

***Dawsonolagus antiquus*, A Primitive Lagomorph from the Eocene Arshanto Formation, Nei Mongol, China**

Author(s) :Chuankui Li, Jin Meng, Yuanqing Wang

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DAWSONOLAGUS ANTIQUUS, A PRIMITIVE LAGOMORPH FROM THE EOCENE ARSHANTO FORMATION,
NEI MONGOL, CHINA

CHUANKUI LI

Research Associate, Section of Vertebrate Paleontology; Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences,
P.O. Box 643, Beijing 100044, China (lichuankui@ivpp.ac.cn)

JIN MENG

Research Associate, Section of Vertebrate Paleontology; Division of Paleontology, American Museum of Natural History, Central Park West at 79th
Street, New York, NY 10024 (jmeng@amnh.org)

YUANQING WANG

Research Associate, Section of Vertebrate Paleontology; Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences,
P.O. Box 643, Beijing 100044, China (wangyuanqing@ivpp.ac.cn)

ABSTRACT

A new lagomorph, *Dawsonolagus antiquus*, **gen. et sp. nov.**, collected from the possible late early Eocene Arshanto Formation of Nei Mongol (Inner Mongolia), China, is described. The material includes a partial skull with P⁴-M² on both sides, two fragmentary mandibles, several isolated teeth, three calcanei and an astragalus. The new genus is characterized by a mosaic combination of features similar to mimotonids and lagomorphs, presenting a morphotype intermediate between a mimotonid and a typical lagomorph.

INTRODUCTION

Lagomorpha consists of two living families, Leporidae (rabbits and hares) and Ochotonidae (pikas) that include 13 genera and 81 species (Nowak 1999), and at least 56 fossil genera (McKenna and Bell 1997). Recent phylogenetic analyses suggest that Asia is probably the center of origin for the group (Meng et al. 2003; Asher et al. 2005), where stem taxa of lagomorphs, such as *Mimotona* (Li 1977; Li and Ting 1985, 1993) and *Gomphos* (Zhegallo and Shevyreva 1976; Dashzeveg and Russell 1988; Asher et al. 2005), have been recorded from middle Paleocene to lowest Eocene beds. On the other hand, lagomorphs of modern aspect were diverse in the Eocene of Asia, represented by at least nine genera including *Lushilagus*, *Shamolagus*, *Gobiolagus*, *Hypsomyilus*, *Strenulagus*, *Dituberolagus*, *Annalagus*, *Desmatolagus*, and *Aktashmys* (Averianov and Lopatin 2005; Meng et al. 2005). In contrast to *Mimotona* and *Gomphos*, for which the dentition and various cranial and postcranial elements have been documented, most Asian Eocene lagomorphs are known only from fragmentary jaws and teeth, restricting our knowledge of morphological transformations among early lagomorphs to their dentition.

Here we report a new genus and species of lagomorph from the possibly late early Eocene Arshanto Formation of Nei Mongol (Inner Mongolia), China. The new taxon is represented by partial skull and jaws as well as some elements of the pes that display a combination of features similar to either mimotonids or lagomorphs. This new taxon is therefore morphologically transitional between mimotonids and lagomorphs. The primitive nature of the taxon is consistent with the interpretation that the Arshanto Formation is probably late early Eocene, not middle Eocene as previously recognized.

TERMINOLOGY AND ABBREVIATIONS

We primarily follow Wood (1940) for terminology related to lagomorph cheek tooth structures. Relevant terms have

been used inconsistently in previous studies of lagomorphs because of different interpretations of their cusp homology (Ehik 1926; Wood 1940; Bohlin 1942; McKenna 1982; Averianov and Lopatin 2005). We follow Novacek (1986) for general terminology related to the mammalian cranium and Krause (1884) for terminology that is specific for lagomorphs. Early works, such as those by Krause (1884), Gerhardt (1909), Dice (1933), and Craigie (1948), employed inconsistent terminology related to lagomorph skull morphology. For tarsal structures, we follow the terminology of Szalay (1985).

Institutional abbreviations are as follows: **AMNH**, American Museum of Natural History, New York; **CM**, Carnegie Museum of Natural History, Pittsburgh; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing; **PIN**, Paleontological Institute, Russian Academy of Sciences, Moscow; **ZIN**, Zoological Institute, Russian Academy of Sciences, St. Petersburg.

SYSTEMATIC PALEONTOLOGY

Order Lagomorpha Brandt, 1855

Family indet.

Dawsonolagus, **gen. nov.**

Type species.—*D. antiquus*, the only species currently known for the genus.

Diagnosis.—A moderately sized Glires with ever-growing incisors covered with enamel band anteriorly and a dental formula of 2?-0-3-3/1-0-2-3. Primitively similar to mimotonids in having flat orbital floor of maxilla, large temporal region on skull, glenoid fossa broad and long, large coronoid process, short diastema, sub-unilateral hypsodonty of cheek teeth, relatively straight outline of upper tooth row, and slight reduction of last upper and lower molars. Differs from mimotonids but similar to lagomorphs in having one pair of lower incisors, grooved upper incisor (also present in *Mimotona*), masseteric fossa on jugal (also present in *Mimotona*), anteriorly extended internal nares, posteriorly extended supraorbital crest and postorbital process that define a larger orbit, and calcaneum with

calcaneofibular facet and calcaneal canal. Resembles Asian Eocene lagomorphs in having essentially bilobate lower cheek teeth, non-molariform trilobate P^{3-4} , and M^1 with mixed features of P^4 and M^2 . Further resembles *Lushilagus*, *Strenulagus* and *Aktashmys* in general tooth morphology and separation of the trigon from the hypocone-shelf on M^2 ; differs from the latter in having symmetrically grooved upper incisor, relatively straight upper tooth row, less hypsodont cheek teeth, anteriorly closed paraflexia and larger labial cusp on P^3 , molars with two separate labial roots, and M^{1-2} subequal in size. Similar to later leporids in having supraorbital crest, distinct postorbital process of the frontal, interorbital constriction of skull, and formation of the anterior zygomatic arch primarily by jugal. Unique in having spaced upper cheek teeth and a coronoid process that is posterior in position (the latter is unknown in *Strenulagus*, *Lushilagus* and *Aktashmys*).

Etymology.—The genus is named to honor Dr. Mary R. Dawson, who has made a lifetime contribution to the study of lagomorphs.

Dawsonolagus antiquus, sp. nov.
(Figs. 1–7)

Holotype.—IVPP V7462, a partial skull with P^4 - M^2 on both sides (Figs. 1–2).

Hypodigm.—Holotype and IVPP V7463, left lower jaw with I_2 , M_{2-3} ; IVPP V7464, anterior part of right lower jaw with M_2 , partial M_1 and alveoli for P_{3-4} ; IVPP V7465.1, right calcaneum; IVPP V7465.2, two left calcanea; IVPP V7465.3, right astragalus; IVPP V7498, left zygomatic fragment with M^1 ; IVPP V7499.1, left M^1 ; IVPP V7499.2, left P^3 ; IVPP V7499.3, right P^4 ; IVPP V7499.4, left M_2 ; IVPP V7499.5, two right M_3 ; IVPP V7499.6, right I^2 ; IVPP V7499.7, left I^2 . All of the specimens were collected from the same pit that yielded numerous rodents as well as specimens of larger mammals. Their correspondence in size and morphology indicate that all of the referred specimens belong to the same lagomorph species.

Horizon and locality.—Lower part of the Arshanto Formation at the Nuhetingboerhe locality, Erlian Basin, Nei Mongol; late early Eocene (see discussion for age estimation of the beds).

Diagnosis.—Same as for the genus.

Etymology.—The trivial name, *antiquus*, implies the primitive nature of the new species.

DESCRIPTION

Skull.—The holotype is a partial skull that preserves most of the skull roof, the left zygomatic arch, and the palate with P^4 - M^2 on both sides (Figs. 1–2). The skull is low and broad, which is not attributable to its slight dorsoventral compression. The incisive foramen is situated anterior to P^2 , as indicated by the position of its posterior edge preserved on the left palatal process of the maxilla. There is no premolar foramen (Bohlin 1942) lingual to P^4 . The maxillary-palatine suture is shaped like a gentle arc ending anteriorly at a level between P^3 and P^4 . The posterior margin of the palate is lingual to the middle of M^2 and has a biconcave outline, with a distinct postpalatine spine pointing posteriorly. Both the palate and posterior nares are relatively broader than those of *Palaeolagus* (AMNH 106111). A pair of palatine foramina emerges on each side of the palatine, with the medial one being slightly anterior. A faint groove leads anteriorly from each foramen.

