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

PHILIP D. GINGERICH
*Museum of Paleontology, The University of Michigan, Ann Arbor, Michigan 48109-1079, U.S.A.*
DEMBERELYIN DASHZEVEG
*Department of Paleontology and Stratigraphy, Geological Institute, Mongolian Academy of Science, Ulan Bator, Mongolian People's Republic.*
DONALD E. RUSSELL
*Institut de Paléontologie, Muséum National d'Histoire Naturelle, 5 Rue de Buffon, Paris 75005, France.*

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 $P_1$. Alveoli show $P_1$ to have been single-rooted and $P_2$ double-rooted. Upper premolars lack a paraconule, and $M^{1-2}$ have a short *Nannopithex*-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 grand que ceux des incisives et de la $P_1$. D'après les alvéoles toujours, $P_1$ était uniradiculée tandis que $P_2$ était biradiculée. Les prémolaires supérieures étaient dépourvues de paraconule, et $M^{1-2}$ possédait un court pli *Nannopithex*, 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.

Manuscrit accepté définitivement le 26.09.1990

Geobios, 1991
n° 24, fasc. 5
p. 637-646

## 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 $P_3$ and crowns or partial crowns of $P_4$-$M_3$. 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 $P_3$-$M_3$. New material also includes two maxillae (PSS 20-61 and PSS no no.) preserving an alveolus for the upper canine, alveoli for $P^{1-2}$, and intact crowns of $P^3$-$M^3$. 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 $P_4$, 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 $P_3$, and crowns of $P_4$-$M_3$. The crown of $P_4$ 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 $P_4$ is short and tucked beneath the overhanging trigonid of $M_1$. The

talonid has two minute cusps flanking a shallow rudimentary basin. Roots of $P_4$ are splayed slightly, and the posterior root is the larger of the two.

$M_1$ is the smallest and narrowest of the molars. It has a high, anteriorly narrowing trigonid overhanging the talonid of $P_4$. 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 $P_4$. 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. $M_1$ 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 $M_2$ in the holotype is slightly larger than that of $M_1$, 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 $M_2$ as they are on $M_1$, 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 $M_1$, but it is still higher than that of $M_3$. The entoconid on $M_2$ is larger than that on $M_1$, 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 $M_1$.

The crown of $M_3$ in the holotype is narrower and much longer than that of $M_2$. The protoconid is lower than it is on $M_2$. 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 $M_3$ does not offset the posterior wall of the trigonid as it does on $M_1$ or to a lesser extent $M_2$, 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 $M_1$ or $M_2$. 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 $I_{1-2}$, an alveolus for $C_1$, an alveolus for a single-rooted $P_1$, and alveoli for a double-rooted $P_2$. Crowns of $P_{3-4}$ and $M_{1-3}$ are preserved intact. Judging from alveoli, $I_1$ and $I_2$ 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 $I_1$ appears to be slightly more appressed mediolaterally than that for $I_2$, which is more nearly circular in outline. Judging from the orientation of its alveolus, $I_1$ was inclined at an angle of about 35° forward of vertical and $I_2$ was slightly less inclined. For comparison, $I_1$ 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 $C_1$. 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 $P_1$. 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 ***Altanius 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'**Altanius 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.*

