a whole was more compact than in IMM 2002-BYGB-1. Two dentary teeth were found associated with the fragmentary skeleton of '*Probactrosaurus*' *mazongshanensis* [11], from the Xinminhao Group of the Gansu Province (northern China). As previously noted by Norman [16], these teeth bear a closer resemblance to those pertaining to *Altirhinus*: they look proportionally longer (mesiodistally) than those of *Probactrosaurus* and IMM 2002-BYGB-1, and they bear a well-developed distal ridge that reaches the apex of the crown.

Dentary teeth of IMM 2002-BYGB-1 therefore appear more primitive than those of *Probactrosaurus*, but more advanced than those of *Altirhinus*. Thus, it may be suggested that IMM 2002-BYGB-1 belongs to a different genus that would occupy an intermediate position in the phylogeny of Hadrosauriformes. The general shape of the dentary also indicates that IMM 2002-BYGB-1 belongs to a distinct taxon. In *Probactrosaurus*, the dentary ramus is distinctly more robust and proportionally higher. In *Altirhinus*, the ventral margin of the dentary ramus is very arched and the rostral part of the dentary consequently projects ventrally, as also observed in lambeosaurine hadrosaurids. The labial shelf between the base of the coronoid process and the dental battery is not really developed in *Altirhinus*: the base of the coronoid process is supported by a curved buttress of bone that sweeps upwards from a broad shelf labial to the dentition, as also observed in *Iguanodon* [15].

Besides *Altirhinus* and *Probactrosaurus*, several other iguanodontian taxa have recently been described from late Early Cretaceous–early Late Cretaceous deposits of eastern Asia. The phylogenetic position of these taxa is still debated [17] and needs to be clarified by further studies. In *Jingzhousaurus yangi* (Yixian Fm., Liaoning Province, China [25]) and especially in *Fukuisaurus tetoriensis* (Kitadani Fm., Fukui Prefecture, Japan [10]), the dentary ramus is short and robust, contrasting with the long and slender condition observed in IMM 2002-BYGB-1. The dentary ramus is also distinctly shorter and more robust in *Equijibus normani* (Xinminbao Group, Gansu Province, China). In this taxon, the dentary teeth retain several plesiomorphic characters: the crown is far longer (mesiodistally) and the enamelled surface bears six or seven weak vertical ridges, but lacks a prominent primary ridge [29]. The dentary of *Shiangmiaosaurus gilmorei*, from the Sunjiawan Formation of the Liaoning Province, is characterised by its long coronoid process, which is strongly inclined backwardly [28]. The dentary ramus in *Shiangmiaosaurus* is also very elongated, as in IMM 2002-BYGB-1, with a length/height ratio = 5, but its ventral margin is distinctly more concave. *Nanyangosaurus zhugeii*, 2000, from the Sangping Formation of the Henan Province, is known only from postcranial material [27].

Outside eastern Asia, late Early Cretaceous–early Late Cretaceous hadrosaurids are also known in North America. The dentary is unknown in *Eolambia caroljonesa*, from the Cedar Mountain Formation (Albian–Cenomanian) of eastern Utah [9]. In *Protohadros byrdi*, from the Woodbine Formation (Cenomanian) of Texas, the dentary can easily be distinguished from IMM 2002-BYGB-1 in being more robust, rostrally deflected and expanded [5].

Non-hadrosaurid hadrosauroids are also represented in later Cretaceous deposits of Inner Mongolia. In *Bactrosaurus johnsoni* and *Gilmoreosaurus mongoliensis*, from the Inner Dabasu Formation (Early Maastrichtian [24]) of Erenhot, the dentary teeth appear more advanced than those of IMM 2002-BYGB-1: the crown is shorter, with a height/width ratio higher than 2, the mesial secondary ridges is less prominent, the distal vertical ridge never reaches the apex of the crown, the subsidiary ridges are very incipient, the marginal crenulations are distinctly less developed, and the rolled edge at the base of the distal margin is very poorly developed or absent [2]. The same differences can be observed with *Telmatosaurus transsylvanicus*, a non-hadrosaurid hadrosauroid from the Sânpetru Formation (Maastrichtian) of the Haţeg Basin in Romania [26].

Advanced hadrosaurids are abundant and diversified in Late Cretaceous deposits of eastern Asia [4,7]. With its long and straight dental ramus, the dentary of *Penelopognathus* superficially resembles that of hadrosaurine hadrosaurids. However, *Penelopognathus* lacks the following hadrosaurid synapomorphies: the coronoid process is not inclined forwardly and the diastema is not developed between the rostral point of the dental battery and the articulation surface with the predentary. Moreover, the morphology of hadrosaurid dentary teeth appears simplified when compared with IMM 2002-BYGB-1: the crown is higher and perfectly symmetrical, a single median ridge ornaments the enamelled side and the marginal crenulations are absent or very poorly developed.