A shallow concave area lateral to P^{3-4} may be identified as the antorbital fossa. The ventral projection of the anterior

zygomatic root is a distinct ridge lateral to P^4 that extends posterolaterally to merge with the zygomatic arch. The posterior edge of the anterior zygomatic root is lateral to the middle of M^1 . The infraorbital foramen measures 1.25 mm in diameter and is low in the facial region anterior to P^3 . As indicated by the maxillary-jugal suture on the lateral and ventral sides of the anterior root of the zygomatic arch, the jugal extends to the facial region. It forms the ventral rim of the orbit and most of the zygomatic arch. The zygomatic process of the maxilla is small, abutting the jugal medially. In lateral view, the jugal is deep and forms a vertical plate with roughly uniform height. On the lateral surface of the zygomatic process of the jugal is a shallow fossa for insertion of the superficial masseter (Meinert 1943; Weijs and Dantuma 1981). Unlike extant taxa, there is no fenestration, or “foramen zygomaticofaciale” of Krause (1884), within the fossa. The posterior portion of the jugal is overlapped dorsally by the zygomatic process of the squamosal and extends posteriorly at least to the level of the glenoid fossa, but does not contribute to the lateral wall of the fossa. The breakage of the jugal at the glenoid fossa suggests a posterior projection of the bone in life. The glenoid fossa is gently concave, conspicuously broad and long, and antero-posteriorly oriented. Its position is relatively low in relation to the tooth row. There is no postglenoid process.

In dorsal view the orbital floor, preserved on the left side, is flat and the ends of tooth roots are almost not exposed yet. The orbit is large, and opens dorsolaterally. The supraorbital crest and postorbital process (supraorbital process) of the frontal are evidently present, although the latter was broken at its base (see lateral view of the skull as well). The nasal is not preserved, but a short segment of the nasal-frontal suture on the left side of the skull roof indicates that the nasal extended posteriorly to the level of M^3 . Because of cracks on the skull roof as well as fusion of bones, there are no identifiable sutures between the frontal, parietal, and squamosal, respectively. The interorbital constriction (Dice 1933) is the narrowest region of the skull, posterior to the base of the postorbital process. Posterior to this region, the roof of the braincase is gently rounded. On each side of the skull a weak ridge extends posteriorly from the base of the postorbital process and gradually fades away toward the lambdoidal crest. This ridge marks the medial border for the origin of the temporalis muscle; its position on the skull roof indicates that the temporalis was large.

On the dorsal roof of the glenoid fossa there is a wide groove (temporal fossa of Craigie 1948, fig. 86) bounded laterally by a vertical ridge of bone for the ventral part of the temporal muscle. On the medial side of the groove, no pronounced ridge (temporal line) appears as in *Lepus*, so the lateral surface of squamosal is smooth.

Mandible.—IVPP V7463 (Fig. 3B–C, E–F) was broken into four pieces, with some parts missing but still connected by matrix when it was found. We reconstructed it based on the shape of *Shamolagus medius* (IVPP V3010). The dentary is slightly slender, judging from the depth of the bone at M_3 . The condyle and angular process were broken, but a

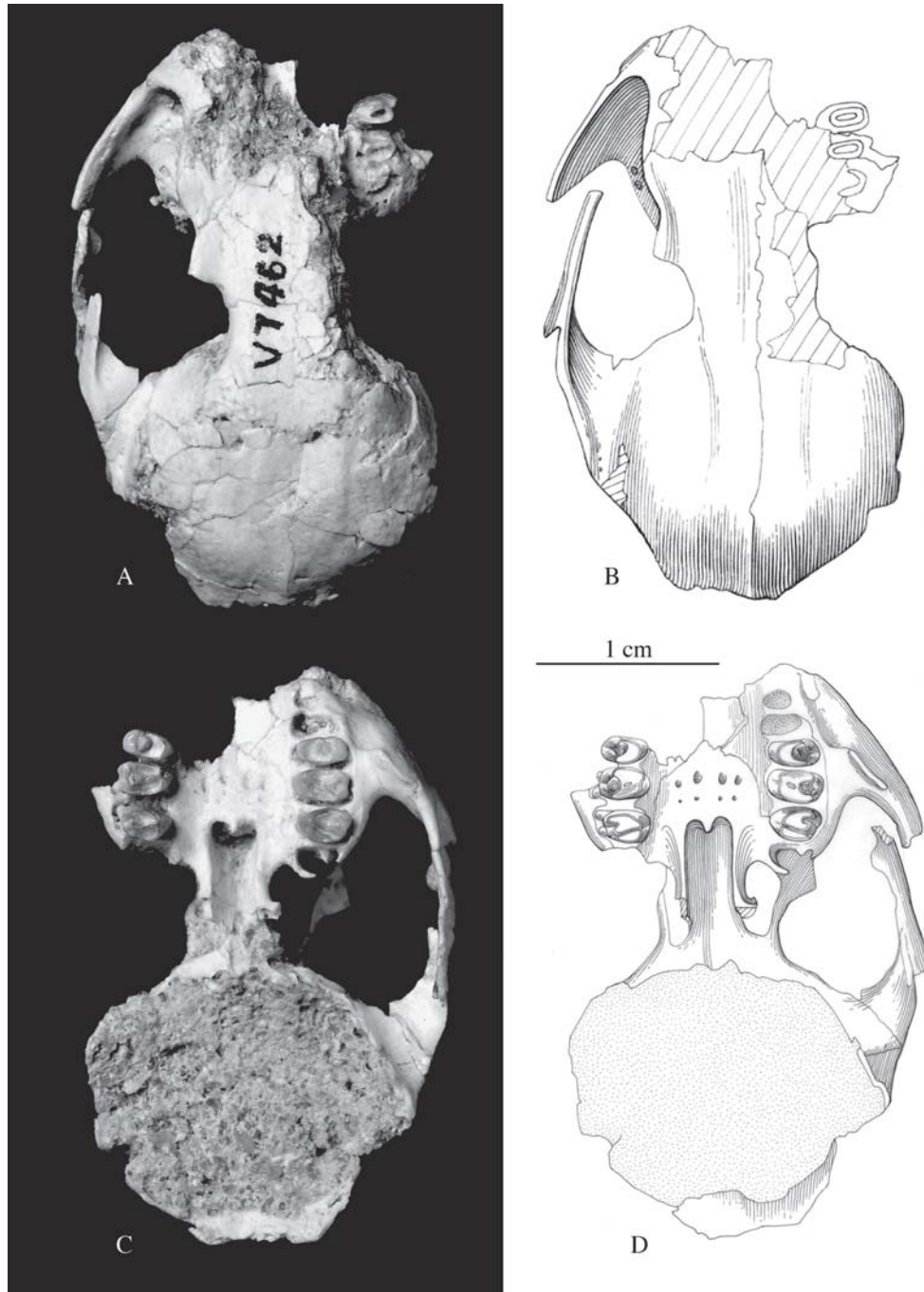


Fig. 1.—*Dawsonolagus antiquus*, partial skull, IVPP V7462 (holotype). A–B, dorsal view; C–D, Ventral view.

large coronoid process is preserved, forming the anterior edge of the ascending ramus. The base of the process is quite posterior to M_3 and there is no coronoid canal (posterointernal canalis mandibularis, Martinez 1985) at this region. The anterior edge of the process is smooth and gently curved. Although the angular process was broken, the preserved portion indicates a deepened region for the attachment of masseter and pterygoid muscles. The ptery-

goid fossa is crushed but it is probably quite deep. On the buccal side, the masseteric fossa is shallow; it extends anteriorly probably behind the level of M_3 . The anterior part of the mandible (IVPP V7464; Fig. 3A, D) is deeper than that of *Shamolagus medius* (IVPP V3010). Although the two species are similar in body size, the diastema of *Dawsonolagus* (4.5 mm) is much shorter than that of *S. medius* (7.0 mm); the same is true for other early lagomorphs. How-