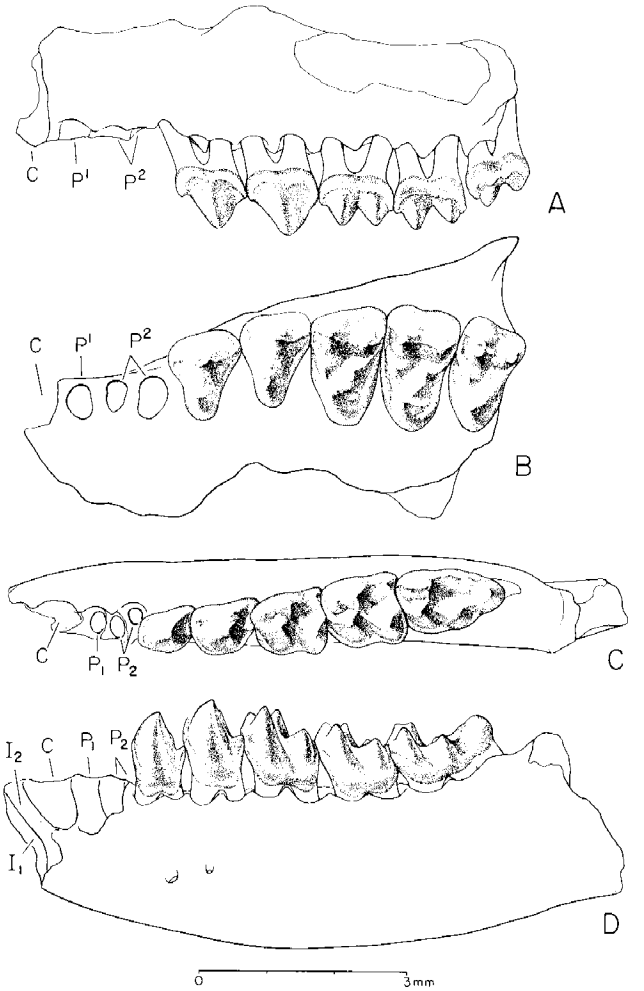


Figure 1 - Dentition of ***Altanius orlovi*** from the Bumban Member of the Naran-Bulak Svita at Tsagan-Khushu (Mongolia). **A, B** : Left maxilla with $P^2$-$M^3$ (PSS 20-61) in lateral and occlusal view. **C, D** : Left dentary with $P_3$-$M_3$ (PSS 20-58) in occlusal and lateral view. Note alveoli for single-rooted $P^1$ and double-rooted $P^2$. Note also equisized alveoli for small vertically implanted $I_1$ and $I_2$, relatively large $C_1$ alveolus, small alveolus for single-rooted $P_1$, and paired alveoli for double-rooted $P_2$.. *Denture d'**Altanius 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 grand, le petit alvéole pour la P1 uniradiculée, et les deux alvéoles correspondant à la P2.*

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

The single alveolus for $P_1$ is anteroposteriorly compressed, measuring approximately 0.2 mm in anteroposterior diameter and 0.4 mm in labiolingual diameter. There are two alveoli for $P_2$, 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 $P_2$ must have overlapped the labial part of the crown of $P_1$, and the back of the crown of $P_2$ must have been overlapped by the lingual side of the crown of $P_3$.

The crown of $P_3$ 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 from the protoconid, curving downward to the anteriormost point on the crown of $P_3$. 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.

$P_4$ in PSS 20-58 is very similar to that in the holotype. The crown of $P_4$, like that of $P_3$, 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 $P_4$ is short and high, like that of $P_3$. 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.

$M_1$, $M_2$, and $M_3$ resemble these teeth in the holotype. The paraconid and metaconid on $M_1$ are well separated, those on $M_2$ are more closely appressed, and the paraconid and metaconid on $M_3$ are confluent. The paraconid on $M_2$ is larger and a little higher than the metaconid. The crista obliqua is the principal crest joining the metaconid on $M_1$. It is strong but subordinate to the protocristid on $M_2$, and it is much weaker than the protocristid on $M_3$. The hypoconid is larger than the entoconid on $M_1$, both are approximately equal in size on $M_2$, and the entoconid is larger than the hypoconid on $M_3$. The hypoconulid is a small posterior swelling on the talonid of $M_1$ and $M_2$. It is a large, basined, posterior lobe on $M_3$.

There is a small mental foramen beneath the anterior root of $P_4$, and a larger mental foramen between the anterior and posterior roots of $P_3$. 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 $M_1$ and intact crowns of $M_2$ and $M_3$. This specimen resembles the holotype and PSS 20-58 very closely. It differs in having a slightly narrower and hence relatively longer $M_2$ crown. The paraconid and metaconid on the trigonid of $M_2$ are more separated than they are on the trigonid of PSS 20-58. In PSS 20-85 the paraconid and metaconid on $M_2$ are almost as well separated as they are on $M_1$ of PSS 20-58.

PSS 20-136 is a left dentary preserving crowns of $P_3$-$M_2$. The teeth are slightly more worn, but otherwise resemble PSS 20-58. The dentary itself preserves enough of an alveolus for $P_2$ to show that the posterior root was positioned lingually, as it is in PSS 20-58. PSS 20-136 has a higher $P_4$ 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 $P^1$ and a double-rooted $P^2$, and crowns of $P^3$-$M^3$ (a second maxillary, PSS 20-168, contains intact crowns of $P^4$-$M^3$ 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 $P^1$ is about 0.4-0.5 mm in diameter. Anterior and posterior alveoli for $P^2$ 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. $P^3$ 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 $P^3$. There is no precingulum and only a weak trace of a postcingulum. Enamel on the lingual edge of $P^3$ is poorly preserved, but there does not appear to have been any lingual cingulum. $P^4$ is very similar to $P^3$, differing in being shorter anteroposteriorly, a little broader labiolingually, and a little higher crowned. $P^4$ also differs in having a stronger protocone. In both premolars, the protocone is isolated, with no crests connecting it to other cusps. $P^3$ and $P^4$ 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 $M^3$, 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

