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## Oldest Plesiadapiform (Mammalia, Proprimates) from Asia and its palaeobiogeographical implications for faunal interchange with North America

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### Abstract

Carpolestid plesiadapiforms are well known in several lineages from the North American Palaeocene, but they are absent from Europe and known, until now, by only two taxa from the Early Eocene of Asia. Here we describe a new genus of Carpolestinae from the Late Palaeocene locality of Subeng in Inner Mongolia (China). In its morphological characteristics, *Subengius mengi* n. gen. n. sp. is phylogenetically close to *Elphidotarsius* and *Carpodaptus* from the western interior of North America. This discovery shows that plesiadapiforms dispersed from North America to Asia long before the mammalian migration waves of the Palaeocene/Eocene boundary. **To cite this article: T. Smith et al., C. R. Palevol 3 (2004).**

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### Résumé

**Le plus ancien plésiadapiforme (Mammalia, Proprimates) d'Asie et ses implications paléobiogéographiques dans les échanges fauniques avec l'Amérique du Nord.** Les plésiadapiformes carpolestidés sont représentés par plusieurs lignées dans le Paléocène nord-américain, mais ils sont absents d'Europe et ne sont connus jusqu'à présent que par deux taxons de l'Éocène inférieur d'Asie. Nous décrivons ici un nouveau genre de Carpolestinae du Paléocène supérieur de la localité de Subeng en Mongolie intérieure (Chine). Par ses caractères morphologiques, *Subengius mengi* n. gen. n. sp. est phylogénétiquement proche de *Elphidotarsius* et *Carpodaptus* de l'Ouest intérieur d'Amérique du Nord. Cette découverte indique que les plésiadapiformes ont migré d'Amérique du Nord vers l'Asie, bien avant les vagues de migrations mammaliennes de la limite Paléocène/Éocène. **Pour citer cet article : T. Smith et al., C. R. Palevol 3 (2004).**

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**Mots clés :** Paléocène ; Bassin d'Erlian ; Mongolie intérieure ; Chine ; Mammifères ; Plesiadapiformes

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## Version française abrégée

### 1. Introduction

Les plésiadapiformes sont un groupe de mammifères arboricoles généralement considérés comme le groupe frère des primates, bien que quelques auteurs les classent encore parmi les primates [12] ou les dermoptères [1–3]. Nous décrivons ici un nouveau *Carpolestinae* du Paléocène supérieur de Subeng en Mongolie intérieure (Chine). Cette localité a été mentionnée par Russell et Zhai [15], mais aucun des spécimens collectés par une équipe de l'IVPP en 1976 n'a encore été décrit. En 1995, durant la première expédition sino-belge en Mongolie intérieure, l'un d'entre nous (T.S.) a exploré la région de Subeng (Fig. 1) et découvert un nouveau niveau riche en restes de mammifères. Cinq cents kilos de sédiments ont été tamisés à l'eau sur des mailles de 0,5 mm durant quelques jours de travail à Subeng, pendant les étés 2000 et 2001. Parmi les centaines de dents déjà obtenues, représentant une vingtaine de taxons, huit dents sont attribuées à un nouveau *Carpolestinae* ici décrit.

### 2. Données géographiques et géologiques

Les affleurements du gisement de Subeng sont situés sur une pente, à 20 km au sud-ouest de la ville d'Erenhot (Fig. 1). Trois unités lithologiques y ont été observées. Une première unité, à la base, est composée d'une siltite blanche, avec des intercalations organiques noires (lithologie 1 sur la Fig. 2). Ces dernières ont fourni un assemblage riche en palynomorphes dominés par des Normapolles et des gymnospermes bisaccates. La deuxième unité, qui a livré de nombreux ostracodes et quelques charophytes, est composée de marnes vertes finement laminées avec des intercalations de calcaires blancs (lithologie 2 sur la Fig. 2). Des lentilles de sables grossiers rouges (lithologie 3 sur la Fig. 2) ont été observées à deux reprises dans ces dépôts laminés. Les marnes vertes ont également fourni un riche assemblage palynologique dominé par deux algues vertes d'eau douce, *Botryococcus* sp. et *Pediastrum* sp. La troisième unité, dans laquelle ont été découverts les restes de mammifères ainsi que de très nombreux fragments de bois silicifiés, est composée de marnes vert-jaune riches en charophytes et pauvres en ostracodes, de sables fins entrecroisés brun-

jaune et de conglomérats calcaires blancs. Les conglomérats sont composés de nodules calcaires (lithologie 5 sur la Fig. 2) et forment le remplissage basal de chenaux, le reste étant rempli avec les sables fins et marnes (lithologie 4 sur la Fig. 2). Par endroits, le développement de paléosols a donné une couleur rouge aux sédiments. Les sédiments finement laminés de la deuxième unité ont une origine lacustre, alors que les sédiments de la troisième unité ont une origine fluviale. Selon la carte géologique régionale [7], trois formations affleurent à Subeng : la formation d'Iren Dabasu (Crétacé supérieur), les formations tertiaires de Nomogen et Bayan Ulan. Les sédiments de la première unité sont considérés comme appartenant à la formation d'Iren Dabasu. En ce qui concerne les dépôts tertiaires, l'interprétation stratigraphique de Meng et al. [13] a été suivie. La deuxième et la troisième unité appartiennent à la formation de Nomogen. Les sédiments de la troisième unité sont attribués aux « Bayan Ulan beds », sur la base de la faune des mammifères, et forment la partie supérieure de la formation de Nomogen. Les études des charophytes et ostracodes en cours devront confirmer cette hypothèse.