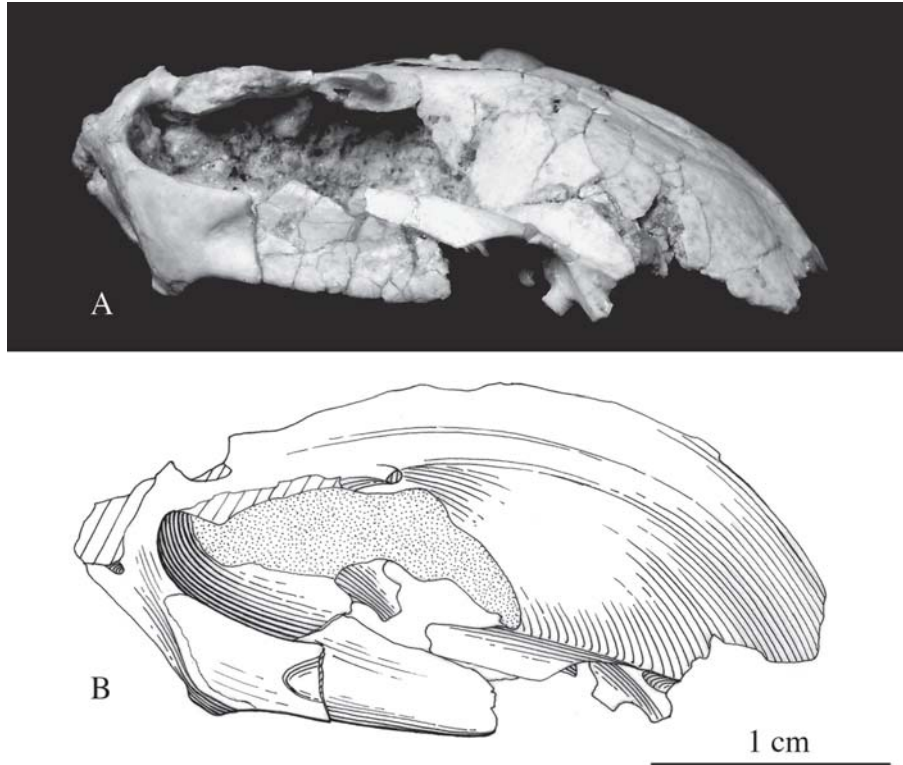


Fig. 2.—*Dawsonolagus antiquus*, partial skull, IVPP V7462 (holotype), left lateral view.

ever, the short diastema of *Dawsonolagus* is similar to those of *Mimotona* and *Gomphos*. A sulcus is situated beneath the posterior half of the diastema, which represents the only preserved mental foramen. Both mandibles indicate that the second lower incisor is absent, as is also the case in mimotonids.

Upper dentition.—IVPP V7499.6 is the anterior part of right I^2 (Fig. 5F, L). A longitudinal sulcus on the anterior surface divides the tooth into two columns of equal width. The medial column extends more anteriorly than the lateral one, so that an acute, asymmetrical V-shaped cutting edge is formed between the anterior tips of the two columns. A contact facet occurs on the medial side of the crown's apex. The enamel layer covers very little of the medial side of the tooth. In lingual view, the wear facet of the occlusal surface is gently concave and the pulp cavity is V-shaped. The upper cheek tooth rows (Figs. 1C–D, 4A) are quite straight, running parallel to the longitudinal axis of the skull. The cheek teeth are separated from each other by narrow gaps and are roughly rectangular but not transversely widened. The M^1 is equal to, or slightly smaller than, the M^2 . The degree of unilateral hypsodonty shown by the upper cheek teeth is not significant (Fig. 5A–C, G–I). There is no cement on any of the upper or lower cheek teeth.

The alveolus for P^2 is preserved on the left side of IVPP V7462; it indicates a small, single-rooted tooth, less than half the width of P^3 . The left P^3 (IVPP V7499.2; see Fig. 4B) is moderately worn and has a strong buccal root. Both

lingual and labial surfaces are smoothly rounded. In occlusal view, the tooth is trilobate. The lingual lobe occupies about two-fifths of the crown surface and is separated from the central lobe by a crescentic valley, the paraflexia (Averianov and Lopatin 2005), which extends to the posterior margin of the tooth. The anteroloph (part of the anteroloph of Wood 1940, fig. 115A C-3 and C-5) is short and joins the anterior base of the central lobe to close the paraflexia anteriorly. The central lobe is higher than the lingual lobe and is comma-shaped, with its tail extending posterolabially to join the posterolabial corner of the labial lobe. The labial lobe is somewhat rounded and situated on the posterolabial corner of the tooth. The short mesoflexia opens anteriorly. An anterolabial cuspsule is absent. The posterior corner of the labial lobe bears a wear facet that inclines posterolingually and is confluent with that of the central lobe.

P^4 (Figs. 1C–D, 4A) is preserved on both sides of the holotype (IVPP V7462) and as an isolated tooth (IVPP V7499.3). It is generally similar to P^3 , but differs in having the labial lobe divided into two cusps and a stronger anteroloph. The tooth possesses a strong buccal and a robust lingual root and lacks the hypostria on the lingual surface of the crown. The lingual lobe of P^4 in IVPP V7462 was considerably worn, revealing thick enamel along its lingual and posterior sides but slightly thinner enamel along the anterior margin of the crown. The central lobe is proportionally smaller than that of P^3 and is isolated from the lingual and

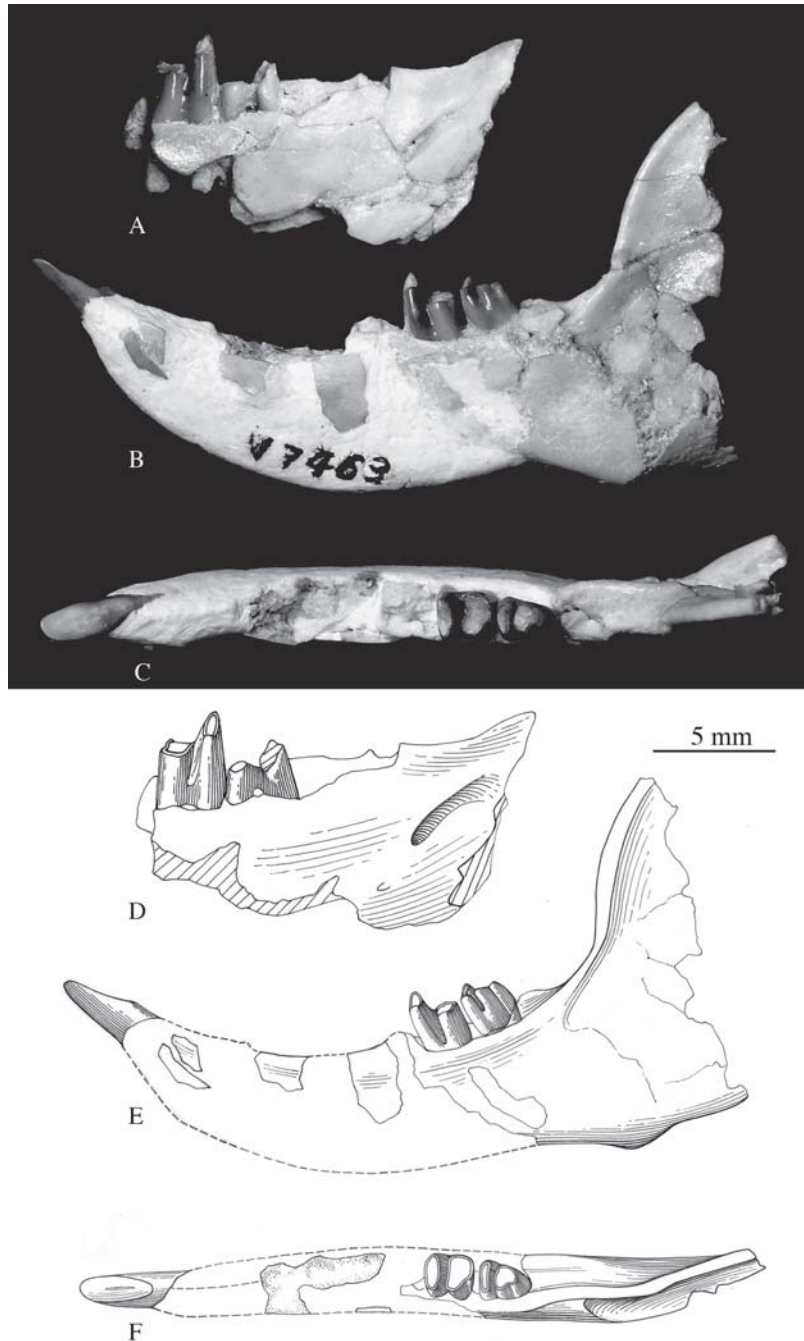


Fig. 3.—*Dawsonolagus antiquus*, fragmentary lower jaws. **A, D**, IVPP V7464, anterior part of right lower jaw with M_2 , partial M_1 , and alveoli for P_{3-4} , lateral view; **B–C, E–F**, IVPP V7463, left lower jaw with I_2 , M_{2-3} ; **B, E**, lateral view; **C, F**, occlusal view.

labial lobes by the paraflexia and mesoflexia. Still, the central lobe bears an inclined wear facet as in P^3 . The labial lobe consists of two equal-sized cusps, the anterolabial cuspsule (Averianov and Lopatin 2005) and a posterolabial cuspsule that may be equivalent to the metastyle of Wood (1940, fig. 115 A-A). The division is not deep and the two cusps are essentially confluent at their base. IVPP V7499.3 is an isolated P^4 , which is probably an unerupted tooth because it

lacks fully-developed roots and any wear facets. It differs from P^4 in IVPP V7462 in having a slightly smaller anterolabial cuspsule and an incomplete anteroloph. Because of its unworn condition, the tooth crown on the lingual side is higher than that of IVPP V7462.

