A new amphilestid mammal from the Early Cretaceous of Inner Mongolia (P.R. China)

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Abstract

A dentary from the Ejinhoro Formation (Early Cretaceous) of the Ordos Basin (Inner Mongolia) can be referred to a new amphilestid mammal *Hangjinia chowi* n. gen., n. sp. Although the dentition is only fragmentarily known, the good state of preservation of the alveoli allows to establish that the number of lower postcanines was reduced to four, differing from all the hitherto known triconodonts. This new species is also characterized by its very stout dentary and by the small relative size of cusps b and c on the last molar. The replacement of the molars is another important feature observed in this species, as it occurs only in few very primitive mammals, among others in another Early Cretaceous amphilestid *Gobiconodon*. A preliminary cladistic analysis, based on only a few dentary and dental characters, shows that *Hangjinia* might constitute the sister-group of *Gobiconodon*.

Key-words: amphilestid mammals, *Hangjinia chowi* n. gen., n. sp. , Early Cretaceous, Inner Mongolia.

Résumé

Un dentaire découvert dans la Formation d'Ejinhoro (Crétacé inférieur) du Bassin de l'Ordos (Mongolie intérieure) peut être référé à un nouveau mammifère amphilestidé, *Hangjinia chowi*. Si la denture n'est connue que de façon fragmentaire, le bon état de conservation des alvéoles permet d'établir que le nombre de postcanines était réduit à quatre, différent de tous les triconodontes connus à ce jour. Cette nouvelle espèce est également caractérisée par son dentaire très robuste et par la petite taille relative des cuspides b et c sur la dernière molaire. Le remplacement des molaires est un autre caractère important observé chez cette espèce: il n'est en effet connu à ce jour que chez quelques mammifères très primitifs, dont un autre amphilestidé du Crétacé inférieur, *Gobiconodon*. Une analyse cladistique préliminaire, basée sur quelques caractères dentaires et de la mandibule, montre qu'*Hangjinia* pourrait former le groupe-frère de *Gobiconodon*.

Mots-clefs: mammifères amphilestidés, *Hangjinia chowi* n. gen., n. sp. , Crétacé inférieur, Mongolie intérieure.

产自中国内蒙古早白垩世地层中的三锥齿兽类哺乳动物一新种

内容提要

产自内蒙古鄂尔多斯盆地早白垩世伊金霍洛组中的一件齿骨化石，被鉴定为一新属新种-----周氏杭锦兽，属于一种新的三锥齿兽类哺乳动物。尽管对其牙列所知甚少，但从齿槽保存的良好状态可以确认下犬后齿减为4个,不同于迄今所知的所有的三锥齿兽类。该新种以粗壮的齿骨以及最后一个臼齿的齿尖b和c相对较小为特征。臼齿的代换是在该标本中观察到的另一个重要特点，因为这种现象只发生在极少数原始的哺乳动物中，比如，在其它一些早白垩世的三锥齿兽类 *Gobiconodon* 中。根据仅有的齿骨和牙齿特征，初步所做的有关遗传方面的分析研究表明，*Hangjinia* 可能构成 *Gobiconodon* 的姊妹群。

