Dorcabune anthracotherioides (Artiodactyla: Ruminantia: Tragulidae) From Hasnot, The Middle Siwaliks, Pakistan

UMAR FAROOQ, MUHAMMAD AKBAR KHAN*, MUHAMMAD AKHTAR AND ABDUL MAJID KHAN

Department of Zoology, University of the Punjab, Quaid-e-Azam Campus, Lahore, Pakistan

Abstract. – *Dorcabune anthracotherioides* is known from the Siwaliks of Pakistan. The fossils were collected from Hasnot (Dhok Pathan Formation) during 1995-2003, but some specimens already present in the palaeontology laboratory of the Zoology Department, Punjab University, Pakistan, are also included in this paper. Most of the collected material is fragmentary in nature and indescribable. Seven specimens are selected for description in this paper including upper and lower dentitions. The identification of the species *D. anthracotherioides* from Hasnot represents an extension of the known age range of *Dorcabune*.

Key Words: Dorcabune anthracotherioides, Hasnot, Dhok Pathan Formation, Siwaliks.

INTRODUCTION

Tragulines are primitive extinct and extant ruminants that flourished during the later Paleogene and gave rise to the pecorans at the beginning of the Oligocene (Vislobokova, 2001). Pecorans. ruminants bearing cranial appendages, are one of the most numerous and widespread groups among recent mammals. Hence, the study of tragulines helps us to understand one of the most significant and intriguing chapters in the evolution of mammals. According to the fossil record, the history of tragulines covers more than 50 million years from the Middle Eocene to the present, but it seems that their history is much longer (Vislobokova, 2001). Even at the early stages of evolution, there was a rather wide spectrum of forms adapted to various plant foods. They inhabited all the continents of the Northern Hemisphere. Most of them remained largely herbivorous, also feeding on some small (mollusks, insects, etc.), as living animals chevrotains do (Vislobokova, 2001). By the latter Middle Miocene it is apparent that the Siwaliks was inhabited by various traguloids, boselaphines, caprines and the smaller Gazella (Barry et al., 1985, 1991, 1995, 2002; Vislobokova, 1997, 1998, 2001).

0030-9923/2007/0006-0353 \$ 8.00/0 Copyright 2007 Zoological Society of Pakistan.

The rank determination and composition of the taxon Tragulina, proposed by Flower (1883) based on the family Tragulidae, as well as the rank determination and composition of some other supraspecific traguline taxa, is still controversial. The Tragulina has been regarded as a suborder of the order Artiodactyla (Osborn, 1910; Colbert, 1941), an infraorder of the suborder Ruminantia (Matthew, 1929; Simpson, 1945; Viret, 1961; Webb and Taylor, 1980; Scott and Janis, 1992; Sudre, 1995), or a parvorder of the infraorder Ruminantia (Geraads et al., 1987). Some researchers regarded all tragulines as one group, Traguloidea (Romer, 1966). Matthew (1934) united all extinct and extant specimens into a single family, Tragulidae, which he placed in the Pecora. Vislobokova (2001) classification is followed in this paper. This research is based on the fossil material from Hasnot that is housed in the Zoology Department, Punjab University, Lahore, Pakistan. As will be shown, the newly described fossil material extends the range of Dorcabune anthracotherioides from14.0-8.4 Ma (Barry et al., 2002) to 14.0 -5.0 Ma.

Abbreviations:PUPC,PunjabUniversityPalaeontological Collection, housed in the Department ofZoology, PunjabUniversity, Lahore, Pakistan; AMNH,American Museum of Natural History, New York, UnitedStates of America; GSI, Geological Survey of India; Ma,

Corresponding author. E-mail: akbaar111@yahoo.ca

Million years ago; M_{1}^{1} , first upper and lower Molar; M_{2}^{2} , second upper and lower molar; M_{3}^{3} , third upper and lower molar; P, premolar.