### 3. Paléontologie

*Ordre.* Proprimates Gingerich, 1989.

*Infra-ordre.* Plesiadapiformes Simons, 1972.

*Super-famille.* Plesiadapoidea Trouessart, 1897.

*Famille.* Carpolestidae Simpson, 1935.

*Sous-famille.* Carpolestinae Simpson, 1935

*Subengius* n. gen.

*Étymologie.* En référence à la localité de Subeng.

*Espèce type.* *Subengius mengi* n. sp.

*Subengius mengi* n. sp.

*Étymologie.* En l'honneur de Meng Jin, qui contribua à la connaissance des faunes mammaliennes du Gashatien de Chine.

*Holotype.* IMM 2001-SB-6, P<sup>4</sup> gauche.

*Matériel attribué.* IMM 2001-SB-1, P<sub>4</sub> droite (partielle) ; IMM 2001-SB-2, M<sub>1</sub> gauche ; IMM 2001-SB-3, M<sub>2</sub> droite ; IMM 2001-SB-4, M<sub>3</sub> droite ; IMM 2001-SB-5, I<sup>1</sup> droite ; IMM 2001-SB-7, M<sup>2</sup> droite ; IMM 2001-SB-8, M<sup>3</sup> gauche.

*Localité type et âge.* Subeng, bassin d'Erlan, Mongolie intérieure, république populaire de Chine ;

« Bayan Ulan Beds », niveau supérieur de la formation de Nomogen, Gashatien, Paléocène supérieur.

*Diagnose.* Petit carpoles-tiné avec une morphologie générale proche de *Elphidotarsius*, différant de *Carpodaptes*, *Carpolestes*, *Carpocristes*, and *Carpomegodon* par l'état primitif de P<sup>4</sup> et P<sub>4</sub>; P<sub>4</sub> plus basse que chez *Elphidotarsius* et les autres carpoles-tinés, avec une cuspide apicale antérieure très petite, suivie par trois cuspides apicales majeures, dont la seconde est la plus haute et la plus grande ; M<sub>1</sub> avec le paraconide antérieur et lingual par rapport au protoconide, et le métaconide complètement postérieur et lingual par rapport au protoconide ; I<sup>1</sup> de morphologie simple avec de petites cuspides et avec un latéroconide moins développé que chez *Carpodaptes* et *Carpolestes*; P<sup>4</sup> courte présentant un faible développement du bord labial, avec seulement deux grandes cuspides et une métacrista portant une troisième cuspide, de petits péricône et hypocone bien développés sur le bord lingual, et deux courtes crêtes longitudinales présentes entre les cuspides labiales et linguales.

#### 4. Analyses phylogénétiques et implications paléobiogéographiques

*Subengius mengi* n. gen. n. sp. est une petite forme qui se situe par un certain nombre de caractères à mi-chemin dans l'évolution « plagiulacoïde » des Carpoles-tidae [14,17] entre le genre le plus primitif *Elphidotarsius* et les genres plus évolués *Carpodaptes*, *Carpolestes*, *Carpocristes* et *Carpomegodon*. Toutefois, *Subengius mengi* présente certains caractères mosaïques par rapport aux lignées américaines. La P<sub>4</sub> l'associe à *Elphidotarsius* : les quatre cuspides apicales situées dans le même axe constituent un caractère plus dérivé que chez *Elphidotarsius florencae* et *E. wightoni*, mais semblable à *E. shotgunensis* et *E. russelli*. D'un autre côté, la P<sub>4</sub> est moins élevé que chez *E. florencae*, qui est considéré comme le carpoles-tiné le plus primitif [4,6]. La M<sub>1</sub> présente un *pattern* du trigonide plus dérivé que chez *Elphidotarsius florencae*, mais moins que chez *E. shotgunensis*. Le bord labial de la P<sup>4</sup>, court et peu développé chez *Subengius mengi*, est moins dérivé que chez *Elphidotarsius wightoni*, mais plus dérivé que chez *E. florencae*. D'autres caractères associent *Subengius* avec *Carpodaptes*, tels que la présence d'un péricône et d'un hypocone sur la P<sup>4</sup>. Les deux courtes crêtes longitudinales situées entre

les cuspides labiales et linguales de la P<sup>4</sup> de carpoles-tidés, tels que *Carpodaptes cygneus*, *C. stonleyi* ou *Carpolestes dubius* sont généralement reliées aux crêtes des bords antérieur et postérieur de la dent, qui se prolongent elles-mêmes jusqu'aux péricône et hypocone. En revanche, chez *Subengius*, ces crêtes longitudinales sont indépendantes. *Carpocristes oriens* est le seul carpoles-tidé à avoir trois crêtes longitudinales indépendantes, comme chez *Subengius*. Fox [11] classe d'ailleurs *Carpocristes oriens* dans un genre monotypique à l'écart de la série *Elphidotarsius–Carpodaptes–Carpolestes*.