关键词：哺乳类 三锥齿兽类 周氏杭锦兽 新属新种 早白垩世 内蒙古

Introduction

The Ordos Basin is located in the central part of northern China, in Inner Mongolia, Ningxia and Shanxi Provinces, and is surrounded by high mountains: the Daqinshan and Langshan Mountains in the north, the Qilian Mountain in the south, the Helan and Liupan Mountains in the west and the Luliang Mountain in the east. During the Early Cretaceous, the Ordos Basin was covered by the large Qingyang lake, of which the widely distributed sediments form the Zhidan Group and the Ejinhoro Formation. The dinosaurs discovered in both formations are representative of the *Psittacosaurus* fauna, distributed throughout the Early Cretaceous basins of Central Asia (DONG, 1992, 1993a). The Zhidan Group, up to 1,300 m thick, is exposed in the Ordos Basin along the valley walls of the Yellow River (DONG, 1993a). The Ejinhoro Formation is distributed south of the great northward bend of the Yellow River, with a thickness of 107-208 m. It comprises a lower unit of red, purplish to bluish mudstones and sandstones, and an upper unit of greyish-green to reddish-orange cross-bedded mudstones and sandstones. (DONG, 1992, 1993a).
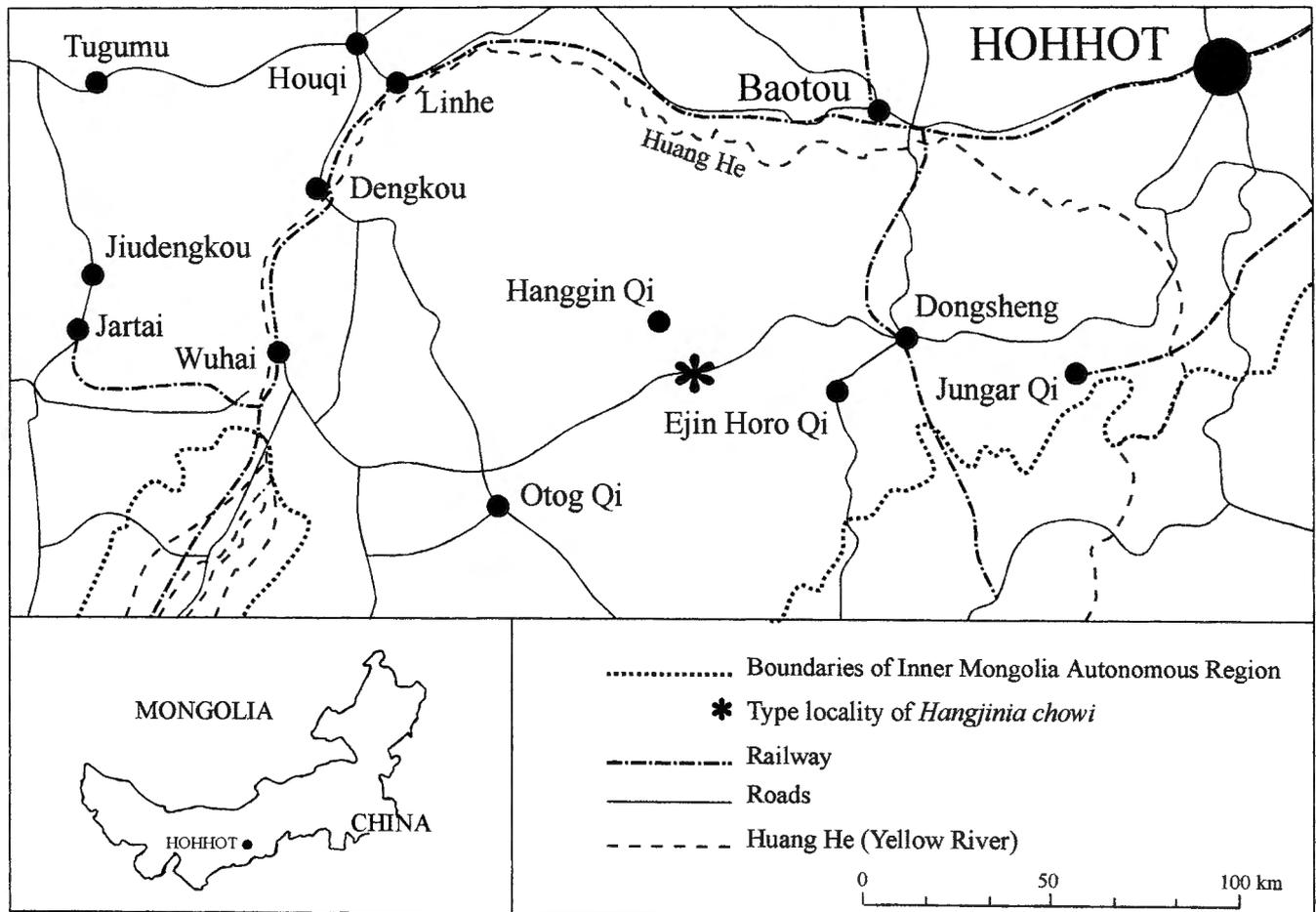
Fig. 1 — — Location of the type locality of *Hangjinia chowi*. Inset map shows the Inner Mongolia Autonomous Region.

The Ejinhoro Formation has yielded the turtles *Ordosemys leios* (BRINKMAN & PENG, 1993a) and *Sinemys gamera* (BRINKMAN & PENG, 1993b), the crocodiles *Eotomistoma multidentata* (YOUNG, 1964), *Shantungosuchus hangjinensis* (WU *et al.*, 1994) and cf. *Theriosuchus* sp. (WU *et al.*, 1996), the champsosaur *Ikechosaurus sunailinae* (SIGOGNEAU-RUSSELL, 1981; BRINKMAN & DONG, 1993), the troodontid *Sinornithoides youngi* (RUSSELL & DONG, 1993), the stegosaur *Wuerhosaurus ordosensis* (DONG, 1993b), the ceratopsian *Psittacosaurus neimongoliensis* and *P. ordosensis* (RUSSELL & ZHAO, 1996) and also ornithopod, sauropod and pterosaur isolated bones. DONG (1993a) mentions the discovery of a single mammal humerus at Laolonghuoze locality. The presence of *Psittacosaurus*, whose fossil record extends from the Valanginian through the Albian (RUSSELL & ZHAO, 1996), speaks for an Early Cretaceous age for the Ejinhoro Formation.

In August 1996, the second Sino-Belgian Dinosaur Expedition in Inner Mongolia (see GODEFROIT *et al.*, 1998) prospected various exposures in the Ejinhoro Formation of Yikezhao League. The mammalian dentary described in the present paper was found about 18 km southeast of Hangjin Qi, together with indeterminate dinosaur fragmentary bones, in slightly consolidated fine reddish-brown sandstones.

Abbreviations: IMM: Inner Mongolia Museum (Hohhot, P.R. China), RBINS: Royal Belgian Institute of natural Sciences (Brussels, Belgium); SBDE: Sino-Belgian dinosaur expedition.

Systematic palaeontology

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Class Mammalia
Order incertae sedis
Family Amphilestidae OSBORN, 1888
Subfamily ?Gobiconodontinae CHOW & RICH, 1984
Genus *Hangjinia* nov. gen.

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Diagnosis: As for the type species, *Hangjinia chowi* nov. sp. (monospecific genus).

Derivatio nominis: From Hangjin Qi (Yikezhao Banner, Inner Mongolia, P.R. China), town near the locality where the holotype was found.

Type species: *Hangjinia chowi* nov. sp.

Hangjinia chowi nov. sp.

