

DENTITION AND SYSTEMATIC RELATIONSHIPS OF *ALTANIUS ORLOVI* (MAMMALIA, PRIMATES) FROM THE EARLY EOCENE OF MONGOLIA

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ABSTRACT

New specimens of *Altanius orlovi* are described from the type area, Tsagan-Khushu, in Mongolia. These include the first dentary preserving alveoli for anterior teeth, which show the lower dental formula of *Altanius* to have been 2.1.4.3. Lower incisors were small, equal in size, and nearly vertical in emplacement. The lower canine alveolus is larger than alveoli for the incisors and larger than that for P₁. Alveoli show P₁ to have been single-rooted and P₂ double-rooted. Upper premolars lack a paraconule, and M¹⁻² have a short *Nannopithec*-fold rather than a full postprotocingulum joining the posterior cingulum. *Altanius* is one of the smallest primates known. Morphological comparisons with *Teilhardina* and *Cantius* indicate that *Altanius* is more generalized and primitive than other Omomyidae or Adapidae. *Altanius* is clearly one of the most primitive primates known to date.

DENTURE ET POSITION SYSTÉMATIQUE D'*ALTANIUS ORLOVI* (MAMMALIA, PRIMATES) DE L'ÉOCÈNE INFÉRIEUR DE MONGOLIE.

RÉSUMÉ

Cet article décrit de nouveaux spécimens d'*Altanius* provenant de la même région que le type, Tsagan-Khushu en Mongolie. Parmi eux se trouve le premier dentaire connu conservant les alvéoles des dents antérieures, d'où l'on peut déduire la formule dentaire d'*Altanius*, 2.1.4.3. L'alvéole de la canine inférieure était plus grande que ceux des incisives et de la P₁. D'après les alvéoles toujours, P₁ était uniradiculée tandis que P₂ était biradiculée. Les prémolaires supérieures étaient dépourvues de paraconule, et M¹⁻² possédait un court pli *Nannopithec*, plutôt qu'un postprotocingulum complet rejoignant le cingulum postérieur. *Altanius* est l'un des plus petits primates connus. La comparaison morphologique avec *Teilhardina* et *Cantius* montre que *Altanius* est plus généralisé et plus primitif que les autres Omomyidés ou Adapidés. Au total, *Altanius* apparaît clairement comme l'un des vrais primates les plus primitifs connus à ce jour.

KEY-WORDS : PRIMATES, TARSIOIDEA, OMOMYIDAE, ALTANIUS, EOCENE, MONGOLIA

MOTS-CLÉS : PRIMATES, TARSIOIDEA, OMOMYIDAE, ALTANIUS, ÉOCÈNE, MONGOLIE.

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INTRODUCTION

Tarsiers are among the most interesting primates of Asia. A single genus, *Tarsius*, survives today in a relict distribution encompassing the Philippine Islands and major land masses of the Sunda shelf: Sumatra, Borneo, and Sulawesi (Niemitz 1984; Musser & Dagosto 1987). Evidence of older tarsier-like primates in the fossil record comes from northern Africa, from south and southeast Asia, from Europe, and from North America. *Altiatlasius koulchii* is an omomyid from late Paleocene sediments of Morocco estimated to be about 56-58 million years [Ma] in age (Sigé *et al.* 1990). *Afrotarsius chatrathi* is an afrotarsiid from Oligocene sediments of Egypt estimated to be about 32 million years in age (Simons & Bown 1985; Afrotarsiidae named by Ginsburg & Mein 1987). *Kohatius coppensi* is an omomyid from early or early middle Eocene sediments of Pakistan estimated to be about 50 Ma in age (Russell & Gingerich 1980, 1987). *Tarsius thailandica* is a tarsiid from lower Miocene sediments of Thailand estimated to be about 18 Ma in age (Ginsburg & Mein 1987). In addition, some 28 genera and more than 50 species of tarsioid primates are known from the Eocene (ca. 54 - 34 Ma) of Europe and North America, all classified in the family Omomyidae (Szalay 1976; Gingerich 1981, 1984; Bown & Rose 1987). Tarsioid primates are not known outside Africa before the beginning of the Eocene. Judging from the fossil record as it is presently known, Omomyidae constitute the principal (perhaps only) Eocene tarsioid radiation, while Afrotarsiidae and Tarsiidae reflect subsequent Oligocene and Miocene-Recent tarsioid diversifications.