M^1 (Figs. 1C–D, 4A) is larger, especially longer, than P^4 . It has a robust lingual root and two sizable buccal roots. On the lingual surface a weak hypostria extends to one-third of

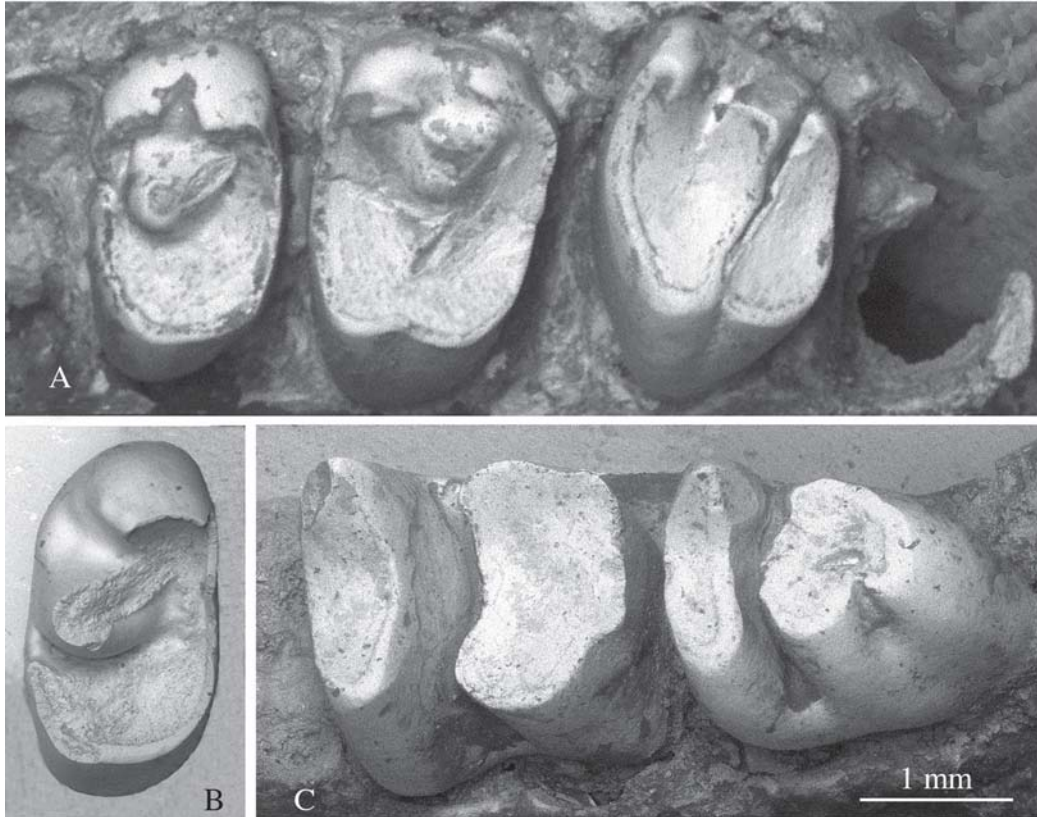


Fig. 4.—*Dawsonolagus antiquus*, SEM microphotographs showing morphology of cheek teeth. A, Occlusal view of left P⁴-M² crowns and alveoli for P³ and M³, IVPP V7462 (holotype); B, Occlusal view of left P³, IVPP V7499.2; C, Occlusal view of left M₂₋₃, IVPP V7463.

the height of the tooth crown, separating the protocone and hypocone shelf (postcingulum of Averianov and Lopatin 2005). The hypocone shelf is larger than the protocone and extends buccally to the posterolabial corner of the tooth. A small enamel island exists near the center of the tooth, which may represent the remnant, the hypofossette, of the hypostria. The centrocone (central lobe) is positioned on the labial half of the tooth. It has a crescentic wear facet inclining lingually. The central valley [crescentic valley of Wood (1940); probably the paraflexia for premolars of Averianov and Lopatin (2005)] surrounds the centrocone on its lingual side, which extends to the posterolabial corner of the tooth and is bounded posteriorly by the labial portion of the hypocone shelf. The lingual portion of M¹ is similar to that of M² in having a well-developed hypocone shelf, whereas the labial region of the tooth is similar to that of P⁴, except that the two labial cusps are anteroposteriorly longer and with the addition of the labial end of the hypocone shelf.

The M² (Figs. 1C–D, 4A) is longer than M¹ owing to an even more expanded hypocone shelf. However, its posterior half is narrower than M¹. Similar to M¹, M² also has two buccal roots. Unlike M¹, which displays some similarities with P⁴, M² is significantly different from P⁴, and thus it also differs from M¹ in several respects. The hypostria is slightly deeper, which may be because the tooth is less worn. In occlusal view, the tooth consists of two parts: the

anterior trigon and the posterior hypocone shelf. Each part is completely surrounded by enamel loops and is separated from the other by a continuous groove that crosses the crown transversely. The thick enamel layer is uniform except for the area between the labial cusps, where it becomes thinner. The trigon is essentially a robust V-shaped structure, with an anteroposteriorly compressed protocone. Within the trigon a centrocone is absent, which is not attributable to wear because M² should have erupted after M¹. Presently, we are unable to interpret the homology of these cusps. The centrocone on M² may have migrated labially to merge with or replace the posterolabial cusp, or it could have been completely lost. The two labial cusps form the arms of the V, with the anterior one more labially extended but shorter than its posterior counterpart. In general, M² is similar to that of *Mimotona* but with an enlarged hypocone shelf (Li 1977); it is also similar to that of *Matutinia* (Ting et al. 2002) but with a less developed hypocone shelf.

M³ is not preserved (Figs. 1C–D, 4A). Its alveolus and the trend toward reduction of M² in IVPP V7462 suggest that it could have been as wide as the posterior half of M². The alveolus also shows that M³ has a large lingual root and two buccal roots.

Lower dentition.—The lower incisor, preserved in IVPP V7463 (Fig. 3B–C, E–F), is slender and extends posteriorly

behind M_2 . The enamel covers more of the lateral side than the medial side of the tooth. The cutting edge of the tip is rounded and the tooth pulp is a longitudinally narrow slit in the concave, oval wear facet.

P_{3-4} are double-rooted, as indicated by alveoli preserved in IVPP V7464. The alveoli suggest that P_3 is triangular in having the trigonid smaller than the talonid and that P_4 consists of two lobes of equal size with a squared contour.

The crown of M_1 was broken in IVPP V7464, but the two roots remain in the jaw. The crown of M_2 (Figs. 3, 4C, 5D, J) is relatively low for a lagomorph and exhibits a weak degree of unilateral hypsodonty. The labial side is slightly higher than its lingual counterpart, showing a ratio of 2.0/1.6 mm in IVPP V7499.4. The tooth possesses two separate roots, of which the anterior root is compressed anteroposteriorly and its pulp shows a tendency toward division. The trigonid is higher, slightly wider, and much shorter than the talonid. Each is surrounded by complete enamel loops. In occlusal view, the trigonid is transversely oval, with the labial side tapered and the lingual portion being higher but shorter than its labial counterpart. The hypostrid crosses the tooth and, unlike in *Aktashmys*, there is no central enamel bridge between the trigonid and talonid. After wear, as shown on M_2 of IVPP V7464, both lobes connect on the lingual side. The talonid is a structureless concave wear surface, except that the enamel indentation at the posterior edge of the tooth indicates the presence of a hypoconulid.

M_3 (Figs. 3B–C, E–F, 4C, 5E, K) is smaller than M_2 ; its two roots are either completely fused or fuse near their junction with the crown. The M_3 trigonid differs from that of M_2 in being only slightly higher than the talonid. There is no enamel bridge between the trigonid and talonid. The talonid is considerably narrower than the trigonid and tapers posteriorly, but the hypoconulid is more distinctive than that of M_2 , forming the third lobe of the tooth. Measurements are given in Table 1.