Diagnosis: Distinguished from all other described Amphilestidae by the presence of only four lower postcanines; dental formula: I_3, C_1, $?P_2$, $?M_2$; first premolar slightly asymmetrical in lateral view; postcanines all double-rooted; dentary particularly short and robust (ratio "height of the dentary below the distal molar / length of the dentary" about 0.19); cusps **b** and **c** very minute on the last molar, about half the height of **a**.

Holotype: IMM 96NMHJLII-1. A cast of the specimen (RBINS M1836) is housed in Brussels.

Derivatio nominis: In honour of Professor CHOW Minchen, famous Chinese palaeontologist, for his invaluable contribution to the knowledge of fossil mammal faunas in China, and particularly in Inner Mongolia.

Locus typicus: 18 km southeast of Hangjin Qi, Hangjinqi Banner, Yikezhao League, Inner Mongolia Province, P.R. China (39°54'323 N, 108°87'676 E, 1325 m. alt.; Figure 1).

Stratum typicum: Ejinhoro Formation, Early Cretaceous.

Description: IMM 96NMHJLII-1 belongs to a medium-sized animal: the estimated length of the dentary is 42 mm. It was thus similar in length to *Gobiconodon borissiaki* TROFIMOV, 1978 (estimated skull length about 48-50 mm; KIELAN-JAWOROWSKA & DASHZEVEG, 1998), but about 1.8 times smaller than *G. ostromi* JENKINS & SCHAFF, 1988.

Dentary (Plate 1) - The posterior portion of the dentary is broken off at the level of the coronoid process. The dentary appears relatively short, deep and robust, with a gently curved lower margin in lateral view: the dentary is 6.5 mm high below the mesial root of P_1 and 7.8 mm high below the distal root of M_2.

In front of the masseteric fossa, the lateral surface of the dentary is slightly convex dorso-ventrally. Its is pierced by four foramina, at mid-height between the ventral and dorsal borders of the dentary: (1) between I_3 and C; (2) between C and P_1; (3) below P_1; (4) below the distal edge of the alveolus for $?P_2$. The dorsolabial border of the coronoid process starts below the alveolus of the distal root of $?M_2$ and forms an angle of about 40° with the long axis of the dentary. The masseteric fossa is particularly wide and deep, suggesting a strong adductor musculature: it is limited anterodorsally by the rounded labiodorsal border of the coronoid process and ventrally by the masseteric crest, which forms a well-developed horizontal shelf.

Between the symphysis and the pterygoid fossa, the lingual side of the dentary is essentially flat. The dorso-lingual border of the dentary bears, at the rear end of the alveolar border and at the foot of the coronoid process, a slit which can be interpreted as a facet for the coronoid. The coronoid can be regarded as the longest-persisting "reptilian" bone in the mammal jaw, in the form of a small thin bony plate inserted against the dentary. Traces of vestigial coronoid or coronoid facet have been recognized in several Late Jurassic and Cretaceous mammal lineages, including gobiconodontines (JENKINS & SCHAFF, 1988), symmetrodonts (HU et al., 1997), dryolestids (KREBS, 1971), tribotherians (DASHZEVEG & KIELAN-JAWOROWSKA, 1984), multituberculates (HAHN, 1977) and even eutherians (KIELAN-JAWOROWSKA, 1981).

The pterygoid fossa is much less wide and deep than the masseteric fossa. It is bordered ventrally by a small pterygoid shelf. At the front end of the pterygoid fossa, the large slit-like dental foramen, through which the inferior alveolar artery and nerve enter the jaw, opens. A shallow and relatively wide groove runs along the ventral border of the dentary, from the anteroventral border of the pterygoid fossa towards the level of the penultimate postcanine. It corresponds to SIMPSON's (1928) "internal groove" which, according to KREBS (1971), held the mylohyoid artery and nerve, but also housed the Meckel's cartilage persisting in adult. This primitive feature of the mammal mandibule also persists in several Jurassic and Cretaceous lineages, including gobiconodontines (KIELAN-JAWOROWSKA & DASHZEVEG, 1998), symmetrodonts (HU et al., 1997) and tribotherians (DASHZEVZEG & KIELAN-JAWOROWSKA, 1984); a remnant of this groove is even distinguishable in the posterior part of the jaw of the Early Cretaceous eutherian *Prokennalestes* (KIELAN-JAWOROWSKA & DASHZEVEG, 1989).

The body of the dentary thickens towards the symphyseal region. As previously described in *Gobiconodon* (JENKINS & SCHAFF, 1988), the rugosity of the symphyseal surface and the steep inclination of its great axis, making an angle of about 35°-40° with the alveolar border surface, are indicative of the presence of a symphyseal ligament and of intra-jaw mobility (SCAPINO, 1981). The distalmost point of the symphysis lies below the alveolus for the canine.

The alveolar border does not face directly dorsally, but becomes inclined labially from back to front.

Teeth - The following dental formula can tentatively be deduced for *Hangjinia chowi*: I_3 C_1 $?P_2$ $?M_2$. The first postcanine is clearly a premolar and the fourth, a molar. The second postcanine is completely broken off and cannot be accurately identified; the third is lost. For description facilities, they have been rather arbitrarily identified respectively as P_2 and M_1. However, it cannot be excluded that the second postcanine is in fact a first molar or, alternatively, that the third postcanine is a third premolar.