Tarsioid primates of the family Omomyidae appear on all three northern continents, Asia, Europe, and North America, at or shortly after the beginning of the Eocene epoch (Dashzeveg 1988). The oldest presumed omomyid known from Asia is *Altanius orlovi* described by Dashzeveg & McKenna (1977) from Tsagan-Khushu in the early Bumbanian of Mongolia (Russell & Zhai 1987). The oldest and therefore presumably most primitive omomyid from Europe is *Teilhardina belgica* described by Teilhard de Chardin (1927; see also Simpson 1940; Gingerich 1977) from the Sparnacian of Belgium. The oldest omomyid from North America is *Teilhardina americana* described by Bown (1976; see also Bown & Rose 1987) from the early Wasatchian of Wyoming.

Here we shall describe newly discovered dental and gnathic remains of *Altanius orlovi* and compare these with earliest Eocene Omomyidae and Adapidae known elsewhere on other continents. Our objective is to clarify the systematic relationships of *Altanius* and its role in early primate evolution. *Altanius orlovi* is noteworthy in being the smallest of known omomyids. The body weight

of *Altanius* is estimated to have been only about 30 gm (based on an all-primate regression of body weight on tooth size) or 10 gm (based on a parallel tarsioid trend; Gingerich 1981, 1984). *Altanius* is, in either case, one of the smallest primates of any age.

Altanius specimens described here were collected from two quarries in the Bumban Member, Naran-Bulak Svita, at Tsagan-Khushu in the Nemegt Basin of southwestern Mongolian People's Republic. The holotype came from a locality called Quarry 1, and other remains described here were found at Quarry 2.

INSTITUTIONAL ABBREVIATION

PSS - Geological Institute Paleontology and Stratigraphy Section, Mongolian Academy of Sciences, Ulan Bator (Mongolian People's Republic).

LOWER DENTITION OF ALTANIUS ORLOVI

The holotype and only specimen of *Altanius orlovi* known previously, PSS 7/20-8, is a left dentary with partially preserved roots of P₃ and crowns or partial crowns of P₄-M₃. New material includes three additional dentaries (PSS 20-58, 20-85, and 20-136) that collectively preserve roots or alveoli for all lower teeth plus intact crowns of P₃-M₃. New material also includes two maxillae (PSS 20-61 and PSS no no.) preserving an alveolus for the upper canine, alveoli for P¹⁻², and intact crowns of P³-M³. The lower dentition of *Altanius orlovi* is described here, followed in the next section by description of the upper dentition.

DESCRIPTION OF HOLOTYPE (PSS 7/20-8)

Dashzeveg & McKenna (1977) described the holotype dentary of *Altanius orlovi*, and it also has been illustrated by Rose & Krause (1984). This dentary is small and relatively deep, with a single mental foramen beneath the roots of P₄, a well developed masseteric fossa, and no trace of an alveolus for the enlarged anterior incisor that characterizes many Omomyidae. The holotype preserves alveoli for P₃, and crowns of P₄-M₃. The crown of P₄ is high, with an anteriorly overhanging trigonid dominated by the protoconid. The paraconid is a small conical cusp smaller than the protoconid and appressed to its lingual surface. The anterior base of the paraconid is connected to the protoconid by a notched paracristid. The protoconid has flattened lingual and posterior surfaces, and a curved sloping buccal face. The metaconid is little more than a small swelling at the posterolingual corner of the protoconid. The talonid of P₄ is short and tucked beneath the overhanging trigonid of M₁. The

talonid has two minute cusps flanking a shallow rudimentary basin. Roots of P₄ are splayed slightly, and the posterior root is the larger of the two.