Sur la base de l'analyse phylogénétique, l'espèce de Subeng est placée dans un nouveau genre d'affinité, encore mal connue au sein des Carpoles-tidae. La morphologie étroitement apparentée entre *Subengius* et plusieurs espèces de *Elphidotarsius* du Torrèjonien et du Tiffanien inférieur implique deux scénarios paléobiogéographiques possibles. Dans le premier, les carpoles-tinés auraient déjà migré vers l'Asie aux alentours du Tiffanien inférieur. Cette hypothèse est renforcée par la persistance de la P<sub>2</sub> chez le récent carpoles-tiné asiatique *Carpocristes oriens*. La P<sub>2</sub> est présente chez les espèces américaines anciennes *Elphidotarsius florencae* et *E. shotgunensis*, alors qu'elle est perdue chez *Elphidotarsius russelli*, *E. wightoni* et les autres carpoles-tidés américains plus évolués [10,11,16]. Dans l'autre scénario, les carpoles-tinés ne se seraient dispersés vers l'Asie qu'à la fin du Tiffanien [4,5]. Ce scénario classique est essentiellement basé sur l'apparition des dinocérates et des ongulés arctostylopidés au Tiffanien 5 en Amérique du Nord, alors que ces groupes sont présents en Asie dès le Nongshanien (début du Paléocène supérieur) [18]. Le scénario de migrations tardives impliquerait que certaines espèces reliques de carpoles-tinés primitifs aient persisté jusqu'à la fin du Tiffanien dans le Nord-Ouest de l'Amérique du Nord, avant de migrer vers l'Asie. Le dernier représentant du genre *Elphidotarsius*, *E. wightoni* du Tiffanien 3 au Canada, est également l'espèce la plus nordique.

## 1. Introduction

Plesiadapiformes are a primitive arboreal mammal group generally considered as the sister-group of primates, although a few authors still consider them to be

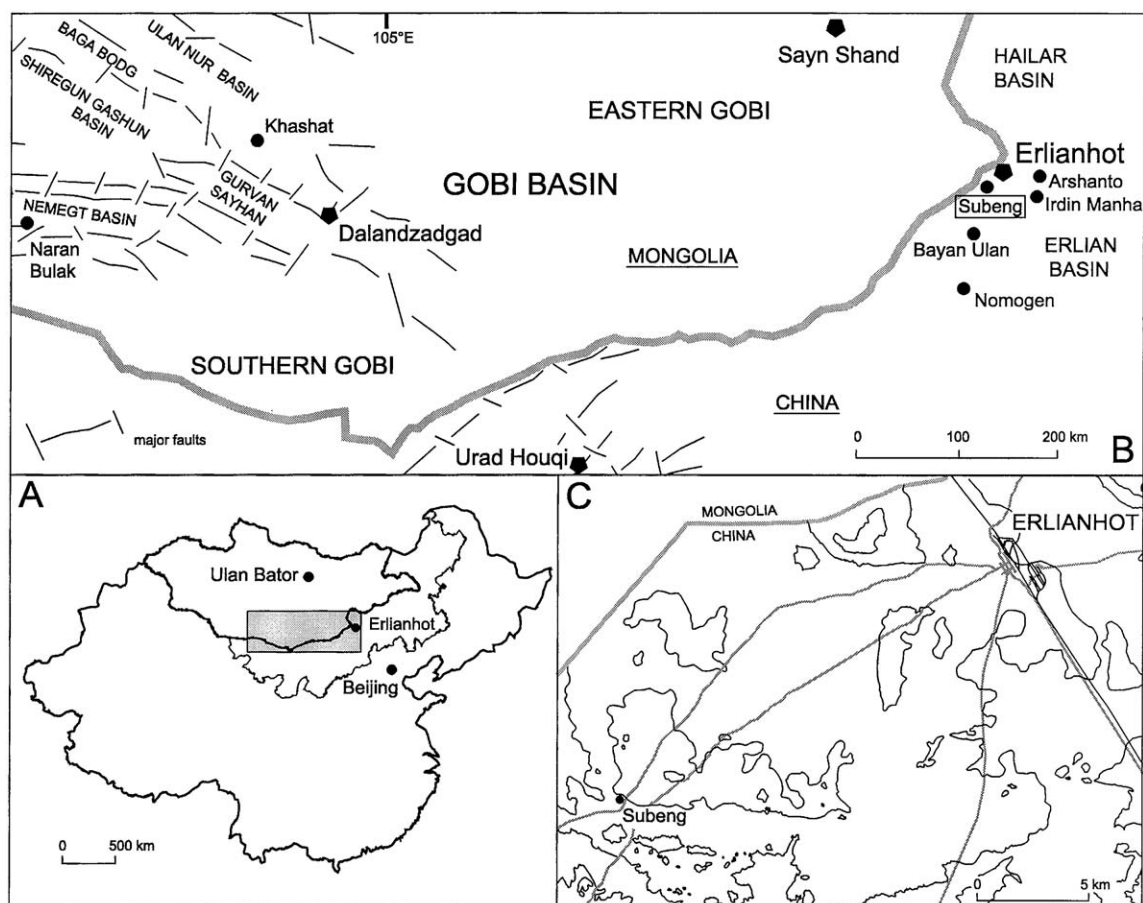


Fig. 1. Map of the Gobi Basin (B), inset map showing the location of the town Erlianhot in Inner Mongolia, China (A) and map with the Subeng mammal site 20 km southwest from Erlianhot (C).