Calcaneum.—The right calcaneum (IVPP V7465.1; Fig. 6) is more nearly complete than two left calcanea at hand (IVPP V7465.2). The calcaneum is similar to that of *Palaeolagus* in general morphology; therefore, it is typical of a lagomorph. The bone measures 10.1 mm in maximum length and 4.0 mm in maximum width. The tuber calcanei is not elongated and takes the shape of a cylinder, being slightly compressed transversely. The ratio of lever arm and load arm (Szalay 1985, fig. 19, x and b) is 1.04 (5.3/4.8 mm). The calcaneal protuberance has a longer medial calcaneo-astragalar facet (CaA) and a lateral convex calcaneofibular facet (CaFi). The CaA consists of a continuous and medially inclined facet that extends far posteriorly to the tuber calcanei on the dorsal surface. The CaFi is only half the length of the CaA and bears a convex surface. The facets are separated by a faint ridge. The distolateral corner of the calcaneum, where the peroneal process is usually present, is broken. A sharp crest on the distomedial edge of the bone shows that the calcaneum has no contact with the navicular. The sustentacular facet (Su) is nearly circular and gently concave and faces distoventrally. Its upper margin (susten-tacular hinge) is roughly level with that of the CaFi. Be-

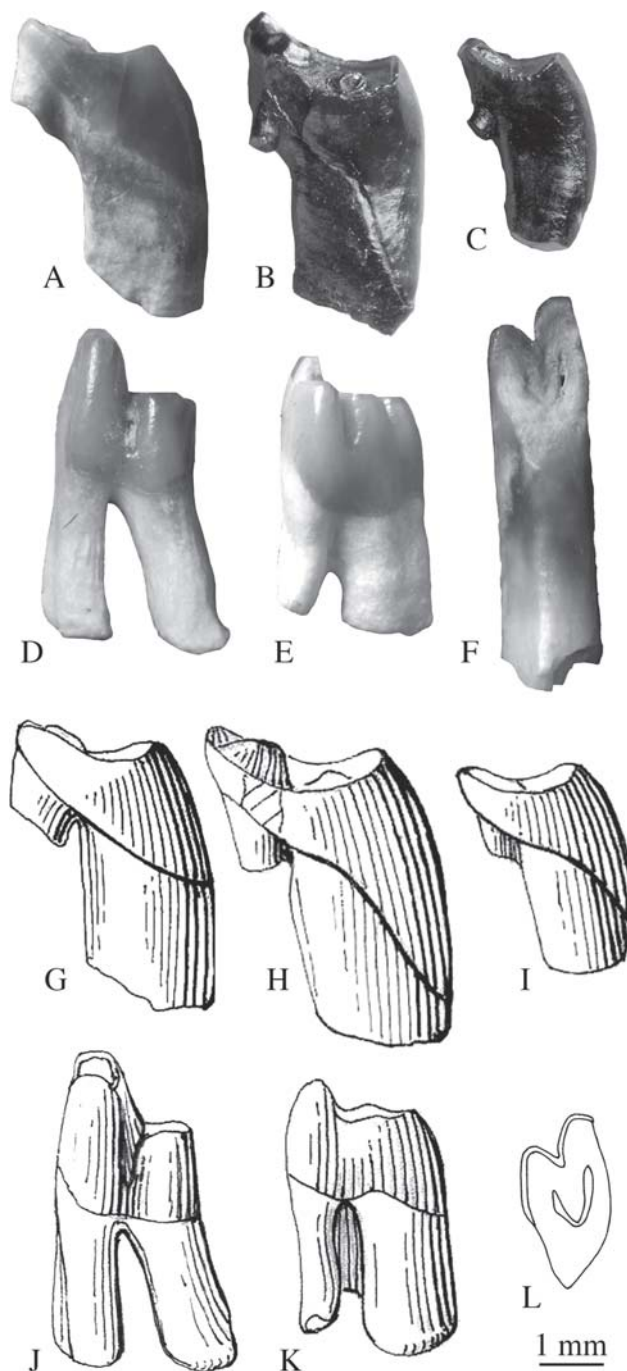


Fig. 5.—Isolated teeth of some Eocene lagomorphs from China, showing details of upper molar unilateral hypsodonty, lower molar root configuration, and upper incisor crown morphology. **A, G,** *Dawsonolagus antiquus*, left M^1 (reversed for comparative purposes), IVPP V7499.1, posterior view [Note relatively minor development of unilateral hypsodonty.]; **B, H,** *Strenulagus shipigouensis* Tong and Lei, 1987, right M^1 , IVPP V10225.34, posterior view; **C, I,** *Lushilagus danjiangensis* Tong and Lei, 1987, right M^1 , IVPP V10230.6, posterior view; **D, J,** *Dawsonolagus antiquus*, buccal view of left M_2 , IVPP V7499.4; **E, K,** *Dawsonolagus antiquus*, buccal view of left M_3 , IVPP V7499.5; **F, L,** *Dawsonolagus antiquus*, section of right I^2 , IVPP V7499.6.

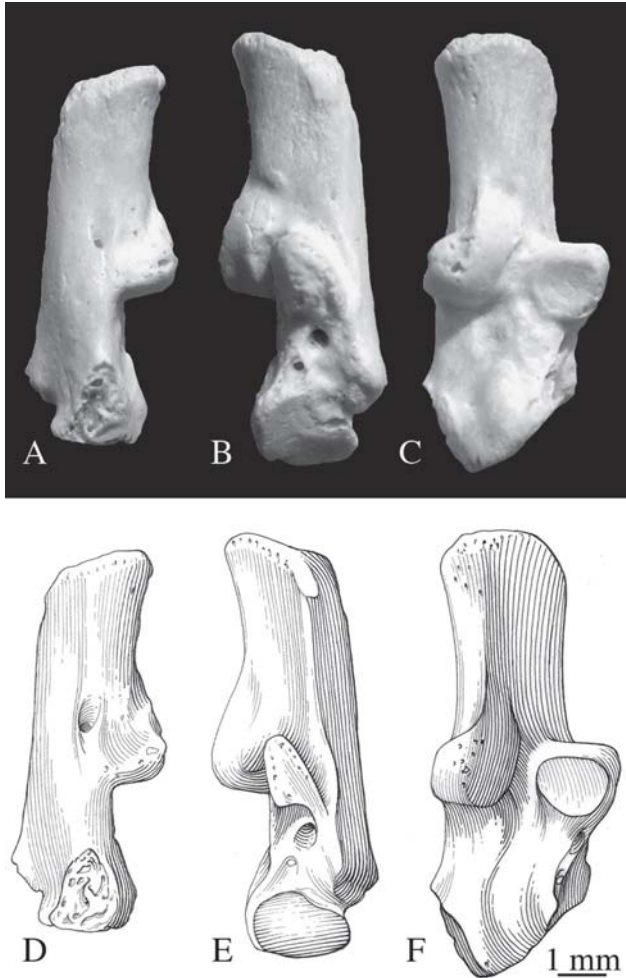


Fig. 6.—*Dawsonolagus antiquus*, right calcaneum, IVPP V7465.1. A, D, lateral view; B, E, medial view; C, F, dorsal view.

tween the Su and CaA there is a broad sulcus calcanei, which extends to the plantar surface of the Su as a groove (gtff) for the tendon of *M. flexor fibularis*. The groove ends distally at the large anterior plantar tubercle (at); the latter medially deviates from the longitudinal axis of the bone. The foramen (Fig. 6B, E) between the Su and the anterior plantar tubercle is the exit of the calcaneal canal (Ecc) (Bleefeld and Bock 2002). The entrance of the Ecc is on the lateral side of the bone (Fig. 6A, D). A smaller opening distodorsal to the exit of the Ecc may be considered as a second exit of the Ecc or as a remnant after the bone was broken. A similar opening has been observed in other lagomorphs. As described by Bleefeld and Bock (2002, p. 182), "On the lateral side of the calcaneal tuber lies a narrow furrow which enters a circular foramen. This foramen serves as an entry way into a tunnel that traverses the calcaneal body, diagonally." On the distal end of the calcaneum is a slightly concave, elliptical, and anteromedially inclined cuboid facet.

Astragalus.—A right astragalus (IVPP V7465.3; Fig. 7) is 3.3 mm wide (measured at the posterior margin of the troch-

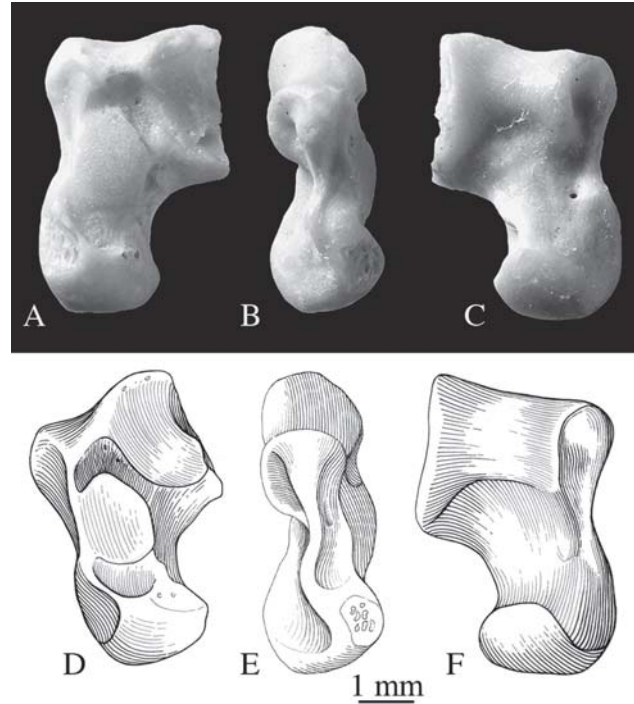


Fig. 7.—*Dawsonolagus antiquus*, right astragalus, IVPP V7465.3. A, D, ventral view; B, E, medial view; C, F, dorsal view.