SYSTEMATIC PALAEONTOLOGY

Order:	Artiodactyla Owen, 1848
Suborder:	Ruminantia Scopoli, 1777
Family:	Tragulidae Milne-Edwards, 1864
Genus:	DORCABUNE Pilgrim, 1910

Type species

Dorcabune anthracotherioides Pilgrim, 1910.

Generic diagnosis

Very large tragulids having bunodont teeth. Isolated parastyle and mesostyle, prominent cingulum and enamel rugosity are the diagnostic characteristics of the upper molars, whereas lower molars are characterized by their broadness, a wide talonid in the third molar, and a pyramidal protoconid with two posteriorly directed folds (Pilgrim, 1910, 1915; Colbert, 1935). The upper molars of Dorcabune anthracotherioides are characterized by their brachydonty and bunodonty. The inner cusps of upper molars are truly selenodont, whereas the outer ones are quite bundont and absolutely conical in their general appearance. The median rib on the labial face of the paracone and metacone is so broad and prominent that it occupies almost all the space between the styles. This feature is very much pronounced in the paracone, the labial surface of which is in fact entirely rib. The parastyle and mesostyle are strong, massive and isolated, whereas the metastyle is very weakly developed. With wear, the mesostyle clearly displays its closer association with the metacone instead of fusing equally to both paracone and metacone. The protocone, instead of being a simple crescent, is more pyramidal in shape and displays three equally strong folds, one proceeding forwards and outwards, the second backwards and a third backwards with a tendency sometimes inwards and sometimes outwards. A strong cingulum runs antero-posteriorly, but is very much pronounced round the protocone. It often rises into a small tubercle at the entrance of the transverse valley between the protocone and hypocone. The enamel is heavy and has moderately fine rugosity (Pilgrim, 1915; Colbert, 1935). The lower molars are also

characterized by well pronounced brachydonty and bunodonty. The anterior arm of protoconid terminates on a broad shelf almost parallel to the anterior margin of the tooth. Entoconid is conical, producing out anteriorly a short process in the direction of the mid line between the two anterior cusps. The hypoconid is crescentic; its anterior arm touches to the external process of the protoconid, while its posterior arm runs inward and completely encircles the posterior base of the entoconid.

Included species

Dorcabune anthracotherioides Pilgrim, 1910; Dorcabune hyaemoschoides Pilgrim, 1915; Dorcabune nagrii Pilgrim, 1915; Dorcabune latidens Pilgrim, 1915; Dorcabune sindiense Pilgrim, 1915; Dorcabune liukengense Han. 1974.

Distribution

The genus *Dorcabune* is known from the Lower Siwaliks of the Chinji Formation, the Middle Siwaliks of the Nagri, and Dhok Pathan Formations and Lower Manchar of Bhagothoro, Pakistan (Pilgrim, 1910, 1915; Colbert, 1935). This genus is also known from China (Han, 1974).

Dorcabune anthracotherioides Pilgrim, 1910

Type specimen

GSI B580, a maxilla with molars present (Colbert, 1935).

Referred specimens

An isolated upper right first molar (PUPC 96/67); A fragment of left maxilla with M^{2-3} (PUPC 87/37); An isolated last upper molar of the left side (PUPC 87/39); An isolated lower left second molar (PUPC 96/65); An isolated second lower molar of the left side (PUPC 96/66); An isolated right lower second molar (PUPC 99/89); A left mandibular ramus with M_3 (PUPC 85/28).

Locality

Hasnot, Jhelum district, the Punjab province, Pakistan.

Stratigraphic range

Lower to Middle Siwaliks.