Fig. 1. Carte du bassin du Gobi (B), incluant une carte avec la localisation de la ville d'Erenhot en Mongolie intérieure, Chine (A) et une carte avec le gisement à mammifères de Subeng, à 20 km au sud-ouest de Erenhot (C).

Primates [12] or Dermoptera [1–3]. They are well known in the Palaeocene and Early Eocene of North America and Europe. In Asia, they are represented only by the family Carpolestidae, but until now, no species has been described before the Early Eocene. Here we describe a new genus of Carpolestinae from the Late Palaeocene locality of Subeng in Inner Mongolia (China). The locality was mentioned by Russell and Zhai [15], but none of the specimens collected by a team of the Institute of Vertebrate Paleontology and Paleanthropology (IVPP) in 1976 have yet been described. In 1995, during the first Sino-Belgian expedition in Inner Mongolia, one of us (T.S.) explored the Subeng area (Fig. 1) and discovered a new level rich in mammalian remains. Five hundred kilograms of sedi-

ments were screen-washed at Subeng using a screen mesh of 0.5 mm during the summers of 2000 and 2001. Among the hundreds of teeth already collected, representing about 20 taxa, eight teeth are attributable to the new carpolestine described here.

## 2. Geographical and geological setting

Outcrops of the Subeng mammal site are situated on a slope 20 km southwest of the city of Erlianhot (Fig. 1). Here gullies have eroded the Quaternary cover and Tertiary sediments are exposed. Outcrops are very rare to non-existent on the plains separated by the slope. At the Subeng site, three different lithological



units have been observed. A first unit is exposed in one locality on the lower plain. Here a white siltstone with black organic-rich intercalations (lithology 1 in Fig. 2) has been observed. The organic-rich deposits have yielded a rich palynomorph assemblage, dominated by *Normapolles* and bisaccate gymnosperms.

The second unit crops out in the lower part of the incline. The dominant lithologies are finely laminated green marls with white limestone intercalations (lithology 2 in Fig. 2). Lens-shaped bodies of coarse pebbly red sands (lithology 3 in Fig. 2) have been observed at two places within these laminated deposits. Both the marls and the limestone have yielded numerous ostracods and a smaller number of charophytes. The green marls have also yielded a rich palynomorph assemblage dominated by *Botryococcus* sp. and *Pediastrum* sp., two freshwater green algae.

The third unit crops out in the upper part of the incline. It is within this third unit that the mammalian fossils have been found. Besides mammals, the third unit is very rich in silicified wood fragments. Even when outcrops are lacking, the limit between units 2 and 3 can be positioned based on the silicified wood that occurs abundantly in the pebble lag covering the sediments. Unit 3 consists of green-to-yellow marls rich in charophytes and poor in ostracods, brown-to-yellow cross-stratified fine sands, and white calcareous conglomerates. The conglomerates consist exclusively of calcareous pebbles (lithology 5 in Fig. 2) and form the basal infill of channel-form incisions. The remainder of such incisions is filled with the fine sands and marls (lithology 4 in Fig. 2). Occasionally, palaeosol development caused red colouring of the sediments.

The finely laminated sediments of unit 2 are lacustrine in origin, while the sediments of unit 3 are fluvial in origin. According to the regional geological map [7], three formations crop out at the Subeng site: the Upper Cretaceous Iren Dabasu Formation, and the Tertiary Nomogen and Bayan Ulan Formations. Sediments of unit 1 are interpreted as belonging to the Iren Dabasu Formation, and further study of the palynomorph assemblage will test this interpretation. Interpretation of the Tertiary deposits follows the stratigraphy of Meng et al. [13], where the Bayan Ulan beds are considered to form the upper part of the Nomogen Formation. Units 2 and 3 both belong to the Nomogen Formation. Based on the mammalian fauna, sediments of unit 3 belong to the Bayan Ulan beds. Further studies of