Judging from the dimensions of its alveolus, the first incisor was the largest of the series. Its alveolus is mesio-distally compressed; it faces nearly perfectly forwards,

indicating that the first incisor was very procumbent. The second incisor, distinctly rectangular in cross-section, is broken off at its base. Its alveolus is less compressed mesio-distally than that of the first one; it faces upwards, forwards and labially. The third incisor is nearly complete, its apex being truncated by post-mortem breaking. It is slightly spatulate in shape and sub-quadrangular in cross-section along its whole height. It is inclined mesially, forming an angle of about 60° with the alveolar border, and slightly labially. Its distal side bears an extensive vertical wear facet, showing the dentine. Its alveolus is comparable in size with that of the second incisor, but it is nearly circular and faces mainly upwards and very slightly forwards and labially. There is no trace of a replacing incisor on the X-ray radiographs.

The canine is not preserved. Its single alveolus is elliptical and very slightly compressed labio-lingually; it faces upwards and very slightly labially. It is less enlarged than the alveolus for the first incisor, but it is slightly larger than that of the second and third incisors. It is separated from the first premolar by a very short diastema.

The reduced number of postcanines is the most striking character observed in IMM 96NMHJLII-1. The first postcanine (Figure 2, A) is damaged. However, the preserved fragment suggests that it was a premolar: the crown is slightly asymmetrical in lateral view and dominated by a very large cusp **a**, flanked mesially and distally by very small cusps **b** and **c**; an incipient cusp **d** can be observed at the distal end of the crown; there is no trace of cingula. The roots are clearly separated along their full height and divergent.The second postcanine is broken off at the level of the alveolar opening. However, X-ray radiographs indicate that this tooth was not fully erupted, contrary to the first postcanine: a part of the crown is still included within the alveolus. The third postcanine is lost. Its alveolus, subdivided by a thin interradicular septum, is in close contact with the preceding one. The alveolus for the mesial root is set more labially than that for the distal one.

The alveolus for the fourth postcanine is fully formed and rectangular in shape; it is subdivided into two sub-equal halves by a partially resorbed interradicular septum. This alveolus was therefore previously occupied by a lost postcanine. Further preparation of the specimen revealed that this alveolus still contains a non-erupted, but fully formed tooth. X-rays radiographs of this area allow a recontruction of the outline of this tooth, but details cannot be discerned (Figure 2, B). The crown is symmetrical in lateral view and dominated by a conical cusp **a**, set in the median part of the crown; mesial cusp **b** and distal cusp **c** are very small, about twice lower than cusp **a**. The three cusps are nearly perfectly aligned mesio-distally. The two roots are completely separated along their full height and are slightly divergent. Because this molar was undoubtedly preceded by another one within the same alveolus, it is thus neither a lacteal nor a monophyseal one; it can consequently be regarded as a repla-
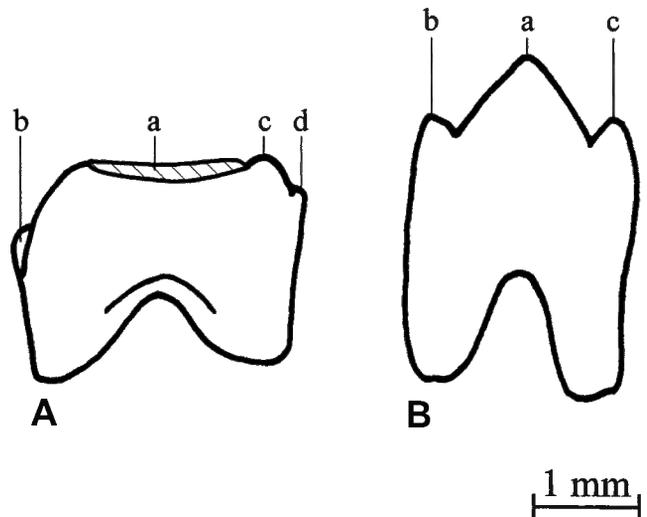
Fig. 2 — Outlines in lateral view of the left P_1 (A) and of the left M_2 (B, deduced from x-rays photographs) of *Hangjinia chowi* (IMM 96NMHJLII-1), from the Early Cretaceous of Inner Mongolia.

cing molar. Molar replacement is very unusual in mammals: although molariform teeth generally appear in the deciduous dentition, molars have no deciduous predecessors, i.e., are not replaced. However, molar replacement has previously been described in the amphilestid *Gobiconodon ostromi* (JENKINS & SCHAFF, 1988). In this species, molar replacement is sequential from front to back and the first replacement molar apparently erupts after the last deciduous molar (see JENKINS & SCHAFF, 1988, fig. 3). If a similar replacement pattern occurred in *Hangjinia chowi*, it can thus be concluded that this animal did not develop more than four postcanines, as replacement can be observed in the last position of the tooth row, in NMM 96NMHJLII-1. ZHANG et al. (1998) recently described molar replacement in the mammaliaform (*sensu* McKENNA & BELL, 1997) *Sinoconodon*, from the Early Jurassic of southern China. Molar replacement pattern in *Sinoconodon* differs from that observed in *Gobiconodon*: in the former, the third replacement lower molar erupts before the fourth deciduous one and, similarly, the fourth replacement lower molar appears before the fifth deciduous one (ZHANG et al., 1998, Fig. 2). If a *Sinoconodon*-like replacement pattern occurred in *Hangjinia chowi*, it cannot be excluded that older adult specimens developed more than four lower postcanines.