Stratigraphic level

Upper Part of the Dhok Pathan Formation, Hasnot; 7-5 Ma (Pilbeam *et al.*, 1977). *Diagnosis*

Dorcabune anthracotherioides is larger than Dorcabune hyaemoschoides and almost equal to that of Dorcatherium crassum (Pilgrim, 1915; Colbert, 1935). The lower margin of the ramus is deep in Dorcabune anthracotherioides. The mandible bears a fairly deep groove starting beneath the P₄ and propagating towards the posterior side behind the teeth. This groove exists also in Dorcatherium maius and minus and in Dorcabune latidens but is absent in Dorcabune nagrii (Pilgrim, 1915). The upper molars of Dorcabune anthracotherioides are very similar to that of Dorcabune hyaemoschoides and differ only by the possession of prominent parastyle. The lower fourth premolar (P_4) is slightly shorter in length than the lower third premolar (P_3) . P₄ is broad and consisting of three lobes, of which middle one is the highest and longest, whereas first and the last lobes are equal in length, though the third lobe is higher in unworn condition. Third lobe is massive and crescent-shaped facing towards the inner and the anterior sides. The posterior arm of the crescent is running out to a level with the internal margin of the tooth. A small notch separates this arm from a long wing which runs backward from the summit of the principal cusp and forms the inner wall of the tooth. This wing is separated by a deep elongated cavity from the crest, which connects the principal cusp to the hinder lobe (Pilgrim, 1915). Dorcabune anthracotherioides differentiates Dorcabune latidens by characterizing a less deep mandible bearing moderately broader molars and possessing much smaller size (Pilgrim, 1915).

Description

PUPC 96/67 is an isolated first right upper molar. It is well preserved and the cusps show that it is in the early stage of wear. The tooth is bunodont and broad crowned. The enamel is extensively wrinkled and indicates a uniform thickness all over the crown of the molar. The cingulum is moderately developed at the antero-posterior face of the tooth but better developed towards the inner side especially at the entrance of the transverse valley between the protocone and hypocone. The molar is

squarish with four cusps; protocone, paracone, metacone and hypocone. The protocone is crescentic in shape. The innermost lingual part of the protocone is pointed. Its posterior limb is free. A very small transverse enamel ridge connects the anterior limb of the protocone with the paracone. The paracone is relatively smaller in anteroposterior length than the metacone. It is pointed in the middle with two sloping sharp anterior and posterior ridges. The metacone is also pointed in the middle with two sharply sloping ridges. The styles are moderately developed. The parastyle is moderately developed and connected to the base of the anterior median rib. The median rib of paracone strongly developed. The mesostyle is strongly developed and is in the form of an isolated pillar. It seems to be more associated with metacone than paracone. It is thin towards its apex and very thick at the base. The metastyle is weakly developed. The parastyle and metastyle are almost equal in height. The median rib of metacone is very weak. The central cavities are wide and very deep. Both central cavities are continuous with one another. Of these cavities, the anterior one is closed at its anterior end and posterior one is closed at its posterior end. The posterior central cavity is also continuous with the transverse valley. The transverse valley is deep and narrow.

The specimen P.U.P.C. No. 87/37 (Fig. 1A, B) is a left maxilla bearing M^{2-3} . The whole part of the palate is broken away but some part of it is preserved in front of M³ and a large portion in front of M^2 . Both the teeth on this maxillary bone fragment are very well preserved. The second upper tooth is very well preserved molar. It is in the early stage of wear and dentine is more exposed in the anterior cones than the posterior ones. The dentine is light reddish-grey in colour due to the light reddish-grey sediments of Hasnot area in which the specimen was preserved. The cingulum is very well developed and borders the inner margin of the tooth. It also extends anteriorly as well as posteriorly to cover partially the base of the both lingual cones. Lingually at the entrance of the transverse valley the cingulum is very much pronounced. The enamel is heavy and rugose. The rugosity is more prominent on the inner cones than on the outer ones. The enamel is thick and the thickness is almost uniform



all over the crown. The average thickness is about 1.5 mm. All the principal cones are inclined towards

the median longitudinal line of the molar. The outer

Fig. 1. *Dorcabune anthracotherioides* A, B (PUPC 87/37), lingual view of the upper second and third molars; (A) and buccal view of the upper second and third molars (B); C (PUPC 99/89), occlusal view of the lower second molar; D (PUPC 85/28), buccal view of the lower third molar.