lea) and 5.2 mm long. In general, the bone shows the basic lagomorph astragal pattern, but is more flat. The trochlea has a square-shaped outline and bears a shallow but broad trochlear groove. The medial trochlear rim is more convex, incomplete, and is about half the length of its lateral counterpart. On the medial side of the bone, a sinuous crest extends from the posteromedial corner of the bone to the posterior margin of the astragal head. In dorsal view, this crest enlarges the area adjacent to the inner side of the medial trochlear rim. The lateral trochlear rim is more gently curved and runs parallel to its medial counterpart. The trochlea terminates anteriorly at a shallow crescentic fossa that joins the distal anterior lip of the tibia. The neck of the astragalus is shorter than that of *Palaeolagus*. The head is broad and slightly offset medially. The navicular facet is transversely broad and is triangular in shape in dorsal view. In plantar view, a small distal astragalotibial facet (ATid) is posterior to the sulcus astragali. The concave calcaneo-astragal facet (CaA) occupies almost the lateral half of the trochlea, with its long axis being diagonal to the long axis of the bone. The CaA is separated from the sustentacular facet by a well-defined sulcus astragali that surrounds the sustentacular facet posterolaterally. The sustentacular facet is convex and its long axis parallels that of the bone. A small facet at the anterolateral side of the head suggests a distal calcaneo-astragal contact. The astragalonavicular facet (AN) extends more posteriorly than in *Palaeolagus* and is separated completely from the sustentaculum by a wide groove (not named by Szalay). Although IVPP V7465.3 is similar to that of lagomorphs in general morphology and

matches the calcaneum described above in size, it possesses several characters that are not typical for lagomorphs, such as its flat body, squared trochlea, incomplete medial trochlear crest, sinuous appendix crest, more medially positioned head, and widely separated Su and AN. Thus, our attribution of this astragalus to *Dawsonolagus* requires further substantiation.

COMPARISONS

Dawsonolagus shares some similarities with mimotonids, including *Mimotona* and *Gomphos*, and others with some Asian Eocene lagomorphs, including *Lushilagus*, *Strenulagus*, and *Aktashmys*. The following comparisons will focus on these taxa. However, because cranial and postcranial specimens of the relevant Asian Eocene lagomorphs are rare, in certain instances we will extend our comparisons to more derived forms (such as *Palaeolagus*) for which better material is available.

Cranium

The incisive foramen of *Dawsonolagus* ends posteriorly anterior to P², which is similar to the condition in *Mimotona* (Li and Ting 1993, fig. 11.4) but more anterior than that of *Gomphos* (Asher et al. 2005) and other earlier Eocene lagomorphs for which this region is known.

On the palate, the premolar foramen is absent in *Dawsonolagus* but present in *Aktashmys montealbus* (Averianov and Lopatin 2005, fig. 2c) and some other lagomorphs such as *Desmatolagus* (Bohlin 1942; Huang 1987; Qi 1988; Zhang et al. 2001) and *Prolagus* (Dawson 1969). This foramen is also absent in several other Asian Eocene lagomorphs, such as *Gobiolagus* (Meng and Hu 2004; Meng et al. 2005). The foramen had been considered to be diagnostic of ochotonids (Bohlin 1942; McKenna 1982), but it is now known to occur in some extant leporids (Martinez 1985). Huang (1987) considered that the premolar foramen shifted posteriorly in geologically younger species, and also observed that the premolar foramen is not a stable feature because its presence varies within a species, such as *D. pusillus* (Huang 1987).

The posterior nares of *Dawsonolagus* lie opposite the middle of M², which is more anterior than that of *Mimotona* (IVPP V7500) and *Gomphos* (Asher et al. 2005), but less so than other lagomorphs, such as *Palaeolagus*, where the structure is known. It is a general observation that the posterior nares shifted anteriorly during the evolution of lagomorphs, thereby making the palate bridge narrower between the nares and incisive foramina.

The orbital floor of *Dawsonolagus* is smooth, similar to that of *Gomphos* and *Mimotona*, probably because of the lower-crowned cheek teeth in these forms, in which the ends of the roots are often exposed but do not project into the orbit. For those taxa having higher-crowned cheek teeth, tooth roots intrude into the orbital floor dorsally rendering it uneven as in *Shamolagus*, *Lushilagus*, and *Strenulagus* or to form a large tuberosity as in *Palaeolagus*

(AMNH 106111) and later leporids. The orbital floor is unknown in *Aktashmys*.

The posterior edge of the anterior zygomatic root is shifted anteriorly in Glires (Meng and Wyss 2001; Meng et al. 2003). In *Dawsonolagus*, it is level with the posterior part of M¹ and is more anterior than that of *Mimotona* (between M² and M³), being similar to those of *Gomphos*, *Aktashmys* (only ZIN 79181 at anterior part of M²), *Lushilagus*, and *Strenulagus*, but more posterior than those of *Desmatolagus*, *Gobiolagus*, and *Mytonolagus*. The construction of the zygomatic arch of *Dawsonolagus* is more similar to that of leporids than to ochotonids in that the jugal forms the main part of the arch and extends anteriorly to the facial region (see Novacek 1985).

The supraorbital crest, the postorbital process of the frontal and the interorbital constriction make the skull of *Dawsonolagus* more similar to that of leporids, such as *Palaeolagus* (Wood 1940; Dawson 1958), than to ochotonids, such as *Prolagus* (Dawson 1969). In ochotonids, both structures are absent, and the orbit is enclosed posteriorly by the anteriorly shifted glenoid process. In *Gomphos*, the postorbital process is present, but more anteriorly located, suggesting a relatively smaller eye compared to that of *Dawsonolagus*. These structures are unknown in other Asian Eocene lagomorphs.

The glenoid fossa of *Dawsonolagus* is primitively similar to those of *Gomphos* (Asher et al. 2005) and other non-lagomorph Glires, such as *Matutinia* (Ting et al. 2002) and *Rhombomylus* (Meng et al. 2003) and early rodents such as *Cocomys* (Li et al. 1989). As discussed by Meng and Wyss (2001), a longitudinally oriented glenoid fossa is present in early Glires, facilitating anteroposterior jaw movement during gnawing and chewing. In advanced forms, such as *Palaeolagus* (Wood 1940; Dawson 1958), the glenoid fossa is shortened and located anterodorsally, much higher than the tooth row, and its articular facet is saddle-shaped.

A large temporal region for attachment of the temporalis muscle can be determined by the position of the temporal lines, which mark the medial extremity of the area for muscle attachment. A large attachment area for the temporalis muscle is similar to the condition found in *Gomphos* (Asher et al. 2005) but differs from those of lagomorphs, such as *Palaeolagus* and later forms, in which the temporal lines are short and more laterally positioned to delimit a reduced attachment area that is partly incorporated into the orbit (Meinertz 1943; Weijs and Dantuma 1981; Martinez 1985). It can be inferred that the temporalis muscle is but a small bundle in *Palaeolagus* and later forms. For all other Asian Eocene lagomorphs, however, this region is unknown.

Mandible

Dawsonolagus is unique in having the coronoid process well posterior to M₃. In other Glires, the anterior base of the coronoid process is usually immediately posterior to M₃ or slightly anterolateral to M₃, as in *Shamolagus* (Li 1965, fig. 4), *Mytonolagus* (Dawson 1970, fig. 13) and *Palaeolagus* (AMNH 106111). Absence of the coronoid canal (postero-in-

TABLE 1. Measurements (in mm) of the dentition of *Dawsonolagus antiquus*, based on IVPP V7462 (left side), IVPP V7463, and IVPP V7499.2. Measurements: **L**, length; **CW**, width of upper tooth crown; **BW**, width of upper tooth base; **CWTR**, width of trigonid crown; **BWTR**, width of trigonid base; **CWTA**, width of talonid crown; **BWTA**, width of talonid base.

tooth locus	L	CW	BW	CWTR	BWTR	CWTA	BWTA
P ³	1.30	2.44	2.55				
P ⁴	1.44	2.18	2.72				
M ¹	1.68	2.20	2.92				
M ²	1.74	2.18	2.94				
M ₂	2.05			1.64	2.10	1.65	2.02
M ₃	1.64			1.24	1.88	1.08	1.64

ternal canalis mandibularis; Martinez 1985) posterior to M₃ in *Dawsonolagus* is similar to that of *Gomphos* (Asher et al. 2005) and *Mimotona*, but different from some lagomorphs in which the canal pierces the anterior base of the coronoid process and is confluent with the mandibular foramen. Although this foramen was considered to be autapomorphic for lagomorphs (Martinez 1985; Meng et al. 2003), it is absent in those Asian Eocene forms for which the relevant anatomy is preserved, such as *Shamolagus* (seen in *S. grangeri*, but unclear in *S. medius*) and *Desmatolagus*.