Comparisons and affinities of *Hangjinia chowi*

The replacing molar of the holotype of *Hangjinia chowi* displays a typical triconodont pattern with three mesio-distally aligned main cusps. According to HOPSON & CROMPTON (1969) and JENKINS & CROMPTON (1979), among others, such a molar structure characterizes the Order Triconodonta OSBORN, 1888, including the Rhaeto-Liassic family Morganucodontidae KÜHNE, 1958, as well

as the more advanced families Triconodontidae MARSH, 1887 and Amphilestidae OSBORN, 1888. However, the monophyly of the Triconodonta in the traditional sense is denied by all the recent phylogenetic analyses (e.g. ROWE, 1988, 1993; WIBLE, 1991; WIBLE & HOPSON, 1993; WIBLE et al., 1995; ROUGIER et al., 1996; JI et al., 1999), with the exception of LUO (1994). McKENNA & BELL (1997) include the families Triconodontidae, Amphilestidae and Austroconodontidae in the distinct mammalian infraclass Triconodonta, but regard the Morganucodontidae, as well as Sinoconodon, as nonmammalian mammaliaforms. MILLS (1971) and KIELAN-JAWOROWSKA & DASHZEVEG (1998) alternatively ally the Amphilestidae with the Kuehneotheriidae KERMACK, KERMACK & MUSSETT, 1968 and, consequently, with the Theria on the basis of the interlocking mechanism between lower molars and of the occlusal pattern between lower and upper molars. It is not the purpose of the present paper to discuss this hypothesis, as the material studied herein does not bring any new information concerning it. It must nevertheless be noted that the study of Kuehneotherium teeth from the Late Triassic of Saint-Nicolas-de-Port (GODEFROIT & SIGOGNEAU-RUSSELL, in press) shows that the interlocking mechanism between adjacent molars was not constant, as the relative development of cusps **d**, **e** and **f** is extremely variable within this genus. For the same reason, the interlocking mechanism in Morganucodon was probably also much more variable than previously described by MILLS (1971). Pending further evidence, it has been decided to follow CIFELLI et al. (1998) and KIELAN-JAWOROWSKA & DASHZEVEG (1998) in using the term "triconodont" in an informal, non-taxonomic sense for the Jurassic and Cretaceous families Triconodontidae MARSH, 1887, Amphilestidae OSBORN, 1888 and Austrotriconodontidae BONAPARTE, 1992.

The dentary of Hangjinia shows apomorphic characters not developed in Morganucodontidae, but shared with more advanced families Amphilestidae and Triconodontidae: the Meckelian groove is shortened and does not reach the symphysis and the pterygoid shelf is well developed (ROWE, 1988, 1993). Within the triconodonts, Hangjinia can be grouped with the Amphilestidae on the basis of the relative size of the cusps on the preserved molar: central cusp **a** is substantially larger and taller than mesial cusp **b** and distal cusp **c**; cusps **b** and **c** are subequal in size. It must be noted that this molar structure is probably plesiomorphic in triconodonts, as it can also be observed in Rhaeto-Liassic Morganucodontidae. In Triconodontidae, the three main cusps have nearly the same size and in Austrotriconodontidae, **a** > **b** > **c**.

Two subfamilies have been distinguished within the Amphilestidae (e.g. CHOW & RICH, 1984; McKENNA & BELL, 1997; KIELAN-JAWOROWSKA & DASHZEVEG, 1998): the Amphilestinae OSBORN, 1888 and the Gobiconodontinae CHOW & RICH, 1984. By the general robustness of its dentary, Hangjinia is reminiscent of the Gobiconodontinae. It has been shown that, in Hangjinia, the shortening of the dentary is correlated with the reduction of the

number of postcanines (only 4). The postcanines are much more numerous in Gobiconodontinae: 4 premolars (P4 disappearing in later ontogenetic stages in G. ostromi) and 5 molars in Gobiconodon (JENKINS & SCHAFF, 1988; KIELAN-JAWOROWSKA & DASHZEVEG, 1998), at least 6 molars in Klamelia (CHOW & RICH, 1984). On the other hand, the dentary of the Gobiconodontinae is greatly foreshortened: in Gobiconodon, it bears only one semiprocumbent incisor and the canine is much smaller than the incisor. In Klamelia, the foreshortening of the dentary is deduced from the presence of a symphyseal region that extends distally towards the level of teeth inferred to be M2-3 (CHOW & RICH, 1984). As in Hangjinia, the premolar crowns of Gobiconodon are asymmetrical, but the asymmetry is more important in Gobiconodon: P1 is clearly caniniform and P2 and P3 are devoid of a mesial cuspule (JENKINS & SCHAFF, 1988; KIELAN-JAWOROWSKA & DASHZEVEG, 1998). In Gobiconodon, at least the first three premolars are single-rooted (JENKINS & SCHAFF, 1988; KIELAN-JAWOROWSKA & DASHZEVEG, 1998), whereas even the first premolar is double-rooted in Hangjinia. Precise comparisons of the lower molar structure are impossible in the current state of our knowledge, because we only know the outline of the replacing ?M2 in Hangjinia. However, cusps **b** and **c** look proportionally higher in Gobiconodon and a large cusp **d** is usually developed distally.