M₁ is the smallest and narrowest of the molars. It has a high, anteriorly narrowing trigonid overhanging the talonid of P₄. The protoconid is slightly higher than the paraconid and metaconid, which are about equal in height. The lingual side of the protoconid is convex rather than flattened as it is on P₄. The paraconid and metaconid are widely separated at their apices, which are conical but somewhat laterally compressed. A very small crest (lingual half of the paracristid) connects the labial base of the paraconid with the anterior base of the protoconid, isolating a very small basin on the trigonid labial to the paraconid. The metaconid is posterolingual to the protoconid and well separated from it. A small crest runs anteriorly from the metaconid. Another crest runs posteriorly from the metaconid connecting it basally to the anterior part of the entoconid across a distinct talonid notch. The third metaconid crest is a continuation of the crista obliqua running up a marked offset in the posterolabial wall of the trigonid. This offset makes the protocristid "stepped." The hypoconid is large, with anterior and posterior faces making an angle of about 85°. The hypoconulid is a very small medial swelling at the posterior edge of the talonid. The entoconid too is small, with a flat anterolabial surface, convex lingual surface, and slightly concave posterior surface. The talonid basin is rounded and smooth. M₁ has a precingulid arising from the labial base of the protoconid and running anterolingually to terminate abruptly as a small cuspule. There is a weak postcingulid descending along the rear of the hypoconid and becoming indistinct near the labial base of this cusp.

The crown of M₂ in the holotype is slightly larger than that of M₁, with a longer and broader talonid basin. The trigonid is damaged and little can be determined regarding details of cusp form and position. The paraconid and metaconid are not so widely separated on M₂ as they are on M₁, and the rear wall of the trigonid is not so strongly offset by the crista obliqua and parallel hypoflexid groove. The protoconid is lower than that of M₁, but it is still higher than that of M₃. The entoconid on M₂ is larger than that on M₁, projecting posterobuccally. There is a deep talonid notch anterior to the entoconid. The hypoconulid is weak. The base of the hypoconid overhangs the labial surface of the dentary making the crown exodaenodont. The talonid basin is rounded and smooth, and a precingulid and postcingulid are developed as on M₁.

The crown of M₃ in the holotype is narrower and much longer than that of M₂. The protoconid is lower than it is on M₂. The paraconid and metaconid are separate but joined labially to the protoconid. The metaconid is

slightly smaller and lower than the paraconid. The protocristid arises from the rear of the metaconid and runs labially to join the back of the protoconid. The remainder of the labial surface of the metaconid is flat and continuous with the convex lingual surface of the protoconid. The lingual surface of the protoconid joins the labial surfaces of the paraconid and metaconid in such a way as to enclose two very small basins at the labial bases of the paraconid and metaconid. The crista obliqua on M₃ does not offset the posterior wall of the trigonid as it does on M₁ or to a lesser extent M₂, joining the posterior wall of the trigonid at a lower point than on either of the two preceding molars. The entoconid is distinct but obscured in being incorporated into a lingual talonid crest. The entoconid is continued posteriorly as a slightly cuspidate lingual crest. There is a deep talonid notch anterior to the entoconid. The hypoconid is smaller than that on either M₁ or M₂. The talonid is much enlarged and elongate. It is expanded posterolabial to the entoconid forming an extended hypoconulid lobe. The precingulid is heavy and ledgelike, running from the hypoflexid groove between the protoconid and hypoconid anteriorly around the base of the protoconid. A smaller labial cingulid borders the hypoconid. There is no postcingulid bordering the hypoconulid lobe posteriorly.

Measurements of the holotype are recorded in Table 1.

DESCRIPTION OF PSS 20-58.