A reduced coronoid process was considered to be a derived feature of lagomorphs (Martinez 1985; Li and Ting 1985), in which there is only a rudimentary bony projection anteroventral to the elevated mandibular condyle. In *Dawsonolagus*, the coronoid process is large, similar to that of *Gomphos* (Asher et al. 2005), which is consistent with a large attachment area for the temporalis muscle on the skull. This structure is unknown in other Asian lagomorphs. In *Palaeolagus* the process is “nearly as high as the condylar process” and “the anterior face of the ascending ramus is grooved in all forms for the insertion of the *temporalis*” (Wood 1940, p. 28). In *P. haydeni* (AMNH 10611) the coronoid process forms a thin sheet adhering to the anterolateral margin of a protruding crest that leads vertically up to the condyle. In *Dawsonolagus*, however, the anterior surface of the coronoid process is not grooved and the process is far above the protruding crest. The crest around the pterygoid fossa runs more horizontally to the condyle. Although the condylar process is not preserved in the specimens at hand, it is probably lower than those of other lagomorphs, judging from both the more horizontal protruding crest and the low position of the glenoid fossa on the skull.

A short diastema is another significant feature of *Dawsonolagus* (Fig. 2C), which is similar to conditions in *Mimotona* (Li and Ting 1993) and *Gomphos* (Asher et al. 2005), but shorter than in *Strenulagus* (Lopatin and Averianov 2006) and *Shamolagus* (Li 1965).

Dentition

The grooved upper incisor of *Dawsonolagus* is similar to those of lagomorphs and *Mimotona* (Li 1977), and the division of the tooth into two nearly symmetrical columns by the groove is comparable to the condition observed in some

leporids, such as *Palaeolagus*. In this regard, *Dawsonolagus* differs from *Aktashmys*, in which the groove on the anterior side of I² “shifted to the distal edge; therefore, the mesial blade is almost twice as large as the distal blade” (Averianov and Lopatin 2005, p. 311). Also differing from *Aktashmys*, the I² pulp of *Dawsonolagus* is V-shaped, rather than being a transverse circle (Fig. 5F, L; Averianov and Lopatin 2005, fig. 3a). In *Mimotona*, the mesial blade is larger than the distal one, but with an inclined longitudinal pulp.

The lower incisor of *Mimotona* (IVPP V7416.1) and *Gomphos* (Meng et al. 2004) extends posterior to M₃. The I₂ of *Dawsonolagus* extends at least behind M₂, which is more posteriorly than in other lagomorphs. For instance, the lower incisor ends beneath M₂ of *Shamolagus grangeri*, *Gobiolagus tolmachovi*, *G. andrewsi*, *Strenulagus solaris* and *Mytonolagus* and beneath the posterior half of M₁ in *S. medius* and *Desmatolagus vetustus*. The lower incisor condition is unknown in *Aktashmys*.

The external margin of the upper dentition of *Dawsonolagus* is quite straight, as in *Mimotona* and *Gomphos*. In other lagomorphs, such as *Strenulagus*, *Lushilagus*, *Desmatolagus*, *Gobiolagus* (except for *G. major*, IVPP V14134; Meng and Hu 2004), and *Mytonolagus*, the external outline of the upper dentition is arched. A complete upper dentition is not preserved in *Aktashmys*, but the available material shows that it is probably arched (Averianov and Lopatin 2005, fig. 2).

The upper cheek teeth of *Dawsonolagus* are spaced apart by gaps, which does not appear to be artificial. In addition, the cheek teeth are not transversely widened. These features make the cheek teeth appear small on the palate. In known mimotonids and other lagomorphs, adjacent upper cheek teeth usually contact each other. The unilateral hypsodonty of upper cheek teeth is common in Glires and varies among different taxa. *Dawsonolagus* is similar to *Mimotona* in having relatively lower-crowned upper cheek teeth, which are higher than in *Gomphos* but lower than in other lagomorphs (Fig. 5A–C, G–I). In *Mimotona* and *Gomphos*, M^{1–2} are more or less square-shaped. These teeth in *Dawsonolagus* are transversely rectangular but not lingually extended. Although *Aktashmys* and *Strenulagus* are similar to *Dawsonolagus* in the shape of the tooth contour, the degree of hyp-

sodonty is quite different among these taxa. In IVPP V7498, a moderately worn right M^1 , the lingual crown height is about twice the buccal height, whereas in other forms, such as *Aktashmys*, the lingual enamel extends deeply and the ratio can reach up to three times or more.

The P^3 of *Dawsonolagus* differs from those of *Aktashmys* (Averianov and Lopatin 2005) and *Strenulagus* (Tong 1997), but is similar to those of *Mimotona* and *Gomphos*, in that the anteroloph closes the paraflexia anteriorly. The paraflexia is open anteriorly in *Aktashmys* and *Strenulagus*. The P^3 central lobe is similar to that of *Lushilagus* but differs from those of *Strenulagus* and *Aktashmys*; in the latter forms, the central lobe is anteroposteriorly oriented. Proportionally, the labial lobe is much larger, and more anteriorly extended, than those of *Aktashmys* and *Strenulagus*. *Aktashmys* and *Strenulagus* differ from *Dawsonolagus* in having the mesoflexia wide open anterolaterally. *Strenulagus shipigouensis* further differs from *Dawsonolagus* in having an anterolabial cuspule on P^3 . In general, the structure of P^3 (and P^4 as well) of *Dawsonolagus* is more similar to that of *Lushilagus* than to those of *Strenulagus*, *Aktashmys* and *Shamolagus*.

It is universally true that the M^1 in lagomorphs, including *Aktashmys*, *Lushilagus*, and *Strenulagus*, is significantly larger than M^2 . But in *Dawsonolagus*, as in *Gomphos* (Asher et al. 2005) and *Mimotona* (Li 1977), M^1 and M^2 are subequal. In addition, the upper molars of *Dawsonolagus* have two sizable labial roots, differing from those of *Aktashmys*, in which “the labial roots of M^1 and M^2 vary in number and structure either a single root or two labial roots fused . . .” (Averianov and Lopatin 2005, p. 312).

Although M^3 is not preserved in *Dawsonolagus*, its alveolus clearly indicates a sizable M^3 that has two labial roots. A similar condition is present in *Mimotona* and *Gomphos*. In other forms, such as *Strenulagus*, *Aktashmys*, *Lushilagus*, *Gobiolagus*, and *Mytonolagus* (some also estimated by preserved alveoli), the size of M^3 is relatively more reduced than in *Dawsonolagus*. Coupled with the reduction in size, the M^3 usually has one labial root, which is often reduced, as in *Aktashmys*. The M^3 of *Shamolagus* and *Desmatolagus* is more reduced, smaller, and simpler than in other forms.

The M_3 of *Mimotona* and *Gomphos* is either larger than or subequal to M_2 , and usually has a projecting hypoconulid that forms a third lobe at the end of the tooth. The M_3 of *Dawsonolagus* and *Aktashmys* is slightly smaller than that of M_2 , and it bears a clear third lobe. In contrast, the M_3 is more reduced to various degrees among *Strenulagus*, *Lushilagus*, *Gobiolagus*, *Shamolagus*, and *Mytonolagus* and distinctively diminished in *Desmatolagus vetustus* (Burke 1941, fig. 8; Meng et al. 2005).

Postcranium

The calcaneum of *Dawsonolagus* is typical of lagomorphs in having the calcaneofibular facet and calcaneal canal. For non-lagomorph Glires for which the calcaneum is known, including *Gomphos* (Meng et al. 2004; Asher et al. 2005),

these features are absent, except for the calcaneofibular facet in *Rhombomylus* (Meng et al. 2003). According to Bleefeld and Bock (2002), the calcaneal canal is a feature that appeared early in the history of lagomorphs, and it occurs in all recognized Recent and fossil lagomorph calcanea, which supports the monophyly of the order. The canal is greatly reduced or lost in extant leporids, which is regarded as a derived lagomorph feature (Bleefeld and Bock 2002). Given the phylogenetic relationships of gliriform mammals (Meng et al. 2003; Asher et al. 2005), these features are deemed derived within Glires.