contact with the preceding tooth to a point at the base of the protocone at its anterolingual corner. On $M^2$ and $M^3$ (and possibly $M^1$), there is a faint swelling directly anterior to the protocone that might be interpreted as a rudimentary pericone cuspule. $M^1$ and $M^2$ have a postcingulum well preserved, arising from the point of interproximal contact with the following molar to a point posterolingual to the protocone. There is a small but distinct swelling that might be interpreted as a rudimentary hypocone on this postcingulum. Pre- and postprotocristae connect the protocone to the paraconule and metaconule, respectively, and these crests continue as preparaconule and postmetaconule cristae. There is only a faint trace of postparaconule and premetaconule cristae. The "*Nannopithex*-fold" on $M^1$ and $M^2$ sweeps down the posterior surface of the protocone about two-thirds of the way to the postcingulum. It ends in a slight swelling that is also possibly homologous with the hypocone in other primates. This *Nannopithex*-fold does not actually join the postcingulum, but remains separated by a distinct notch or gap. The posterior surface of the protocone is not well preserved on $M^3$, precluding any determination of the conformation of cusps and crests in this area.

The lower border of the infraorbital foramen is preserved on the maxilla directly above $P^3$. It is relatively large, measuring approximately 0.5 mm in diameter. Measurements of this specimen are listed in Table 2.

| Tooth | | PSS 20-61 | PSS 20-168 |
|---|---|---|---|
| $P^3$ | L | 1.00 | -- |
| | W | 1.26 | -- |
| | H | 0.96 | -- |
| $P^4$ | L | 0.96 | 0.95 |
| | W | 1.37 | 1.62 |
| | H | 1.08 | 1.07 |
| $M^1$ | L | 0.98 | 1.11 |
| | W | 1.69 | 1.72 |
| | H | 0.81 | 1.00 |
| $M^2$ | L | 0.98 | 1.07 |
| | W | 1.80 | 1.92 |
| | H | 0.88 | 0.95 |
| $M^3$ | L | 0.98 | 0.87 |
| | W | 1.47 | 1.62 |
| | H | 0.78 | 0.73 |
| $P^3$-$M^3$ | L | 4.97 | -- |
| $P^4$-$M^3$ | L | -- | 3.60 |

Table 2 - Measurements of upper teeth of early Eocene ***Altanius orlovi*** from the Bumban Member of the Naran-Bulak Svita at Tsagan-Khushu. Abbreviations as in Table 1. All measurements in mm. ***Mesures des dents supérieures d'Altanius orlovi de l'Eocène inférieur du Bumban Member de Naran-Bulak Svita à Tsagan-Khushu. Abréviations comme pour le tabl. 1. Toutes les mesures sont en mm.***

## COMPARISON WITH OTHER EARLY EOCENE OMOMYIDAE

Dashzeveg & McKenna (1977) described *Altanius orlovi* as an omomyid, and it is thus logical to compare *Altanius* with the earliest Omomyidae in Asia, Europe, and North America. *Kohatius coppensi*, based on an isolated $M_1$ of early or early middle Eocene age, is still the only other omomyid known from Asia (Russell & Gingerich 1980, 1987), and it resembles North American early Eocene *Tetonius* in size and general form. A $P_4$ referred to *Kohatius* is more similar to *Altanius* than it is to *Tetonius* in having an oblique occlusal outline with distinct labial bulges above the roots. It differs from *Altanius* in lacking a well developed paraconid and metaconid.

One tooth of a possible omomyid has been described from the Oligocene of Oman (Thomas *et al.* 1989). This lower molar is small, but it is still about twice the size of lower molars of *Altanius*, and it differs in having a prominent entoconid and hypoconulid twinned near the lingual margin of the tooth (more often seen in Adapidae). *Decoredon elongatus* from the middle Paleocene of China has been proposed as a possible omomyid (Szalay & Li 1986), but the illustrated specimens appear so different from any known primate, fossil or living, that they are unlikely to represent this order. *Decoredon* was originally described as a condylarth (Xu, 1977), which remains a possible allocation.

*Teilhardina belgica* from the Sparnacian locality of Dormaal in Belgium is the earliest and most primitive omomyid known from Europe (Simpson 1940 ; Szalay 1976 ; Godinot *et al.* 1978). The dental formula cannot be determined with certainty, but it was probably both 2.1.4.3 and 2.1.3.3 with the population being variable. The holotype of *T. belgica* has alveoli like those of *A. orlovi* for two equisized, slightly procumbent incisors (Gingerich 1977). Some specimens retain two alveoli between $C_1$ and $P_3$, while others retain only a single premolar alveolus in front of $P_3$ (Gingerich 1977). Specimens with two premolar alveoli in front of $P_3$ may have retained $P_1$ as well as $P_2$, or alternatively $P_1$ may have been lost in all specimens and the number of roots of $P_2$ remained variable. Retention of $P_1$ in some specimens is at least a possibility, and consequently the dental formula is best expressed as 2.1.3-4.3. Lower cheek teeth of *T. belgica* are generally similar to those of *A. orlovi* but differ in having a less developed paraconid and metaconid on $P_4$, a reduced entoconid on $M_{1-2}$, and a reduced hypoconulid lobe on $M_3$. Upper cheek teeth of *Teilhardina belgica* were illustrated by Szalay (1976). Judging from these illustrations, upper cheek teeth of *T.*

*belgica* differ from those of *A. orlovi* in having blunter cusps and reduced conules, in having protocones more expanded anteroposteriorly on $P^3$-$M^2$, in having the *Nannopithex*-fold a little more strongly developed on $M^{1-2}$, and in having a more reduced $M^3$.