PSS 20-58 (Fig. 1C,D) is a left dentary preserving alveoli for I₁₋₂, an alveolus for C₁, an alveolus for a single-rooted P₁, and alveoli for a double-rooted P₂. Crowns of P₃₋₄ and M₁₋₃ are preserved intact. Judging from alveoli, I₁ and I₂ were approximately the same size: neither was clearly larger than the other. Both alveoli are small, measuring approximately 0.2 mm in diameter. The alveolus for I₁ appears to be slightly more appressed mediolaterally than that for I₂, which is more nearly circular in outline. Judging from the orientation of its alveolus, I₁ was inclined at an angle of about 35° forward of vertical and I₂ was slightly less inclined. For comparison, I₁ in extant *Tarsius* is inclined at only about 20° forward of vertical. Neither incisor can be considered to be enlarged, and neither incisor alveolus extends beneath or behind that for C₁. Without intact crowns, one can only speculate as to whether the incisors of *Altanius* were pointed or spatulate.

The canine alveolus in PSS 20-58 is larger than that for either of the preceding incisors or the following P₁. It is nearly circular in cross-sectional outline, measuring approximately 0.5 mm in diameter. The canine alveolus is slightly inclined anteriorly, but the crown is unlikely to have been procumbent to any significant

Tooth (holotype)		PSS 7/20-8	PSS 20-58	PSS 20-85	PSS 20-136
P ₃	L	--	0.96	--	0.78
	W	--	0.72	--	0.71
	H	--	0.86	--	0.86
P ₄	L	0.93	0.92	--	0.94
	W	0.88	0.87	--	0.80
	H	0.82	1.02	--	0.84
P ₄ L/W index		1.07	1.06	--	1.18
M ₁	L	1.09	1.13	--	1.13
	W	1.15	1.05	--	0.92
	H	0.80	0.83	--	0.76
M ₂	L	1.08	1.17	1.14	1.16
	W	1.22	1.15	1.05	1.07
	H	0.92	0.89	0.90	0.79
M ₃	L	1.58	1.62	1.58	--
	W	1.15	1.08	0.92	--
	H	0.82	0.87	0.88	--
Mandibular depth beneath M ₂		2.40	2.12	2.38	--
P ₃ -M ₂	L	--	--	--	3.79
P ₄ -M ₃	L	4.45	5.22	--	--
M ₂ -M ₃	L	--	--	2.67	--

Table 1 - Measurements of lower teeth of early Eocene *Allantius orlovi* from the Bumban Member of the Naran-Bulak Svita at Tsagan-Khushu. Abbreviations : L, crown length. W, crown width. H, crown height (measured on labial side). All measurements in mm. *Mesures des dents inférieures d'Allantius orlovi de l'Eocène inférieur du Bumban Member de Naran-Bulak Svita à Tsagan-Khushu. Abréviations : L, longueur de la couronne ; W, largeur de la couronne ; H, hauteur de la couronne (mesurée du côté labial). Toutes les mesures sont en mm.*

degree. There was clearly no diastema in front of or behind the lower canine.

The single alveolus for P₁ is anteroposteriorly compressed, measuring approximately 0.2 mm in anteroposterior diameter and 0.4 mm in labiolingual diameter. There are two alveoli for P₂, both measuring between 0.2 and 0.3 mm in diameter. These are oriented at a 10-15° angle to the sagittal plane, indicating that the front of the crown of P₂ must have overlapped the labial part of the crown of P₁, and the back of the crown of P₂ must have been overlapped by the lingual side of the crown of P₃.

The crown of P₃ is simple, trapezoidal in occlusal outline, with a single, high, pointed protoconid. There is no paraconid, and only a faint swelling in the position of the metaconid. A convex anterior crest extends forward