cones are relatively higher vertically than the inner cones. In protocone the thickness of anterior limb gradually decreases towards the parastyle. The length of anterior limb is greater than the posterior one. The posterior limb of the protocone is very thick and is free. It is much expanded in the middle and due to expansion the transverse valley between protocone and hypocone has become very narrow anteriorly. The anterior limb of the protocone is continuous with the parastyle of paracone. The innermost lingual part of the protocone is blunt and would be almost rounded in the late stage of wear. The parastyle is well developed. The paracone is well developed and its median rib is so strongly developed that it occupies almost all the space between the styles on the labial side. The paracone is comparatively higher than the protocone. It is almost spindle-shaped, with thickness in the middle. The mesostyle is an isolated pillar and strongly developed and seems to be closely associated with metacone. The metacone is relatively higher than the paracone in length. Anteriorly, it is connected with paracone while posteriorly linked with hypocone through a small, thin narrower and low ridge. Unlike the paracone it is moderately transversely thick in the middle as its median rib is much weaker than that of the paracone. The metastyle is weakly developed. It is more distinct anteriorly. The hypocone is strongly V-shaped in its general appearance. Both limbs of the hypocone are equally longer. The central cavities are well developed but here they have been filled with

sandstone during preservation. The posterior central cavity is wider than the anterior one. The transverse valley is deep and long. It is continuous with the

anterior central cavity only. The third upper tooth is

Number	Position	Length	Width	W/L ratio
PUPC 96/67	M^1	13.75	16.80	12.00
AMNH 19562	M^1	15.50	19.50	
GSI B.580	M^1	18.00	23.10	
PUPC 87/37	M^2	17.55	17.70	13.40
AMNH 19652	M^2	18.00	22.50	
GSI B.580	M^2	21.70	26.70	
PUPC 87/37	M^3	17.30	17.75	16.00
PUPC 87/39	M^3	20.80	17.20	20.60
AMNH 19652	M^3	19.50	22.50	
AMNH 29998	M^3	18.00	22.00	
GSI B.580	M^3	21.40	25.80	13.10
PUPC 96/65	M_2	20.30	13.30	11.00
PUPC 96/66	M_2	19.00	12.00	14.00
PUPC 99/89	M_2	19.60	11.55	12.90
AMNH 19355	M_2	17.50	13.00	
GSI B.682/683	M_2	19.50	14.70	
PUPC 85/28	M ₃	26.00	13.00	14.00
AMNH 19353	M ₃	28.00	14.00	
GSI B.682/683	M ₃	30.90	16.00	12.20

 Table I. Comparative measurements of the cheek teeth of Dorcabune anthracotherioides in millimeters.

very good in the state of preservation except the anterior limb of the metacone, which is slightly damaged. The tooth is just touched by wear. PUPC 96/65, PUPC 96/66 and PUPC 99/89 (Fig. 1C) are the second lower molars. The molars are nicely preserved. The teeth are sub-hypsodont and narrow crowned. The central cavities are long, narrow and curved. The enamel is strongly rugose over the lateral sides. PUPC 85/28 (Fig. 1D) is a fragment of left mandible bearing M_3 . It is a well preserved fragment of left mandibular ramus bearing M₃. The mandible is damaged anteriorly, posteriorly and slightly ventrally. It is moderately thick, deep enough. The maximum preserved vertical depth below M₃ is about 30 mm and thickness is about 13.5 mm. The third lower molar is in a good state of

preservation. The metaconid is slightly damaged anteriorly. It is in the middle stage of wear. It is hypsodont and narrow crowned. The enamel is heavy, thick and very rugose. It is very prominently wrinkled all around the tooth except the lingual side, where it becomes slight. The enamel is fairly thick with an average of 1.4 mm. The cingulum is very strong and well developed at the anterior and labial sides of protocone. It is in the form of an extraordinary high and stout tubercle at the entrance of transverse valley. A small singular tubercle is also present between the hypoconid and talonid on the labial side. The cingulum is absent on all other sides of the tooth. The comparative measurements of the molars are provided in Table I.