In the Amphilestinae, the dentary is always more slender than in Hangjinia and in Gobicondontinae (compare with SIMPSON, 1928, fig. 19). The number of teeth is never reduced, neither in the mesial nor in the distal part of the mandible: the dental formula is I3or4, C1, P4, M5 in Amphilestes and I4, C1, P2, M5 in Phascolotherium (SIMPSON, 1928); Phascolodon possessed more than 4 molars (SIMPSON, 1925). The amphilestine lower canine is always much larger than the incisors. The lower canine is apparently double-rooted in Amphilestes, but single-rooted in Phascalotherium. However, this character appears variable and of poor phylogenetic value within the triconodonts: in Triconodontidae, Triconodon possessed double-rooted deciduous lower canines, whereas the permanent lower canines of Trioracodon had apparently only one root (SIMPSON, 1928); in the Rhaeto-Liassic mammaliaform Morganucodon, the lower canines can either be single-rooted or double-rooted (MILLS, 1971). Unlike in Hangjinia and in Gobiconodon, the amphilestine premolars are symmetrical in lateral view. All the premolars are double-rooted, as in Hangjinia. It must be noted that the latter condition is probably plesiomorphic in amphilestids, as it is also observed in triconodontids (SIMPSON, 1928), and in the mammaliaform Morganucodon (MILLS, 1971). With its apparent quite simple morphology and the relative small size of its cusps **b** and **c**, the replacing ?M2 of Hangjinia particularly resembles the lower molars of the Late Jurassic amphilestine Aploconodon (SIMPSON, 1925).

JI et al. (1999) very recently described a new remarkably preserved triconodont mammal, Jeholodens jenkinsi, from the Early Cretaceous of China. The phylogenetic

Table 1 — Distribution of mandibular and dental characters for *Hangjinia chowi* and 5 selected accurately known triconodont mammals, with *Morganucodon* regarded as outgroup. **1:** Angular process present (0), or absent (1); **2:** Meckelian groove reaching the symphysis (0), or shortened (1); **3:** Pterygoid shelf absent (0), or present (1) (ROWE, 1988, 1993); **4:** Lingual cingulum very developed and cuspulate (0), or less developed (1); **5:** Cups a of lower molars much larger than cusps b and c (0), or cusps a, b and c nearly or quite equal in size (1); **6:** One-to-one opposition between upper and lower molars (0), or two-to-one opposition (1) (CROMPTON & JENKINS, 1979); **7:** Lower premolars asymmetrical in lateral view (0), or symmetrical and molariform (1); **8:** Dentition diphyodont (0), or lower molars undergo replacement (1); **9:** At least 7 lower postcanines (0), or 4 lower postcanines (1); **10:** At least 3 lower incisors (0), or one single lower incisor (1); **11:** Lower molars double-rooted (0), or essentially single-rooted (1).

	1	2	3	4	5	6	7	8	9	10	11
Outgroup	0	0	0	0	0	0	0	0	0	0	0
Hangjinia	1	1	1	1	0	?	0	1	1	0	0
Gobiconodon	1	1	1	1	0	1	0	1	0	1	1
Amphilestes	1	1	1	1	0	1	1	0	0	0	0
Phascalotherium	1	1	1	1	0	1	1	0	0	0	0
Triconodon	1	1	1	1	1	0	0	0	0	?	0
Trioracodon	1	1	1	1	1	0	0	0	0	?	0

position of this new species within triconodontids still needs to be clarified. However, it clearly differs from *Hangginia* by the presence of four incisors and six post-canines; the lower canine is particularly small and cusps **b, c** and **d** are distinctly larger on the lower molars.

Replacement of lower molars is shared by both *Hangjinia* and *Gobiconodon*: this character is convincingly demonstrated for *G. ostromi* (JENKINS & SCHAFF, 1988, fig. 8), whereas strong differential wear and dentary structure give indirect evidence of molar replacement in *G. borissiaki* (JENKINS & SCHAFF, 1988; KIELAN-JAWOR-OWSKA & DASHZEVEG, 1998). Molar replacement has not been described in any other mammal, but is well documented in *Sinoconodon* (ZHANG *et al.*, 1998). LUO (1994) argues that *Haldanodon*, Kuehneotheriidae, *Megazostrodon*, Morganucodontidae, Triconodontidae and more derived mammals form a monophyletic group characterized, among others, by a diphyodont dentition. PARRINGTON (1971) concluded to a diphyodont replacement pattern in *Morganucodon*, on the basis of a detailed analysis of the abundant material representing this genus. Nevertheless, GOW (1986) showed that the Early Jurassic mammaliaform *Megazostrodon* should be an exception, as differential tooth wear suggests that the second molar would be replaced, but this hypothesis needs to be confirmed by study of more nearly complete growth series for the taxon. PARRINGTON (1978, fig. 4d) illustrated a dissected fragmentary dentary of *Kuehneotherium*, showing M_4 with roots and roots of M_3 and M_5, on which no trace of molar replacement can be discerned. As *Kueneotherium* is otherwise known only by isolated teeth and edentulous dentaries, it is currently impossible to demonstrate positively the molar replacement in this genus on such incomplete material. This problem occurs in fact in most Mesozoic mammals. That is why it is difficult to state whether the molar replacement observed in *Hang-*

jinia and *Gobiconodon* is really a synapomorphy (or a reversion) closely uniting both taxa, a plesiomorphic character preserved in the amphilestid lineage, or a phenomenon independently appearing in several early mammal lineages and illustrating the plasticity of the dental germinative process. Tooth replacement in adulthood may represent, as noted by JENKINS & SCHAFF (1988) in *Gobiconodon*, a compensatory mechanism renewing heavily abraded molars and, therefore, maintaining life-long efficient puncturing-shearing capabilities.