*Teilhardina americana* is the oldest and most primitive North American omomyid (Szalay 1976 ; Bown 1976, 1979 ; Bown & Rose 1987). It comes from the middle Sandcouleean subdivision of the Wasatchian land-mammal age (zone $Wa_1$, early Eocene), but it has not been found to date in early Sandcouleean sediments (zone $Wa_0$) considered closely correlative with the European Sparnacian (Gingerich 1989). Thus *T. americana* is probably a little younger geologically than *T. belgica*. *T. americana* has a dental formula of 2?.1.3-4.3 (Bown & Rose 1987) like that inferred for *T. belgica*. *T. americana* differs from *T. belgica* in having a moderately enlarged $I_1$, a slightly reduced canine, and broader cheek teeth (Bown & Rose 1987), and these are further differences from *A. orlovi*.

*Altanius orlovi* appears to be more primitive than both *Teilhardina belgica* and *T. americana*. It is primitive in retaining three alveoli between $C_1$ and $P_3$ for a single-rooted $P_1$ and double-rooted $P_2$. Small size may be primitive. The presence of alveoli for small, equisized, vertically implanted $I_1$ and $I_2$, a characteristic shared with *T. belgica*, is probably primitive as well. In being as or more primitive than *Teilhardina* in characteristics compared here, *Altanius* is probably more primitive than all other Omomyidae known to date.

## COMPARISON WITH EARLY EOCENE ADAPIDAE

*Altanius* can also be compared with early Eocene Adapidae. Adapidae are poorly known in the early Eocene of Asia. Three species, *Panobius afridi*, cf. *Agerinia* sp., and Adapidae indet., are represented by a total of four teeth (Russell & Gingerich 1987), and these are all from the latter part of the early Eocene. All represent primates much larger than *Altanius*. *Panobius* is similar to European *Donrussellia* and differs from *Altanius* as *Donrussellia* does.

*Cantius eppsi*, *Donrussellia provincialis*, and *Donrussellia magna* are the oldest and most primitive European Adapidae (Russell *et al.* 1967 ; Godinot 1978, 1981 ; Godinot *et al.* 1987 ; Russell *et al.* 1988). All are much larger than *Altanius*. The anterior dentition of *Cantius eppsi* is unknown, but it probably had small, vertically-implanted lower incisors, a large projecting $C_1$, single-rooted $P_1$, and double-rooted $P_2$ like later *Cantius*. $P_4$ is longer than it is wide (L/W = 1.33), with distinct paraconid and metaconid cusps well separated. Lower molar cusps are blunt and talonids are broadly basined. Trigonids resemble those of *Altanius* in being open on $M_1$ but more closed on $M_2$ and $M_3$, with paraconids and metaconids closely appressed and even confluent. Upper $P^{3-4}$ and $M^{1-3}$ differ from *Altanius* in having blunter cusps and anteroposteriorly elongated, basined trigons. Upper molars of *C. eppsi* resemble those of *A. orlovi* in having relatively large conules and in having a similarly developed *Nannopithex*-fold.

*Donrussellia provincialis* is the only species of *Donrussellia* for which the front of the dentary is known, and it preserves alveoli showing that the lateral incisor was small, the canine relatively large, $P_1$ single-rooted, and $P_2$ double-rooted (Godinot 1981), a configuration very much like that in *Altanius*. $P_4$ is longer than it is wide in *D. magna* (L/W = 1.51) and in *D. provincialis* (L/W = 1.47). These two species have more open trigonids on lower molars, with more centrally placed paraconids. Upper molars of *D. provincialis* have small conules, and the *Nannopithex*-fold is weak or missing.

*Cantius torresi* is the oldest and most primitive North American adapid (Gingerich 1986, 1989). It resembles European *C. eppsi* closely, differing principally in having a shorter and broader $P_4$ (L/W = 1.17-1.25 for three specimens - overlapping the range for *A. orlovi* in Table 1).

*Altanius orlovi* differs from all early Adapidae in being much smaller. It is equally primitive in dental formula, and the conformation of incisor and premolar alveoli is very similar to that seen in Adapidae.