The material under study comprises isolated

upper and lower molars, a fragment of left maxilla with M^{2-3} , and left mandibular ramus with M_3 . All the specimens reveal almost all those characteristics, which are being exhibited by the species *Dorcabune* anthracotherioides Pilgrim, 1910 e.g., their inner cusps are truly selenodont whereas outer cusps show more affinity towards bunodonty. There seems to be a slight trend towards the brachydonty. As far as the upper molars are concerned their median ribs on the labial face of the outer cusps are so broad and prominent that they occupy almost all the space between the styles, this characteristic is more pronounced in paracone. Parastyle and mesostyle are isolated, strong and stout. Metastyle is mostly very weakly developed. Mesostyle reveals its close association with metacone. Protocone displays pyramidal shape. Strong cingulum runs antero posteriorly but it is very much pronounced around the protocone. Enamel is heavy and rugose. In lower molars each of the two anterior conids are bifurcated posteriorly. Anterior arm of the protoconid terminates in a broad shelf, almost parallel to the anterior margin of the tooth. Entoconid is conical with a short anterior process proceeding between the two anterior cusps. Hypoconid is crescentic in shape; its anterior arm mostly touches the posterior external process of the protoconid, whereas its posterior arm runs inwards and completely encircles the posterior base of the entoconid. Talonid is broader bearing a crenulated tubercle. The inner and outer arms of talonid are almost equal in height. The specimens under study also show closer resemblances in their measurements with the type specimens. First upper molar represented by PUPC 96/67, is compared with AMNH 19652 and GSI B580 which indicates that the difference in length and width is in the normal range. Second upper molar PUPC 87/37 is compared with AMNH 19652 and GSI B580, again variations in length and width are within the normal range of species. Two specimens of third upper molars i.e., PUPC 87/37 and 87/39 are compared with AMNH 19652 and 29998 and GSI B580. PUPC 87/37 shows closer measurements with the type specimens in almost all respects but PUPC 87/39 differs greatly due to the reason that its anterior face is completely scratched, whereas lingual face is scratched along the base only. Table I reveals the comparison of second molars of the lower dentition including PUPC 96/65, 96/66 and 99/89 with the type specimens AMNH 19355 (Colbert, 1935) and GSI B682/683 (Pilgrim, 1915). As far as the third lower molar PUPC 85/28 is concerned, it is compared with AMNH 19353 (Colbert, 1935) and GSI B682/683 (Pilgrim, 1915). All the above said facts lead to the conclusion that the specimens are attributable to *Dorcabune anthracotherioides* Pilgrim collected from Hasnot, the Middle Siwaliks.

DISCUSSION

The genus Dorcabune was founded by Pilgrim (1910) and he regarded Dorcabune anthracotherioides as its type-species, from the Lower Siwaliks of the Chinji Formation, Pakistan. The original description of this species was not based on one specimen as type specimen but on several specimens (Colbert, 1935). In addition to the species Dorcabune anthracotherioides, three more species of the genus Dorcabune from the Siwaliks of Pakistan were erected by Pilgrim (1915), which are: i) Dorcabune hyaemoschoides, ii) Dorcabune nagrii, and iii) Dorcabune latidens. Of these species two are known from the Lower Siwaliks and remaining two from the Middle Siwaliks. The species belonging to the Lower Siwaliks are Dorcabune anthracotherioides and Dorcabune hyaemoschoides, both known from the Chinji Formation. Of the Middle Siwalik species, Dorcabune nagrii is known from Nagri and Dorcabune latidens known from Hasnot, district Jhelum, the Punjab province, Pakistan (Pilgrim, 1910, 1915). In this present study Dorcabune anthracotherioides is also found from Hasnot being described for the first time from the upper part of the Dhok Pathan Formation. Based on the morphology of the lower molars of some selected genera, Moya-Sola (1988) retained only the Tragulidae (including Tragulus, Hyemoschus, Dorcatherium, and, possibly, Dorcabune and Yunnanotherium) in the Tragulina and excluded Archaeomeryx, leptomerycids, and hypertragulids from the Ruminantia. This point of view conflicts with the opinion of most other researchers. Following Gentry (1978), Dorcabune, known only from dental materials (Pilgrim, 1910), is excluded