For a better understanding of the phylogenetic affinities of *Hangjinia*, a preliminary cladistic analysis has tentatively been performed, based on 11 dental and mandibular characters and 7 taxa. The newly described *Jeholodens jenkinsi* has not been included in this analysis, pending further informations about this specimen and, particularly, about the morphology of the postcanine roots. An exhaustive search for most parsimonious trees has been performed using the "Hennig86" programme (FARRIS, 1988).The Rhaeto-Liassic mammaliaform *Morganucodon*, known by abundant material and presenting a triconodont-like dentition, has been first chosen as outgroup. The resulting character-taxon matrix is presented in Table 1. In this quite simple case, a single cladogram has been generated, with a length of 11 steps, a consistency index (C.I.) and a retention index (R.I.) of 1 (Figure 3, A). *Hangjinia* is more closely related to *Gobiconodon* than to amphilestine genera (*Amphilestes* and *Phascalotherium*); it could consequently be grouped within the monophyletic subfamily Gobiconodontinae. However, the monophyly of *Hangjinia* and *Gobiconodon* is only based on the replacement of the lower molars, whose polarity, as discussed above, remains conjectural.

For this reason, it may also be tentatively postulated that molar replacement is in fact plesiomorphic in *Hang-*
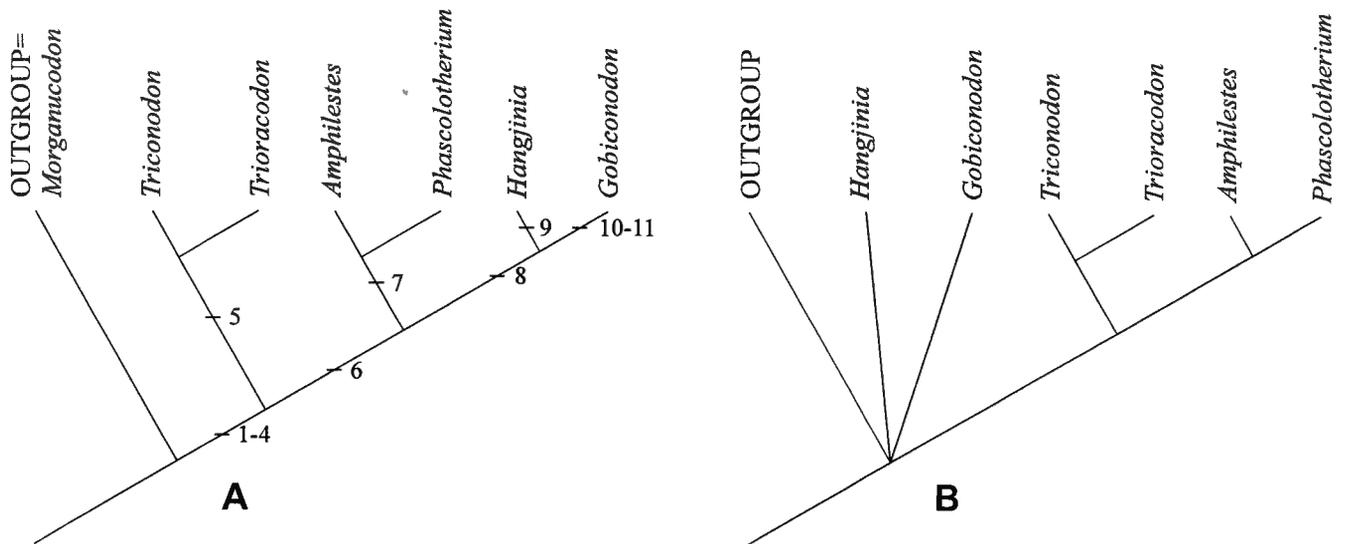
Fig. 3 — Cladogram showing the phylogenetic relationships of *Hangjinia chowi* with selected accurately known triconodont mammals. A: using *Morganucodon* as outgroup and regarding molar replacement as apomorphic in triconodonts; B: regarding molar replacement as plesiomorphic in triconodonts, or eliminating this character from this analysis. **1:** Angular process present (0), or absent (1); **2:** Meckelian groove reaching the symphysis (0), or shortened (1); **3:** Pterygoid shelf absent (0), or present (1) (ROWE, 1988, 1993); **4:** Lingual cingulum very developed and cuspulate (0), or less developed (1); **5:** Cups a of lower molars much larger than cusps b and c (0), or cusps a, b and c nearly or quite equal in size (1); **6:** One-to-one opposition between upper and lower molars (0), or two-to-one opposition (1) (CROMPTON & JENKINS, 1979); **7:** Lower premolars asymmetrical in lateral view (0), or symmetrical and molariform (1); **8:** Dentition diphyodont, or lower molars undergo replacement (character of uncertain polarity); **9:** At least 7 lower postcanines (0), or 4 lower postcanines (1); **10:** At least 3 lower incisors (0), or one single lower incisor (1); **11:** Lower molars double-rooted (0), or essentially single-rooted (1).

jinia and *Gobiconodon*. *Sinoconodon* may in this case be chosen as outgroup. However, recent phylogenies clearly indicate that this genus is probably too distant from the advanced triconodont trunk and also by far too specialized to be regarded as a good outgroup in our analysis (see, e.g., CROMPTON & SUN, 1995; CROMPTON & LUO, 1993; LUO, 1994); we can nevertheless imagine an hypothetic *Morganucodon*-like outgroup with replacement molars for advanced triconodonts. This alternative hypothesis generates eight equally most parsimonious trees, with a length of 12 steps, a C.I. of 0.91 and a R.I. of 0.83. Nelson' s consensus cladogram recovered from this analysis (Figure 3, B) indicates unresolved relationships between *Hangjinia*, *Gobiconodon* and the monophyletic group formed by the Triconodontidae and the Amphilestinae. It means that the phylogenetic position of *Hangjinia* cannot be clarified on the basis of the available material if molar replacement is regarded as plesiomorphic in triconodonts. If this latter character is removed from the analysis, an identical Nelson's consensus cladogram, based on three equally parsimonious trees with a length of 10 steps, a C.I. and a R.I. of 1, is generated.