## COMPARISON WITH PALEOCENE CARPOLESTIDAE

Dashzeveg & McKenna (1977) noted similarities of the holotype of *Altanius* to the primitive carpolestid *Elphidotarsius* from the middle Paleocene of North America. Rose & Krause (1984) extended this comparison and concluded that significant resemblances of *Altanius* to *Elphidotarsius* are at least as numerous and detailed as those to any omomyid. Rose & Krause further suggested that relationships of *Altanius* lie with Plesiadapiformes rather than tarsiiform Omomyidae. New specimens of *Altanius* described here make it possible to extend this comparison further and to evaluate relationships to primitive Carpolestidae (*Elphidotarsius*) in the context of primitive Omomyidae (*Teilhardina*) and Adapidae (*Cantius*). *Elphidotarsius* and Carpolestidae are reviewed in Rose (1975) and Krause (1978).

Eighteen points of comparison of *Altanius* to *Elphidotarsius*, *Teilhardina*, and *Cantius*, are listed in Table 3. These are taken from Rose & Krause and from specimens described above. Character 4, $I_1$

| Character | Range (0 to 1 or 2) | *Altanius* | *Elphido.* | *Teilhard.* | *Cantius* |
|---|---|---|---|---|---|
| 1 .Overall size | Small - Large | 0 | 1 | 1 | 2 |
| 2. $I_1$ size | * Small - Large | 0 | 1 | 0 | 0 |
| 3. $I_1$ inclination | * Vertical - Procumbent | 0 | 1 | 0 | 0 |
| 4. $I_1$ shape | * Pointed - Spatulate | - | 0 | - | 1 |
| 5. $P_1$ alveolus | * Present - Absent | 0 | 2 | 1 | 0 |
| 6. $P_3$ crown | * Large - Reduced | 0 | 1 | 0 | 0 |
| 7. $P_4$ trigonid | * Triangular - Bladelike | 0 | 1 | 0 | 0 |
| 8. $M_1$ trigonid | * High - Low | 0 | 0 | 1 | 2 |
| 9. $M_1$ trigonid | * Wide - Compact | 1 | 1 | 0 | 0 |
| 10. $M_1$ paraconid-metaconid | * Separated - Connate | 0 | 0 | 0 | 0 |
| 11. $M_1$ protocristid | Stepped - Flat | 0 | 0 | 1 | 0 |
| 12. $M_1$ talonid | * Narrow - Broad | 1 | 1 | 0 | 1 |
| 13. $M_1$ talonid | * Short - Long | 0 | 0 | 1 | 1 |
| 14. $M_2$ paraconid size | * Large - Small (rel. metaconid) | 0 | 1 | 1 | 1 |
| 15. $M_{2-3}$ lingual cusps | High - Low | 0 | 0 | 1 | 1 |
| 16. $M_{1-3}$ crowns | "Normal" - Exodaenodont | 1 | 2 | 0 | 0 |
| 17. $P^{3-4}$ paraconule | * Absent - Present | 0 | 1 | 0 | 0 |
| 18. $M^{1-2}$ crest | Postprotocingulum - *Nannopithex*-fold | 1 | 0 | 1 | 1 |

Table 3 - Characters used in comparison of ***Altanius*** with primitive plesiadapiform ***Elphidotarsius,*** primitive omomyid ***Teilhardina***, and primitive adapid ***Cantius.*** Character state scores range from 0 to 1 (or 2). Asterisks mark character states initially assumed to be primitive in beginning comparative analysis. ***Caractères utilisés dans la comparaison de Altanius avec le plesiadapiforme primitif Elphidotarsius, l'omomyidé primitif Teilhardina, et l'adapidé primitif Cantius. Les astérisques indiquent les caractères suggérés primitifs au début de l'analyse comparative.***

shape, is known only in *Elphidotarsius* and *Cantius*, and it thus has limited value in comparison. Character 10, separation of the paraconid and metaconid on $M_1$, appears not to differ among taxa compared, and thus it too has limited value. Most characters can be scored from 0 to 1, but in some cases, where intermediate states are known, it is appropriate to score from 0 to 2.

Comparing the lists of character states for pairs of genera in Table 3, it is immediately clear that *Teilhardina* and *Cantius* differ least from each other. The sum of differences between the *Teilhardina* and *Cantius* lists is 5. *Teilhardina* and *Cantius* together differ from *Altanius* by a sum of differences of 9-10, and they differ from *Elphidotarsius* by a sum of differences of 15-16. *Altanius* differs from *Elphidotarsius* by a sum of differences of 11, and it is thus phenetically slightly closer to Omomyidae- Adapidae than it is to Carpolestidae. This difference is slight however.