from the family composition. According to Gentry (1978)Dorcabune is most probably an anthracotheriid, however a number of collected dental specimens from the Middle Siwaliks after Pilgrim (1910) evidently prove its inclusion in the Tragulina. According to Barry et al. (2002), the range of Dorcabune in the Siwaliks is limited to 14.0-8.4 Ma. The studied specimens of Dorcabune anthracotherioides were collected from the Hasnot near the Bhandar Bed which is located in the eastnorth of Hasnot and considered the youngest part of the Dhok Pathan Formation. The magnetostratigraphy and biostratigraphy (Pilbeam et al., 1977; Johnson et al., 1982; Barry et al., 1982) of the Hasnot indicates that the outcrops in the immediate vicinity of the Hasnot and particularly to the north near Bhandar are younger than the sediments that lie in some distance to the west and southeast. The age of the deposits towards the northeastern side is 5.0 Ma and of that south of the village Hasnot most likely range between 6.5 and 5.3 Ma old, based on their correlation of the Kaulial section (Barry et al., 2002) to the geomagnetic reversal time scale of Mankinen and Dalrymple (1979). Therefore, the age of the Hasnot localities ranges from 7 to 5 Ma and the findings of Dorcabune anthracotherioides in the area extend its range from 14.0-5 Ma.

REFERENCES

- BARRY, J. C., JOHNSON, N. M., RAZA, S. M., AND JACOBS, L. L., 1985. Neogene mammalian faunal change in Southern Asia: Correlations with climatic, tectonic, and eustatic events. *Geology*, **13**: 637-640.
- BARRY, J. C., LINDSAY, E. H. AND JACOBS, L. L., 1982. A biostratigraphic zonation of the middle and upper Siwaliks of the Potwar Plateau of northern Pakistan. *Palaeogeog. Palaeoclimat. Palaeoecol.*, **37**: 95-130.
- BARRY, J. C., MORGAN, M. E., FLYNN, L. J, PILBEAM, D., JACOBS, L. L., LINDSAY, E. H., RAZA, S. M. AND SOLOUNIAS, N., 1995. Patterns of faunal turnover and diversity in the Neogene Siwaliks of northern Pakistan. *Palaeogeog. Palaeoclimat. Palaeoecol.*, 115: 209-226.
- BARRY, J. C., MORGAN, M. E., WRINKLER, A. J., FLYNN, L. J, LINDSAY, E. H., JACOBS, L. L. AND PILBEAM, D., 1991. Faunal interchange and Miocene terrestrial vertebrates of southern Asia. *Paleobiology*, 17: 231-245.
- BARRY, J., MORGAN, M., FLYNN, L., PILBEAM, D., BEHRENSMEYER, A. K., RAZA, S., KHAN, I.,

BADGELY, C., HICKS, J. AND KELLEY, J., 2002. Faunal and Environmental change in the Late Miocene Siwaliks of Northern Pakistan. *Paleobiology*, **28**: 1-72.