It can therefore be concluded that the phylogenetic position of *Hangjinia* within triconodonts remains conjectural, although this genus appears closely related to *Gobiconodon*. The present analysis is, of course, very restrictive because it is only based on a few dental and mandibular characters. The recent study of the complete holotype of *Jeholodens jenkinsi* (JI *et al.*, 1999) demonstrates that phylogenetic analyses based only on a few dental characters do not necessarily closely fit the reality. A more definitive assessment of the amphilestid phylogeny must therefore await an analysis of the whole skeleton and, in particular, the discovery of more complete material of *Hangjinia* in Inner Mongolia.

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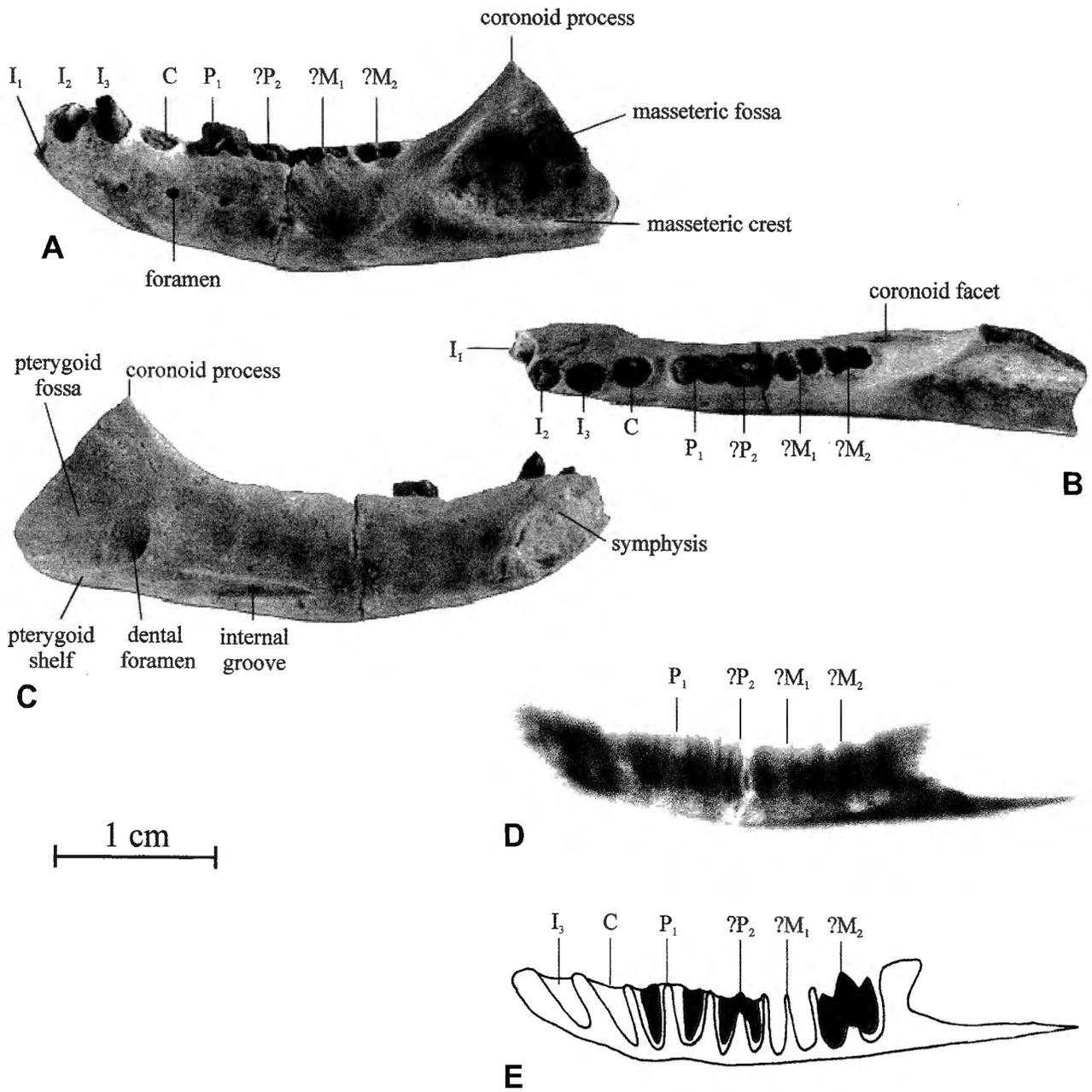
PLATE 1

Left dentary of *Hangjinia chowi* (IMM 96NMHJLII-1), from the Early Cretaceous of Inner Mongolia. A: labial view; B: occlusal view; C: lingual view; D: x-ray radiograph in lateral view; E: interpretation of x-ray radiographs (with tooth or root fragments in black).