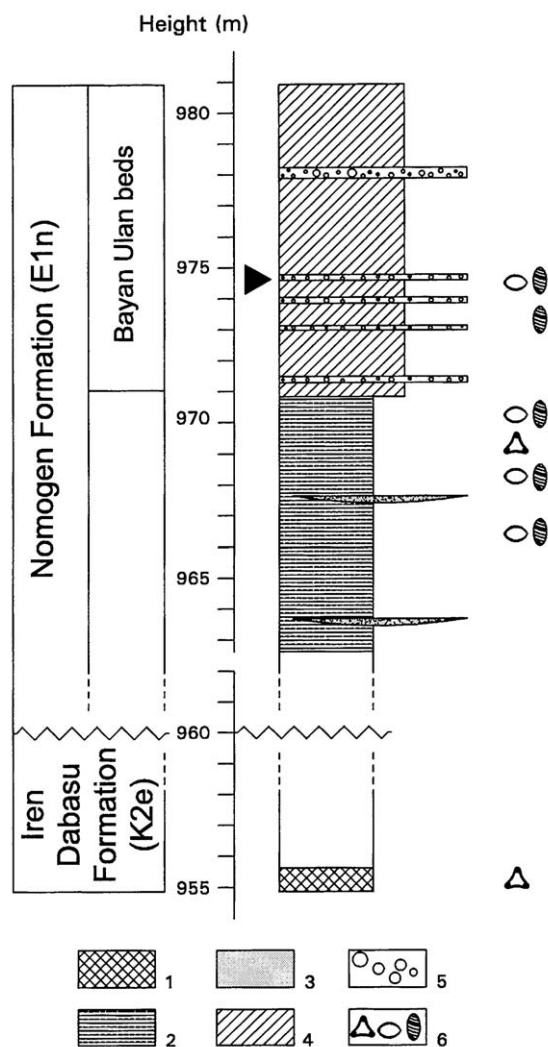


Fig. 2. Subeng stratigraphic section with the three different lithological units. Unit 1: white siltstone with black organic rich intercalations (lithology 1); Unit 2: finely laminated green marls with white limestone intercalations (lithology 2), and lens-shaped bodies of coarse pebbly red sands (lithology 3); Unit 3: fine sands and marls (lithology 4), and conglomerates of calcareous pebbles (lithology 5). Palynomorphs, ostracods and charophytes (6) are present at different levels. The black triangle indicates the position of the mammal level. Fig. 2. Section stratigraphique de Subeng avec les trois unités lithologiques différentes. Unité 1: siltite blanche avec intercalations organiques noires (lithologie 1); unité 2: marnes vertes finement laminées avec intercalations des calcaires blancs (lithologie 2) et lentilles de sables rouges (lithologie 3); unité 3: sables fins et marnes (lithologie 4), et conglomérats de nodules calcaires (lithologie 5); palynomorphes, ostracodes et charophytes (6) sont présents à différents niveaux. Le triangle noir indique la position du niveau à mammifères.

charophytes and ostracods have been initiated to test this hypothesis.

### 3. Systematic palaeontology

**Order.** Proprimates Gingerich, 1989.

**Infraorder.** Plesiadapiformes Simons, 1972.

**Superfamily.** Plesiadapoidea Trouessart, 1897.

**Family.** Carpolestidae Simpson, 1935.

**Subfamily.** Carpolestinae Simpson, 1935.

*Subengius* n. gen.

**Etymology.** Named for the locality of Subeng.

**Type species.** *Subengius mengi* n. sp.

*Subengius mengi* n. sp.

**Etymology.** Named for Meng Jin who contributed to the knowledge of the Gashatan mammal faunas from China.

**Holotype.** IMM 2001-SB-6, left P<sup>4</sup>.

**Referred material.** IMM 2001-SB-1, right P<sub>4</sub> (partial); IMM 2001-SB-2, left M<sub>1</sub>; IMM 2001-SB-3, right M<sub>2</sub>; IMM 2001-SB-4, right M<sub>3</sub>; IMM 2001-SB-5, right I<sup>1</sup>; IMM 2001-SB-7, right M<sup>2</sup>; IMM 2001-SB-8, left M<sup>3</sup>.

**Type locality and age.** Subeng, Erlian Basin, Inner Mongolia, People's Republic of China; Upper 'Bayan Ulan' beds of the Nomogen Formation, Gashatan Land Mammal Age, Upper Palaeocene.

**Diagnosis.** Small carpolestine close to *Elphidotarsius* in general morphology, differing from *Carpodaptus*, *Carpolestes*, *Carpocristes*, and *Carpomegodon* in the primitive condition of the P<sup>4</sup> and P<sub>4</sub>; P<sub>4</sub> lower than that in *Elphidotarsius* and the other carpolestines, with a very small anterior apical cusp followed by three major apical cusps, the second of these is the highest and largest apical cusp; M<sub>1</sub> with the paraconid anterior and lingual to the protoconid, and the metaconid completely posterior and lingual to the protoconid; I<sup>1</sup> of simple morphology with small cusps and a laterocone less developed than in *Carpodaptus* and *Carpolestes*; P<sup>4</sup> short, showing weak development of the labial border, with only two large cusps and a metacrista bearing a third cusp, small well-developed pericone and hypocone cusps on the lingual border,

and two short spur-like ridges present between the labial and lingual cusps.

#### Description (Fig. 3)

**P<sub>4</sub>.** P<sub>4</sub> is modified into the plagiaulacoid blade typical of carpolestids. Its serrated crest consists of a very small, anterior apical cusp, followed by three major apical cusps, with the second of these being the highest and largest apical cusp. The posterior part of the tooth is lacking. In occlusal view, P<sub>4</sub> is slightly sigmoid, with the part in front of the small anterior cusp turning labially and the part posterior to the last apical cusp directed lingually. The lingual side of the tooth is lower-crowned than the labial side.

**M<sub>1</sub>.** The trigonid of M<sub>1</sub> is anteroposteriorly elongated. The paraconid, with a well-developed paralophid, is situated anterolingually to the protoconid. The protoconid is the largest trigonid cusp and is situated anterolabially to the metaconid. The metaconid is well behind the paraconid, and the trigonid basin is wide open lingually. The oblique crest connects the hypoconid to the summit of the metaconid. The hypoconulid is anteroposteriorly compressed. The anterolabial cingulum is well developed and a small anterolingual cingulum is present.