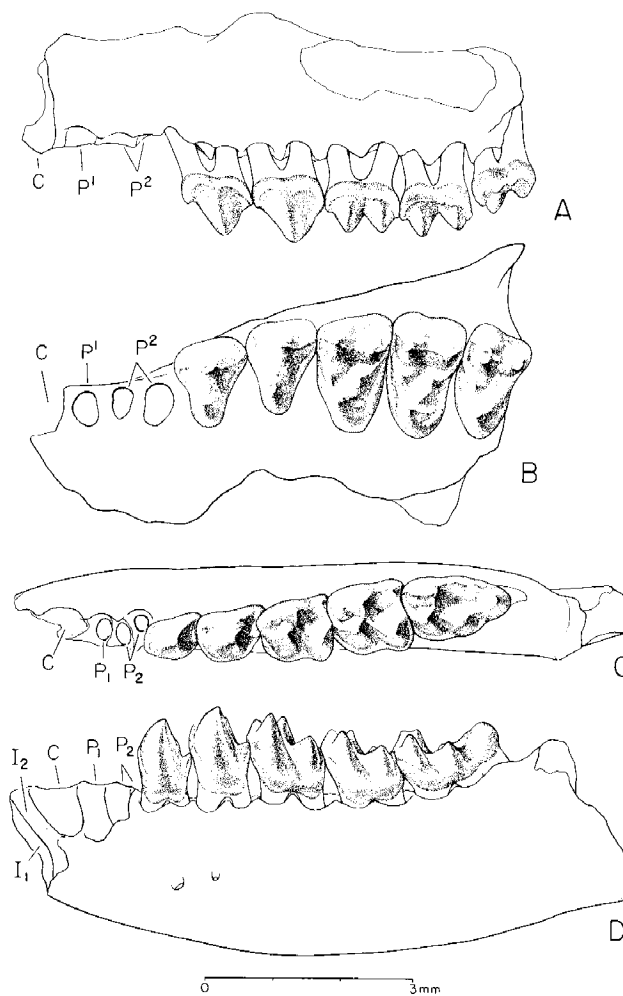


Figure 1 - Dentition of *Allantius orlovi* from the Bumban Member of the Naran-Bulak Svita at Tsagan-Khushu (Mongolia). A, B : Left maxilla with P₃-M₃ (PSS 20-61) in lateral and occlusal view. C, D : Left dentary with P₃-M₃ (PSS 20-58) in occlusal and lateral view. Note alveoli for single-rooted P₁ and double-rooted P₂. Note also equisized alveoli for small vertically implanted I₁ and I₂, relatively large C₁ alveolus, small alveolus for single-rooted P₁, and paired alveoli for double-rooted P₂. *Denture d'Allantius orlovi provenant du Bumban Member de Naran-Bulak Svita à Tsagan-Khushu (Mongolie). A,B : maxillaire gauche avec P₃-M₃ (PSS 20-61) en vue latérale et occlusale. C,D : mandibule gauche avec P₃-M₃ (PSS 20-58) en vue occlusale et latérale. Remarquer les alvéoles pour une P₁ uniradiculée et une P₂ biradiculée. Remarquer également les alvéoles de même taille des I₁ et I₂ à implantation verticale, l'alvéole de C relativement grande, le petit alvéole pour la P₁ uniradiculée, et les deux alvéoles correspondant à la P₂.*

from the protoconid, curving downward to the anteriormost point on the crown of P₃. Here it meets labial and lingual portions of the precingulid. A concave posterior crest joins the protoconid to the metaconid swelling at the posterolingual corner of the trigonid before descending posteriorly. A faint postcingulid curves to merge posteriorly into a short, high, convex talonid. This talonid is slightly basined, with the narrow

basin opening medially. A faint crista obliqua runs from the superior part of the talonid up the back of the protoconid.

P₄ in PSS 20-58 is very similar to that in the holotype. The crown of P₄, like that of P₃, is trapezoidal in occlusal outline. There is a high, well developed trigonid with distinct protoconid, paraconid, and metaconid. The protoconid is the largest, the metaconid is next largest, and the paraconid is the smallest of trigonid cusps. The protoconid and metaconid are positioned close together, while the paraconid is more distant. A curved paracristid connects the anterior surface of the protoconid to the anterior margin of the paraconid. The protocristid connecting the protoconid and metaconid is short and sharply notched. The talonid on P₄ is short and high, like that of P₃. It is more basined, with a better developed hypoconid and sharper crista obliqua defining the labial margin of the basin. The talonid basin is open lingually. There is a precingulid arising from the base of the protoconid and extending forward and upward to join the paracristid at its lowest point. A postcingulid curves upward to connect the posterior base of the crown to the hypoconid.