IMM 2002-BYGB-1 does not belong to any hadrosauroid dinosaur described to date. For that reason, it has been decided to regard it as a new taxon, *Penelopognathus weishampeli*. Autapomorphic characters include its elongated straight dental ramus and the numerous, sparsely distributed foramina on the lateral side of this ramus.

4. Palaeobiogeography of basal Hadrosauroidea

Styracosterna is defined as all ankylopollexans closer to *Parasaurolophus* than to *Camptosaurus* [21]. By the Early Cretaceous, non-hadrosauroid Styracosterna had achieved a virtually cosmopolitan distribution, ranging across Euramerica (several species of *Iguanodon*: Valanginian–Aptian), Asia (*I. bernissartensis*: Aptian–Albian), Africa (*Lurdusaurus*: Aptian), and Australia (*Muttaburrasaurus*: Albian). Hadrosauroidea emerged from this stock of basal styracosternans during the Early Cretaceous. *Jingzhousaurus yangi*, from the Barremian of the Liaoning Province in northeastern China [17,25] and *Probactrosaurus gobiensis*, from the Barremian of Inner Mongolia, China [23], can be regarded as the oldest known representatives of the hadrosauroid clade. Basal hadrosauroids quickly diversified in eastern Asia during the late Early Cretaceous: '*Probactrosaurus*' *mazongshanensis* (Barremian–Albian of the Gansu Province, China [11]), *Penelopognathus weishampeli* (Albian of Inner Mongolia, China), *Altirhinus kurzanovi* (Late Albian of eastern P.R. Mongolia [6]), *Fukuisaurus tetoriensis* (Aptian–Albian of the Fukui Prefecture, Japan [10]), and *Nanyangosaurus zhugeii* (? Albian of the Henan Province, China [27]). *Equijibus normani*, from the Barremian–Albian of the Gansu Province, is regarded as a basal hadrosauroid by You et al. [29], but as a non-hadrosauroid Styracosterna by Norman [17]. Outside eastern Asia, Early Cretaceous hadrosauroids are represented in Africa by *Ouranosaurus nigeriensis*, from the Late Aptian of Niger [22], and also by morphologically or stratigraphically ambiguous material from Central Asia (*Gilmoreosaurus* sp. and?*G.* ?*atavus*, from the ?Albian–?Cenomanian Khodzhakul Formation in Uzbekistan [13]), Europe ('*Trachodon' cantebrigensis* from the Albian Cambridge Greensand in England [12]), and North America (two partial femora from the Albian–Cenomanian Dakota sandstone in Nebraska and Cedar Mountain Formation in Utah [1,5]. By early Late Cretaceous time, non-hadrosaurid Hadrosauroidea were unambiguously present in eastern Asia (*Shuangmiaosaurus gimorei*, from the Cenomanian–Turonian of Liaoning, China [28]) and North America (*Eolambia caroljonesa*, from the Early Cenomanian of Utah, and *Protohadros byrdi*, from the Cenomanian of Texas [5,9]). Advanced hadrosaurids apparently developed from the Turonian both in Asia [19] and in North America [18]. Although hollow-crested lambeosaurines clearly have an Asian origin [3,4], the situation remains unclear for flat-headed or solid-crested hadrosaurines. From the Campanian till the Maastrichtian, Hadrosauridae reached their zenith and were apparently spread worldwide: North America, Central America, South America, Europe, Asia and apparently even Antarctica [7]. Primitive hadrosauroids maintained until the Early Maastrichtian in a few isolated places, where they had not to face the concurrence of advanced hadrosaurids, with their more efficient masticatory apparatus. The latest non-hadrosaurid hadrosauroids include *Telmatosaurus* from the Sânpetru Formation of Romania [26], *Bactrosaurus* and *Gilmoreosaurus* from the Iren Dabasu Formation of Inner Mongolia [4,24].

It can therefore be concluded that basal hadrosauroid dinosaurs, including *Penelopognathus weishampeli* described in the present paper, were already well diversified in eastern Asia by late Early Cretaceous time. Therefore, an Asian origin for the hadrosauroid clade is a reasonable hypothesis. However, the phylogenetic relationships between basal hadrosauroids and the timing of dispersal between Laurasian continental areas during mid-Cretaceous times cannot be accurately resolved in the current state of our knowledge. A better understanding of these topics requires a deeper analysis of several Asian taxa (*Jinzhousaurus*, *Equijibus*, *Fukuisaurus*, '*Probactrosaurus*' *mazongshanensis*) and the discovery of more complete material for other forms (*Shuanmiaosaurus*, *Nanyangosaurus*, *Penelopognathus*).

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