**M<sub>2</sub>.** M<sub>2</sub> shows the general morphology of this tooth in Carpolestidae: the trigonid basin is shorter but larger, the metaconid lies immediately behind the paraconid, and both are directly lingual to the protoconid. The protoconid and metaconid are subequal. The talonid is longer than on M<sub>1</sub>, with an oblique crest that is more anteriorly directed toward the base of the protoconid instead of the base of the metaconid.

**M<sub>3</sub>.** The trigonid of M<sub>3</sub> resembles that of M<sub>2</sub> greatly, but here the metaconid is clearly the largest trigonid cusp. The talonid of M<sub>3</sub> is even longer than that on M<sub>2</sub> and it has a large, rounded hypoconulid lobe.

**I<sup>1</sup>.** I<sup>1</sup> has a simple morphology, and is J-shaped in lateral view. The height of the crown is about 1.5 times the length, and the crown has four distinct cusps. The anterocone is the highest of the two apical cusps. The laterocone is posterolateral to the anterocone but also somewhat larger. The anterocone is connected to a small mediobasal cusp by a long medial crest. Anteromedially, this crest bears a very small elongated bulge, but no mediocone. The mediobasal cusp is posterior to the laterobasal cusp.

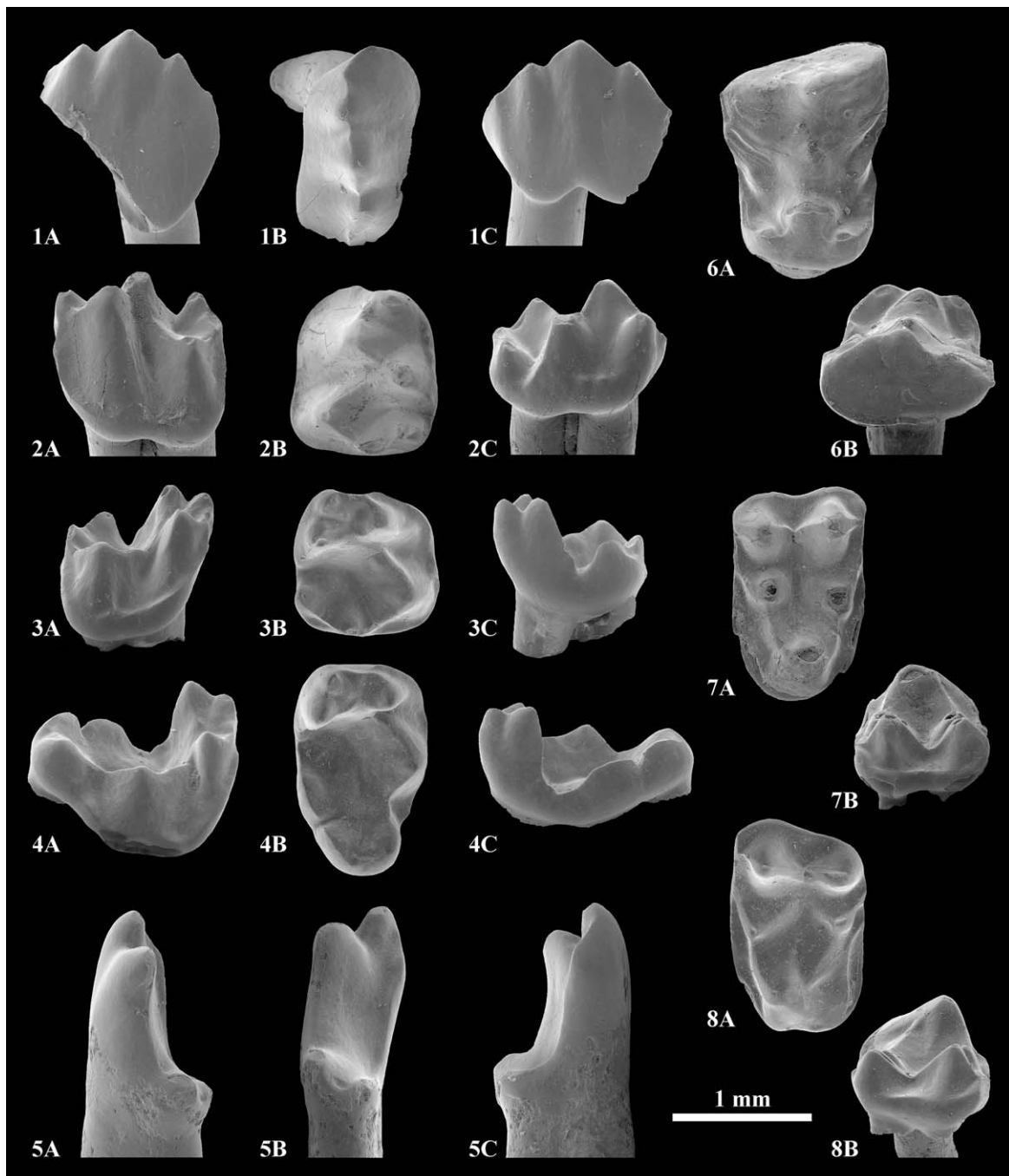


Fig. 3. *Subengius mengi* n. gen. n. sp. 1. IMM 2001-SB-1, partial right P<sub>4</sub>. 2. IMM 2001-SB-2, left M<sub>1</sub>. 3. IMM 2001-SB-3, right M<sub>2</sub>. 4. IMM 2001-SB-4, right M<sub>3</sub>. 5. IMM 2001-SB-5, right I<sup>1</sup>. Labial (A), occlusal (B) and lingual views (C). 6. IMM 2001-SB-6, left P<sup>4</sup>. 7. IMM 2001-SB-7, right M<sup>2</sup>. 8. IMM 2001-SB-8, left M<sup>3</sup>. Occlusal (A) and labial (B) views.

Fig. 3 *Subengius mengi* n. gen. n. sp. 1. IMM 2001-SB-1, P<sub>4</sub> droite (partielle). 2. IMM 2001-SB-2, M<sub>1</sub> gauche. 3. IMM 2001-SB-3, M<sub>2</sub> droite. 4. IMM 2001-SB-4, M<sub>3</sub> droite. 5. IMM 2001-SB-5, I<sup>1</sup> droite. Vues labiale (A), occlusale (B) et linguale (C). 6. IMM 2001-SB-6, P<sup>4</sup> gauche. 7. IMM 2001-SB-7, M<sup>2</sup> droite. 8. IMM 2001-SB-8, M<sup>3</sup> gauche. Vues occlusale (A) et labiale (B).

**P<sup>4</sup>.** P<sup>4</sup> has the outline of an irregular square. The lingual side is shorter than the labial side, and the anterior side is shorter than the posterior side. The labial border of P<sup>4</sup> is formed by a ridge, with the anterior portion lower than the posterior portion. This ridge bears two large cusps followed posteriorly by a metacrista. A first cusp is present in the middle of the anterior half. The second and largest cusp is situated at the beginning of the posterior half, which is often regarded as the paracone. A small third cusp is visible on the metacrista, behind the supposed paracone, that would be homologous to the metacone [14]. Centrally, a cusp thought to be the paraconule is present. From this paraconule, a crescentic ridge stretches labially toward the anterior and posterior sides of the crown, with the posterior part of this ridge containing a small cusplule.