The general shape of the calcaneum of *Dawsonolagus* is similar to that of *Palaeolagus*. The ratio of lever arm and load arm, for instance, is almost identical to that of *Palaeolagus* (Szalay 1985, fig. 19). This suggests that the function of the pes in the two forms may have been similar. Tarsal elements from the Eocene Andarak 2 locality have been assigned to Lagomorpha and were considered very similar to those of modern lagomorphs and *Palaeolagus* (Averianov 1991). However, the illustration provided by Averianov (1991, fig. 6; PIN 3486/159) shows that, although the calcaneum assigned to Lagomorpha bears a calcaneofibular facet, it is quite different from those of *Palaeolagus* and extant lagomorphs in being significantly elongated (Dawson 1969; Szalay 1985; Bleefeld and Bock 2002). The calcaneofibular facet is also present on the calcaneum of *Rhombomylus* and is therefore not unique to lagomorphs among Glires. In addition, the calcaneum described by Averianov (1991) lacks the calcaneal canal, making its taxonomic assignment problematic. In fact, all of the tarsal elements from the Andarak 2 locality, including those assigned to Mixodontia, are similarly elongated and differ not only from those of lagomorphs but also from those of *Rhombomylus* (Meng et al. 2003) and *Gomphos* (Meng et al. 2004; Asher et al. 2005). It may be expected that these elongated calcanea would give rise to a greater ratio of lever arm to load arm and represent species with a specialized pes and mode of locomotion.

DISCUSSION

Taxonomy

Traditionally, the Lagomorpha have been classified into two families: Ochotonidae Thomas, 1897 and Leporidae Fischer de Waldheim, 1817 (McKenna and Bell 1997). Additional families have been proposed, such as Palaeolagidae Dice, 1929, Mytonolagidae Burke, 1941, Desmatolagidae Burke, 1941, and Prolagidae Gureev, 1962, although these family rank taxa are not stable and have often been recognized as subfamilies, such as Mytonolaginae, Palaeolaginae, and Archaeolaginae by various authors (Dice 1929; Dawson 1958; Averianov 1999). Recently, Averianov and Lopatin (2005) proposed a new family, Strenulagidae, which includes five Eocene Asian lagomorph genera, including *Lushilagus*, *Aktashmys*, *Strenulagus*, *Shamolagus*, and *Gobiolagus*. As Averianov and Lopatin (2005, p. 310) remarked: “The new family comprises the most primitive

Asian lagomorphs and is ancestral to the Palaeolagidae, Desmatolagidae, Prolagidae, Ochotonidae, and Leporidae.” Because our knowledge of these genera is restricted to fragmentary jaws, the dentition, or even isolated cheek teeth, whether these genera possess similarly primitive, or more derived, features in the temporal region of the skull, shape of the glenoid fossa, and development of the coronoid process, are unknown. The preceding dental comparisons, including incisor condition, tooth row shape, and cheek tooth morphology (premolar morphology, crown height, occlusal contour, tooth size variations, root condition) shows a mosaic distribution within these early lagomorphs. In the dentition alone, *Dawsonolagus* displays some similarities with some of the genera in question. For instance, the separated trigon and hypocone shelf on M² appears similar to those of *Aktashmys* and *Strenulagus*. On the other hand, *Dawsonolagus* shares some features of the dentition, cranium and mandible, which are probably primitive, with *Mimotona* and *Gomphos* (see above). More importantly, there seems to be no single derived character shared by *Dawsonolagus* and those genera included in the Strenulagidae. In fact, the diagnosis for the Strenulagidae consists of essentially all primitive features (Averianov and Lopatin 2005), which indicates that Strenulagidae likely represents a grade rather than a clade of early lagomorphs. Without a phylogenetic analysis of the Asian Eocene taxa and their relatives as a basis for their classification, we are not convinced of the validity of the Strenulagidae. Therefore, we choose to place *Dawsonolagus* as family indet. within Lagomorpha.

Mastication

Lagomorphs have reduced temporalis muscles, an anterodorsally positioned glenoid fossa that is anteroposteriorly short, a high mandibular process, a greatly reduced coronoid process, an expanded angular process, and transversely elongated and ridged cheek teeth. The lagomorph jaw apparatus has been considered to be intermediate between those of ungulates and rodents (Weijs and Dantuma 1981). In plotting ratios of the moment arm of the ventral-most fibers for the superficial masseter to the resistance arms of the molar and incisor, lagomorphs differ from rodents, *Rhombomylus*, and other mammals in having the greatest ratios, which result from deepening of the angular process and elevation of the mandibular condyle (Meng et al. 2003). In addition, the moment arm of the anterior deep masseter in lagomorphs is comparable to those of many rodents. Again, the relatively long moment arm for the anterior deep masseter in lagomorphs results from the dorsal elevation of the mandibular condyle, not from anterior shifting of the masseteric fossa as in rodents. Instead, as indicated by the position of the anterior edge of the masseteric fossa, the anterior deep masseter in lagomorphs is not shifted significantly anteriorly. These features indicate that, compared to rodents, anterior movement of the lower jaw in lagomorphs is not so significant and that incisive biting in lagomorphs is less efficient than in rodents.

The masticatory apparatus of *Dawsonolagus* can be characterized by the following features. The temporal region and coronoid process are large, suggesting a temporalis muscle that was larger than those of later lagomorphs. The glenoid fossa is broad and anteroposteriorly oriented, which allows anteroposterior and transverse movements of the lower jaw during mastication. The glenoid is also low in position, indicating a low mandibular condyle. The incisors are similar to those of more derived lagomorphs, but the cheek teeth combine a mixture of features that are otherwise characteristic of either mimotonids or lagomorphs. With these features, it can be inferred that the masticatory pattern of *Dawsonolagus* is probably different from that of younger lagomorphs. It is also different from that of early rodents because of its transversely oriented tooth ridges and more posteriorly positioned masseter muscles. When the skull, mandible and tooth morphology are considered altogether, the masticatory pattern of *Dawsonolagus* probably resembles those of mimotonids and eurymylids.

Age implication

The specimens of *Dawsonolagus* come from the Nuhetingboerhe locality, Erlian Basin, Nei Mongol. This locality is somewhat nearby the site labeled as “7 miles west of Camp Margetts” by the Central Asiatic Expedition. Most of the beds in these areas were considered as “Irdin Manha beds” (Granger 1930; see also Qi 1980, 1987, 1990; Meng 1990; Meng et al. 1998). As noted by Radinsky (1964, p. 5), “The available evidence thus suggests that the relationship between the beds called ‘Irdin Manha’ in the Camp Margetts area and the type Irdin Manha beds is complex and not yet fully understood. The solution to this problem requires careful stratigraphic investigations in the critical areas and the collection of additional faunal samples with accurate stratigraphic data. At least until such is done, the terms ‘Irdin Manha’ and ‘Houldjin’ should be placed in quotation marks when strata in the Camp Margetts area are referred to indicate that correlation is still uncertain.”

Recently, new stratigraphic data show the potential existence of early Eocene Bumbanian equivalent beds, the *Gomphos* beds, in the nearby area (Meng et al. 2004; Bowen et al. 2005). Our fieldwork in 2004–2005 in these areas also demonstrated that at Nuhetingboerhe the beds contain a late Paleocene fauna, similar to the Bayan Ulan fauna (Meng et al. 1998), the potential early Eocene fauna containing *Gomphos elkema*, and the fauna yielding *Dawsonolagus* in a demonstrable superpositional sequence. Based on new stratigraphic data, we think the beds containing *Dawsonolagus* occur in the lower part of the Arshanto Formation, which is separated from the underlying beds by a hiatus.

The Arshanto Formation is traditionally regarded as the early middle Eocene, and its fauna has been the basis for the regional land mammal age known as the Arshantan. However, our field observations demonstrate that stratigraphic problems, as recognized by Radinsky (1964), are real, and that the Irdin Manha and Arshanto faunas are formed by

fossils collected from distantly separated localities and, even worse, from beds of different ages. To clarify these problems requires systematic field investigations as well as a review of fossils previously collected from these areas. A paper dealing with the stratigraphy of this region is being undertaken. At present, the stratigraphic data and the nature of the faunas from these beds present persuasive evidence that enables us to consider the Arshanto Formation as being late early Eocene in age.

The earliest known Asian lagomorph represented by a reasonable sample is *Aktashmys montealbus* (Averianov 1994), which came from the Andarak 2 locality in Kyrgyzstan, from beds dated as terminal early Eocene (Averianov and Lopatin 2005). Other forms, such as *Lushilagus* and *Strenulagus*, are from beds of Irдинmanhan or younger age. As our preceding comparisons indicate, *Dawsonolagus* is morphologically more primitive than *Aktashmys* in having less unilateral hypsodonty, unfused labial roots of upper molars, and more mimotonid-like premolars, suggesting that the beds yielding *Dawsonolagus* are no younger than those yielding *Aktashmys*. This lends support to our preliminary assessment that the Arshanto Formation could be late early Eocene.

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