- COLBERT, E. H., 1935. Siwalik mammals in the American Museum of Natural History. *Trans. Am. Phil. Soc.*, 26: 1-401.
- COLBERT, E. H., 1941. The osteology and relationships of *Archaeomeryx*, an ancestral ruminant. *Am. Mus. Novitat.*, **1135**:1–24.
- FLOWER, W. H., 1883. On the arrangement of the orders and families of existing mammalian. *Proc. zool. Soc. London*: 178–186.
- GENTRY, A.W., 1978. Tragulidae and Camelidae, in evolution of African mammals, Harward University Press Cambridge, pp. 536–539.
- GERAADS, D., BOUVRAIN, G. AND SUDRE, J., 1987. Relations phylétiques de *Bachitherium* Filhol, ruminant de l'Oligocene d'Europe occidentale, *Palaeovertebrata*, 17: 43–73.
- HAN, DE-FEN, 1974. First discovery of *Dorcabune* in China. *Verteb. Palasiat.*, **12**(3): 217-221.
- JOHNSON, G. D., ZEITLER, P., NAESER, C. W., JOHNSON, N. M., SUMMERS, D. M., FROST, C. D., OPDYKE, N.D. AND TAHIRKHELI, R. A. K., 1982. The occurrence and fission-track ages of Late Neogene and quaternary volcanic sediments, Siwalik group, northern Pakistan. *Palaeogeog. Palaeoclimat. Palaeoecol.*, 37: 63-93.
- MATTHEW, W. D., 1929. Critical observations upon Siwalik Mammals. Bull. Am. Mus. nat. Hist., 56: 435-560.
- MATTHEW, W. D., 1934. A phylogenetic chart of the Artiodactyla. J. Mammal., 15: 207–209.
- MOYA -SOLA, S., 1988. Morphology of lower molars of the ruminants (Artiodactyla Mammalia): Phylogenetic implication. *Paleontol. Evol.*, **22**: 61–70.
- OSBORN, H. F., 1910. The age of mammals in Europe, Asia and North America. Macmillan Co, New York, pp. 635.
- PILBEAM, D., BARRY, J., MEYER, G. E., SHAH, S. M. I., PICKFORD, M. H. L., BISHOP, W. W., THOMAS, H. AND JACOBS, L. L., 1977. Geology and palaeontology of Neogene strata of Pakistan. *Nature*, 270: 684-689.
- PILGRIM, G. E., 1910. Notice of new mammalian genera and species from territories of India. *Rec. geol. Surv. India*, 40: 63-71.
- PILGRIM, G. E., 1915. Dentition of tragulid genus Dorcabune. Rec. geol. Surv., India, 45: 226-238.
- ROMER, A.S., 1966. Vertebrate paleontology. University of Chicago, Chicago–Illinois:
- SCOTT, K. M. AND JANIS, C.M., 1992. Relationships of the Ruminantia (Artiodactyla) and an analysis of the characters used in ruminant taxonomy. In: *Mammal phylogeny, placentals* (eds. F. S. Szalay, M. J. Novacek and M.C. McKenna), pp. 282–302. Springer-Verlag,

New York.

- SIMPSON, G. G., 1945. The principles of classification and a classification of mammals. *Bull. Am. Mus. nat. Hist.*, 85: 1-350.
- SUDRE, J., 1995. Le Garouillas et les sites contemporains (Oligocene, MP25) des phosphorites du Quercy (Lot, Tarn-et-Garonne, France) et leurs faunes de vertebras, *Paleontographica A*, **236**: 205-256.
- VIRET, J., 1961. Artiodactyla. In: *Traite de Paléontologie*, vol. 1, pp. 887-1021, Masson et Cie, Paris.
- VISLOBOKOVA, I.A., 1997. Eocene–Early Miocene ruminants in Asia, Mém. Trav. E.P.H.E., Inst. Montpellier, 21: 215–223.
- VISLOBOKOVA, I.A., 1998. A new representative of the Hypertraguloidea (Tragulina, Ruminantia) from the Khoer-Dzan locality in Mongolia, with remarks on the relationship of the Hypertragulidae. *Am. Mus. Novitat.*, **3225**: 1–24.
- VISLOBOKOVA, I. A., 2001. Evolution and Classification of Tragulina (Ruminantia, Artiodactyla). *Paleontol. J. Suppl.*, 35: 69–145.
- WEBB, S. D. AND TAYLOR, B. E., 1980. The phylogeny of hornless ruminants and a description of the Cranium of Archaeomeryx, Bull. Am. Mus. nat. Hist., 167: 117–158.

(Received 3 March 2007, revised 21 July 2007)