On P<sup>4</sup>, anterolingual and posterolingual to the base of the paraconule, two short spur-like ridges are visible curving labially. The anterior ridge is better developed and widens at its lingual end, developing into a small accessory cusplule. The lingual base of the paraconule is connected to the protocone by a broad ridge. The protocone is the largest cusp and is compressed transversely. A lingually directed ridge runs toward the pericone and hypocone from both the antero- and posterolingual parts, respectively, of the base of the protocone. Both of these cusps are well developed, but clearly smaller than the protocone. A labially oriented ridge springs from both these cusps, forming the anterior and posterior borders of P<sup>4</sup>. However, each ridge becomes lower passing the protocone and disappears before attaining the midway inflexions.

**M<sup>1–3</sup>.** Upper molars show a more conventional cusp pattern. The three cusps of the trigon are readily distinguished; the para- and metaconule are smaller but well developed. These cusps are connected by a series of ridges, and a labial cingulum, a precingulum and a postcingulum are present. M<sup>3</sup> differs in the degree of reduction of the cingulum on the posterolabial portion of the molar, and in having a well-developed talon that contains the reduced hypocone.

#### 4. Phylogenetic analysis and palaeobiogeographical implications

The new Chinese carpolestid *Subengius mengi* is a small form and only the third plesiadapiform reported

in Asia. *Carpocristes oriens* Beard & Wang, 1995, one of the two other species known from the Bumbanian (Early Eocene) of Asia, is the only species that is significantly smaller than *Subengius mengi*. Carpolestids are characterized by their 'plagiaulacoid' evolution [14,17]. This includes hypertrophy of P<sub>4</sub>, which becomes a high, serrated crest that eventually also continues onto the anterior part of M<sub>1</sub>. In association with this, P<sup>3</sup> and P<sup>4</sup> are also often enlarged, and have a crown with a pattern of longitudinal ridges composed of numerous cusps. The more posteriorly situated molars are less modified and therefore less diagnostic. *Subengius* exhibits a number of characteristics that place it midway in plagiaulacoid evolution, between the more primitive genus *Elphidotarsius* and the more evolved genera *Carpodaptus*, *Carpolestes*, *Carpocristes*, and *Carpomegodon*.