Phylogenetic analysis using parsimony (Swofford, 1985) yields a similar result (Figure 2). A phylogenetic tree was constructed by a parsimony algorithm from data in Table 3. All possible tree topologies were compared and the tree of shortest length (22 steps) is the one shown. It has a consistency index of 0.955. The tree is rooted at the midpoint of greatest patristic distance (midpoint between *Elphidotarsius* and *Teilhardina*). Characters marked by asterisks in Table 3 were assumed to be primitive *a priori*, based on evolutionary trends observed in Carpolestidae and early primates in general (initial polarities were not assigned in all cases). Alternatively, the oldest genus, *Elphidotarsius*, was used as a hypothetical ancestor in determining character polarities. For characters unordered in beginning the analysis (those without asterisks in Table 3), phylogenetic analysis using parsimony indicates that intermediate overall size like that in *Elphidotarsius* and *Teilhardina* is primitive (Character 1), a stepped $M_1$ protocristid like that in

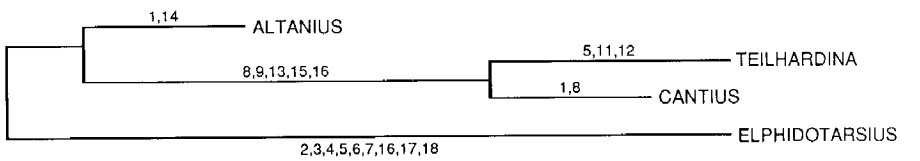


Figure 2 - Phylogenetic tree showing postulated relationships of ***Altanius, Teilhardina, Cantius,*** and ***Elphidotarsius.*** Branch lengths are proportional to number of changes assigned to each branch. Numbers written above or below branches denote characters in Table 3 changing along each branch segment. Note that ***Altanius*** is closer to ***Teilhardina*** and ***Cantius*** than it is to ***Elphidotarsius,*** but ***Altanius*** falls outside the ***Teilhardina - Cantius*** clade. See text for discussion. ***Relations phylogénétiques envisagées entre Altanius, Teilhardina, Cantius, et Elphidotarsius. La longueur des branches est proportionnelle au nombre de changements attribués à chaque branche. Les nombres indiquent les caractères du tableau 3 changeant le long de chaque segment. Noter qu'Altanius est plus proche de Teilhardina et Cantius que d'Elphidotarsus, mais Altanius est hors du clade Teilhardina - Cantius. Voir discussion dans le texte.***

*Altanius*, *Elphidotarsius*, and *Cantius* is primitive (Character 11), high $M_{2-3}$ lingual cusps like those in *Altanius* and *Elphidotarsius* are primitive (Character 15), and intermediate to full exodaenodonty like that in *Altanius* and *Elphidotarsius* is primitive (Character 16). The postprotocingulum - *Nannopithex*-fold difference separating *Elphidotarsius* from *Altanius*, *Teilhardina*, and *Cantius* cannot be polarized (Character 18). Phylogenetic analysis using parsimony contradicts our initial assumptions that a wide $M_1$ trigonid is primitive (Character 9), that a narrow $M_1$ talonid is primitive (Character 12), and that a large $M_2$ paraconid is primitive (Character 14).

Overall similarity and phylogenetic analysis using parsimony agree in placing *Altanius* closer to *Teilhardina* - *Cantius* than to *Elphidotarsius*. Relationships of *Altanius* appear to lie with Omomyidae and Adapidae rather than plesiadapiform Carpolestidae.

## DISCUSSION AND CONCLUSIONS

Similarity of *Altanius* to earliest Omomyidae and Adapidae, similarity of the latter groups to each other (evidenced by a history of difficulty in distinguishing them), and appearance of *Altanius*, Omomyidae, and Adapidae in faunas of similar age on northern continents, taken together, are evidence of their close relationship. Overall similarity and phylogenetic analysis using parsimony indicate that *Teilhardina* and *Cantius* are similar to each other, sharing derived characteristics that include characters 8, 9, 13, 15, and 16 from Table 3 (see Fig. 2). The first species of *Teilhardina*, *T. belgica*, was described by Teilhard de Chardin (1927), who recognized its affinities to *Omomys* and Omomyidae. The second species of *Teilhardina*, *T. gallica*, was described by Russell *et al.* (1967). This subsequently proved to be an adapid and it was redescribed as *Donrussellia* by Szalay (1976). The first species of *Cantius*, *C. eppsi*, was described by Cooper (1932) who placed it in the adapid genus *Protoadapis*. This species was redescribed as an omomyid by Simons (1962) when he placed it in the new genus *Cantius*. Russell *et al.* (1967) returned *Cantius* to Adapidae (Notharctidae) and correctly recognized that *Cantius* was congeneric with most species then referred to *Pelycodus*.