M₁, M₂, and M₃ resemble these teeth in the holotype. The paraconid and metaconid on M₁ are well separated, those on M₂ are more closely appressed, and the paraconid and metaconid on M₃ are confluent. The paraconid on M₂ is larger and a little higher than the metaconid. The crista obliqua is the principal crest joining the metaconid on M₁. It is strong but subordinate to the protocristid on M₂, and it is much weaker than the protocristid on M₃. The hypoconid is larger than the entoconid on M₁, both are approximately equal in size on M₂, and the entoconid is larger than the hypoconid on M₃. The hypoconulid is a small posterior swelling on the talonid of M₁ and M₂. It is a large, basined, posterior lobe on M₃.

There is a small mental foramen beneath the anterior root of P₄, and a larger mental foramen between the anterior and posterior roots of P₃. Measurements of this specimen are included in Table 1.

DESCRIPTION OF PSS 20-85 AND PSS 20-136.

PSS 20-85 is a left dentary with the broken base of the crown of M₁ and intact crowns of M₂ and M₃. This specimen resembles the holotype and PSS 20-58 very closely. It differs in having a slightly narrower and hence relatively longer M₂ crown. The paraconid and metaconid on the trigonid of M₂ are more separated than they are on the trigonid of PSS 20-58. In PSS 20-85 the paraconid and metaconid on M₂ are almost as well separated as they are on M₁ of PSS 20-58.

PSS 20-136 is a left dentary preserving crowns of P₃-M₂. The teeth are slightly more worn, but otherwise

resemble PSS 20-58. The dentary itself preserves enough of an alveolus for P₂ to show that the posterior root was positioned lingually, as it is in PSS 20-58. PSS 20-136 has a higher P₄ L/W index than either PSS 20-58 or the holotype.

Measurements of PSS 20-85 and PSS 20-136 are included in Table 1.

UPPER DENTITION OF ALTANIUS ORLOVI

DESCRIPTION OF PSS 20-61.

PSS 20-61 (Fig. 1A,B) is a left maxilla preserving the posterior edge of the upper canine alveolus, alveoli for a single-rooted P¹ and a double-rooted P², and crowns of P³-M³ (a second maxillary, PSS 20-168, contains intact crowns of P⁴-M³ but no additional alveoli). Judging from its preserved posterior edge, the canine alveolus in PSS 20-61 was approximately 0.5-0.6 mm in diameter. The alveolus for P¹ is about 0.4-0.5 mm in diameter. Anterior and posterior alveoli for P² measure about 0.4 mm and 0.5 mm, respectively, in average diameter. Both are slightly compressed anteroposteriorly.

All of the preserved cheek teeth are high crowned. P³ is roughly triangular in occlusal outline, with a large paracone in the center of the labial margin of the crown. A very small parastyle precedes the paracone. There is a small but distinct protocone lingual to and well separated from the paracone. A strong postparacrista runs down the back of the paracone to the posterior edge of the crown, where it joins a weak labial cingulum running from the parastyle to the posterior edge of P³. There is no precingulum and only a weak trace of a postcingulum. Enamel on the lingual edge of P³ is poorly preserved, but there does not appear to have been any lingual cingulum. P⁴ is very similar to P³, differing in being shorter anteroposteriorly, a little broader labiolingually, and a little higher crowned. P⁴ also differs in having a stronger protocone. In both premolars, the protocone is isolated, with no crests connecting it to other cusps. P³ and P⁴ both lack paraconules.

All three upper molars are similar in form, with a high, pointed paracone and metacone forming the labial half of each crown, and a prominent protocone, paraconule, and metaconule forming the lingual half of each crown (except on M³, where the metaconule and to some extent the metacone are reduced). The lingual portion of each molar appears to be twisted forward relative to its labial complement. All three upper molars have narrow but distinct labial cingula. All three have precingula as well, running from the interproximal