*Subengius mengi* displays some mosaic characters in comparison with the American lineages. P<sub>4</sub>, with three major apical cusps and one small anterior apical cusp, associates *Subengius* with *Elphidotarsius*. The four apical cusps of P<sub>4</sub> are in the same anteroposterior axis, which is more derived than in *Elphidotarsius florencae* Gidley, 1923 (USNM 9411, Fort Union Formation, Torrejonian 3, latest Early Palaeocene, Montana, USA) and *E. wightoni* Fox, 1984 (UA 21001, Paskapoo Formation, Tiffanian 3, middle Late Palaeocene, Alberta, Canada). For this character state, *Subengius mengi* is close to *E. shotgunensis* Gazin, 1971 (AMNH 88311, Fort Union Formation, Tiffanian 1, earliest Late Palaeocene, Wyoming, USA) and *E. russelli* Krause, 1978 (Paskapoo Formation, Tiffanian 1, earliest Late Palaeocene, Alberta, Canada). On the other hand, P<sub>4</sub> is low-crowned and less high than in *E. florencae*, which is considered as the most primitive of the carpolestines [4,6]. The small anterior apical cusp on P<sub>4</sub> is also less developed in *Subengius mengi* than in *Elphidotarsius florencae*. The paraconid of M<sub>1</sub> in *Subengius* is situated completely anterolingual to the protoconid, and the metaconid is fully posterolingual to the protoconid. The diagnosis of *Carpodaptus* puts the paraconid in line with the protoconid, or just slightly lingual to this axial situation [14], which is more derived than in *Elphidotarsius* and *Subengius*. M<sub>1</sub> of *Subengius mengi* presents a somewhat more derived trigonid pattern than in *Elphidotarsius florencae* but less than in *E. shotgunensis*.

I<sup>1</sup> of *Subengius* is primitive in comparison with those of *Carpodaptus* and *Carpolestes*, where the lat-



erocone is more strongly developed than the anterocone [8]. The number of labial cusps on  $P^4$  is four in *Elphidotarsius*, and five or six in *Carpodaptes*, *Carpolestes*, *Carpocristes* and *Carpomegodon* [9]; *Subengius* clearly shows three labial cusps but the presence of a fourth one lost by wear cannot be excluded. The short and weakly developed labial border of  $P^4$  in *Subengius mengi* is less derived than in *Elphidotarsius wightoni* but more derived than in *E. florencae*.  $M^3$  of *Elphidotarsius* and *Subengius* has no hypocone, but in *Carpodaptes* this cusp is well developed.

A few characters do associate *Subengius* with *Carpodaptes*.  $P^4$  of *Subengius* has both a pericone and a hypocone, a condition seen in *Carpodaptes* and *Carpolestes*. The rather limited development of these cusps in *Subengius* is only present in *Carpodaptes hazelae* Simpson, 1936 (AMNH 33854, Fort Union Formation, Tiffanian 2, Late Palaeocene, Montana, USA), which is seen as the most primitive species within this genus [4].

In addition, *Subengius* shows some distinct characters setting it apart from all genera mentioned above.  $P^4$  in *Subengius* has a medial longitudinal ridge and two short spurs. Most carpolestids have only the longitudinal medial ridge. Two spur-like structures are variably developed in *Carpodaptes cygneus* and *C. stonleyi*, two species of uncertain phylogenetic affinities (4 versus 11), and in *Carpolestes dubius*, a much more advanced carpolestid. But in all three species, these spurs are closely related to the ridges that form part of the anterior and posterior border of  $P^4$ , running labially from the pericone and hypocone respectively. In these three species, the latter ridges are very well developed and, in passing the protocone, they curve centrally and link to the spurs. In *Subengius* however, the ridges are much less developed, do not curve centrally and the spurs are independent of them. Also in *Subengius*, the anterior, and possibly the posterior, of the spurs show a small accessory cuspule, which is not seen in any other carpolestid. *Carpocristes oriens* is the only carpolestid having three medial longitudinal ridge systems. These are, as in *Subengius*, independent of the labially oriented ridges, but they do not contain any accessory cuspules. Fox [11] put *Chronolestes simul*, the other Asian Plesiadapiform, outside Carpolestidae, leaving *Carpocristes oriens* as the only true Asian carpolestid known. Fox [11] also placed the latter species in a monotypic genus, separate from the *Elphidotarsius*–*Carpodaptes*–*Carpolestes* series.

Based on phylogenetic analysis, the species found at Subeng is put within the Carpolestidae in a new separate genus of imperfectly known affinities. The closely related morphology of *Subengius mengi* and several species of the Torrejonian–Early Tiffanian *Elphidotarsius* suggests two possible paleobiogeographical scenarios. In the first one, carpolestines dispersed into Asia already around the Early Tiffanian (earliest Late Palaeocene). This hypothesis is reinforced by the retention of  $P_2$  in the recent Chinese carpolestine *Carpocristes oriens*.  $P_2$  is present in the Early American *Elphidotarsius florencae* and *E. shotgunensis*, but is lost in *Elphidotarsius russelli*, *E. wightoni* and the other more derived American carpolestids [10,11,16].

The alternative is a late-dispersal scenario suggesting that carpolestines dispersed into Asia only near the end of the Tiffanian [4,5]. This classical scenario is essentially based on the first occurrence of dinoceratans and arctostyloid ungulates in Tiffanian 5 in North America, whereas these groups are already present in Asia from the Nongshanian (early Late Palaeocene) [18]. The late migration scenario would require that some relict species of primitive carpolestines persisted in the northwestern part of North America until the end of the Tiffanian before migrating to Asia. The last occurrence of *Elphidotarsius* is represented by *E. wightoni* from the middle Late Palaeocene (Tiffanian 3) of Canada, which is also the most northern species.

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