Midpoint rooting places *Altanius* closer to *Teilhardina-Cantius* than it does to *Elphidotarsius*. We retain *Altanius* in Omomyidae because we consider evidence available to date insufficient to justify placement in a distinct family by itself. Comparing *Altanius* with Omomyidae and Adapidae, we consider its primitive size resemblance to Omomyidae to be more important than other primitive characteristics of resemblance to Adapidae (like the full 2.1.4.3 dental formula and stepped $M_1$ protocristid). Omomyidae are small tarsier-like prosimians with pointed incisors and tubular ectotympanics; if *Altanius* should eventually prove to have had spatulate incisors (or a free ectotympanic ring), this new evidence would support classification with Adapidae rather than Omomyidae. It is important to recognize that *Altanius* is more generalized and primitive morphologically than other Omomyidae (and Adapidae). Combining this with its early Eocene age, *Altanius* is properly regarded as one of the most primitive true Primates or "Euprimates" (sensu Hoffstetter, 1977) known to date. Another very primitive true primate is *Altiatlasius* from North Africa described by Sig), Jaeger, Sudre & Vianey-Liaud (1990).

Resemblances to *Elphidotarsius*, while arguably all in primitive characteristics, might be construed as evidence of the morphological (largely dental) continuity linking plesiadapiform Proprimates (*sensu* Gingerich, 1989) to true Primates. The question of relationship here remains open, however, and in recent years the gap between Proprimates and Primates has widened. Many authors doubt that Plesiadapiformes belong in Primates at all (hence their removal to Proprimates). Information sufficient to resolve this uncertainty is not yet available. We can state, though, while reiterating the omomyid character of *Altanius*, that plesiadapiform Proprimates were apparently absent in Asia.

**Acknowledgements** - Specimens in Figure 1 were illustrated by Karen Klitz. We thank Drs. Jens L. Franzen, Gregg F. Gunnell, Robert Hoffstetter, David W. Krause, and Kenneth D. Rose for comments on the manuscript.

## REFERENCES

BOWN T.M. 1976 - Affinities of *Teilhardina* (Primates, Omomyidae) with description of a new species from North America. *Folia Primatol.*, **25** : 62-72.

BOWN T.M. 1979 - Geology and mammalian paleontology of the Sand Creek facies, lower Willwood Formation (lower Eocene), Washakie County, Wyoming. *Mem. Geol. Surv. Wyoming*, **2** : 1-151.

BOWN T.M. & ROSE K.D. 1987 - Patterns of dental evolution in early Eocene anaptomorphine primates (Omomyidae) from the Bighorn Basin, Wyoming. *Paleont. Soc. Mem.* (suppl. vol. 61, n°. 5 *J. Paleont.*), **27** : 1-162.

COOPER C.F. 1932 - On some mammalian remains from the lower Eocene of the London Clay. *Ann. Mag. Nat. Hist.*, 10, **9** : 458-467.

DASHZEVEG D. 1988 - Holarctic correlation of non-marine Palaeocene-Eocene boundary strata using mammals. *J. Geol. Soc.*, **145** : 473-478.

DASHZEVEG D. & MCKENNA M.C. 1977 - Tarsioid primate from the early Tertiary of the Mongolian

People's Republic. *Acta Palaeont. Polonica*, **22** : 119-137.

GINGERICH P.D. 1977 - Dental variation in early Eocene *Teilhardina belgica*, with notes on the anterior dentition of some early Tarsiiformes. *Folia Primatol.*, **28** : 144-153.

GINGERICH P.D. 1981 - Early Cenozoic Omomyidae and the evolutionary history of tarsiiform primates. *J. Human Evol.*, **10** : 345-374.

GINGERICH P.D. 1984 - Paleobiology of tarsiiform primates. *In* NIEMITZ C. (ed.) : Biology of Tarsiers. Gustav Fischer Verlag : 31-44.

GINGERICH P.D. 1986 - Early Eocene *Cantius torresi*- oldest primate of modern aspect from North America. *Nature*, **320** : 319-321.

GINGERICH P.D. 1989 - New earliest Wasatchian mammalian fauna from the Eocene of northwestern Wyoming : composition and diversity in a rarely sampled high-floodplain assemblage. *Univ. Mich. Pap. Paleont.*, **28** : 1-97.

GINSBURG L. & MEIN P. 1987 - *Tarsius thailandica* nov. sp., premier Tarsiidae (Primates, Mammalia) fossile d'Asie. *C. R. Acad. Sci. Paris*, II, **304** : 1213-1215.

GODINOT M. 1978 - Un nouvel Adapidé (Primate) de l'Éocène inférieur de Provence. *C. R. Acad. Sci. Paris*, II, **286** : 1869-1872.

GODINOT M. 1981 - Les mammifères de Rians (Éocène inférieur, Provence). *Palaeovertebrata*, **10** : 43-126.

GODINOT M., BROIN F. de, BUFFETAUT E., RAGE J.-C. & RUSSELL D.E. 1978 - Dormaal : une des plus anciennes faunes éocènes d'Europe. *C. R. Acad. Sci. Paris*, II, **287** : 1273-1276.

GODINOT M., CROCHET J.-Y., HARTENBERGER J.-L., LANGE-BADRÉ B., RUSSELL D.E. & SIGÉ B. 1987 - Nouvelles données sur les mammifères de Palette (Éocène inférieur, Provence). *Münchner Geowiss. Abh. (A)*, **10** : 273-288.

HOFFSTETTER R. 1977 - Phylogénie des Primates : confrontation des résultats obtenus par les diverses voies d'approche du problème. *Bull. Mém. Soc. d'Anthrop. Paris*, **4** : 327-346.

KRAUSE D.W. 1978 - Paleocene primates from western Canada. *Can. J. Earth Sci.*, **15** : 1250-1271.

MUSSER G.G. & DAGOSTO M. 1987 - The identity of *Tarsius pumulus*, a pygmy species endemic to the montane mossy forests of central Sulawesi. *Am. Mus. Novitates*, **2867** : 1-53.

NIEMITZ C. 1984 - Taxonomy and distribution of the genus *Tarsius* Storr, 1780. *In* NIEMITZ C. (ed.) : Biology of Tarsiers. *Gustav Fischer Verlag* : 1-16.

ROSE K.D. 1975 - The Carpolestidae : early Tertiary primates from North America. *Bull. Mus. Comp. Zool., Harvard University*, **147** : 1-74.

ROSE K.D. & KRAUSE D.W. 1984 - Affinities of the primate *Altanius* from the early Tertiary of Mongolia. *J. Mammal.*, **65** : 721-726.

RUSSELL D.E., GALOYER A., LOUIS P. & GINGERICH P.D. 1988 - Nouveaux vertébrés sparnaciens du Conglomérat de Meudon à Meudon, France. *C. R. Acad. Sci. Paris*, II, **307** : 429-433.

RUSSELL D.E. & GINGERICH P.D. 1980 - Un nouveau primate omomyide dans l'Eocène du Pakistan. *C. R. Acad. Sci. Paris*, II, **291** : 621-624.

RUSSELL D.E. & GINGERICH P.D. 1987 - Nouveaux primates de l'éocène du Pakistan. *C. R. Acad. Sci. Paris*, II, **304** : 209-214,

RUSSELL D.E., LOUIS P. & SAVAGE D.E. 1967 - Primates of the French early Eocene. *Univ. California Publ. Geol. Sci.*, **73** : 1-46.

RUSSELL D.E. & ZHAI R.-J. 1987 - The Paleogene of Asia : mammals and stratigraphy. *Mém. Mus. Nat. Hist. Natur., Sér. C, Sciences de la Terre*, **52** : 1-488.

SIGÉ B., JAEGER J.-J., SUDRE J. & VIANEY-LIAUD M. 1990 - *Altiatlasius koulchii* n. gen. et sp., primate omomyidé du Paléocène supérieur du Maroc, et les origines des euprimates. *Palaeontographica, A*, **214** : 31-56.

SIMONS E.L. 1962 - A new Eocene primate genus, *Cantius*, and a revision of some allied European lemuroids. *Bull. Brit. Mus. Nat. Hist., Geol.*, **7** : 1-36.

SIMONS E.L. & BOWN T.M. 1985 - *Afrotarsius chatrathi*, first tarsiiform primate (?Tarsiidae) from Africa. *Nature*, **313** : 475-477.

SIMPSON G.G. 1940 - Studies on the earliest primates. *Bull. Am. Mus. Nat. Hist.*, New York, **77** : 185-212.

SWOFFORD D.L. 1985 - Phylogenetic Analysis using Parsimony (PAUP), version 2.4. *Illinois Nat. Hist. Surv.*, Champaign.

SZALAY F.S. 1976 - Systematics of the Omomyidae (Tarsiiformes, Primates) : taxonomy, phylogeny, and adaptations. *Bull. Am. Mus. Nat. Hist.*, **156** : 157-450.

SZALAY F. S. & LI C.-K. 1986 - Middle Paleocene euprimate from southern China and the distribution of Primates in the Paleogene. *J. Human Evol.*, **15** : 387-397.

TEILHARD de CHARDIN P. 1927 - Les mammifères de l'éocène inférieur de la Belgique. *Mém. Musée Royal d'Hist. Natur. Belgique*, **36** : 1-33.

THOMAS H., ROGER J., SEN S., BOURDILLON-DE-GRISSAC C., & AL-SULAIMANI Z. 1989 - Découverte de vertébrés fossiles dans l'Oligocène inférieur du Dhofar (Sultanat d'Oman). *Geobios*, **22** : 101-120.

XU Q. 1977 - Two new genera of old Ungulata from the Paleocene of Qianshan Basin, Anhui. *Vertebrata PalAsiatica*, **15** : 119-125.