

New artiodactyl ruminant mammal from the late Oligocene of Pakistan

GRÉGOIRE MÉTAIS, PIERRE-OLIVIER ANTOINE, LAURENT MARIVAUX,
JEAN-LOUP WELCOMME, and STÉPHANE DUCROCQ



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Dental and postcranial material of the bovid-like ruminant *Palaeohypsodontus zinensis* sp. nov. is reported from the Oligocene of the Bugti Hills (Balochistan, Pakistan). This finding extends the geographic distribution of this dentally highly derived ruminant, which was previously restricted to the early Oligocene of Mongolia and China. The inclusion of *Palaeohypsodontus* within the Bovidae is disputed on the basis of astragalus characters, and the taxonomic status of the Oligo-Miocene Eurasian bovid-like ruminants is briefly discussed. It is concluded that the assignment of *Palaeohypsodontus* to the Bovidae would be premature. More dental and postcranial material of this genus as well as additional fossils of early bovids are necessary to shed new light on the phylogenetic relationships within the first representatives of that family in Eurasia.

Key words: Mammalia, Ruminantia, Bovidae, Oligocene, Pakistan, Bugti Hills.

Grégoire Métais [metais@isem.univ-montp2.fr], Pierre-Olivier Antoine [poa@isem.univ-montp2.fr], Laurent Marivaux [marivaux@isem.univ-montp2.fr], Jean-Loup Welcomme [welcomme@isem.univ-montp2.fr], Stéphane Ducrocq [ducrocq@isem.univ-montp2.fr], Institut des Sciences de l'Evolution, Université de Montpellier II, Place Eugène Bataillon, F-34095 Montpellier, France.

Introduction

The Tertiary continental formations of the Bugti Hills (Balochistan) in the Sulaiman geological Province of the Lower Indus Basin (Fig. 1), have yielded one of the richest fossil mammal faunas from South Asia. Fossil remains have been known in the area since the nineteenth century (Vickary 1846; Blanford 1883), and large mammals have been the object of several monographies (Lydekker 1883, 1884; Pilgrim 1910, 1912; Forster-Cooper 1924, 1934). Blanford (1883) first recognized the Oligocene age of the lowermost levels of the Bugti Hills, and Pilgrim (1908), based on invertebrate fauna common with that of the Oligocene marine Nari Formation, considered these basal littoral layers as possibly late Paleogene. However, due to the apparent mixture of heterochronic vertebrate fossils, including some typical Oligocene taxa associated with characteristic early Miocene taxa in collections, several authors (following Pilgrim himself who, from 1912, believed the Bugti fauna as Miocene in age) assumed an early Miocene age for the whole Bugti fauna. These authors advocated an endemic evolution and/or reworking phenomenon to explain the persistence of typical Oligocene taxa such as the ruminants *Prodremotherium* and *Gelocus*. The revision of previously collected specimens (Welcomme and Ginsburg 1997), combined with seven seasons of fieldwork by the “Mission Paléontologique Française au Balouchistan”, have led to propose new interpretations of the biostratigraphy of the Bugti Hills (Welcomme et al. 2001). New collectings—from

thirty localities and twelve successive and distinct bone beds—have challenged the classical hypothesis concerning the early Miocene age previously attributed for all the Bugti fossil mammals. The lowermost levels of the Bugti continental sequence (Lower Chitarwata Formation, Hemphill and Kidwai 1973) are thus definitively Oligocene in age as detailed in Welcomme et al. (2001).

The base of the Oligocene deposits of the Chitarwata Formation laying unconformably on the Eocene marine Kirthar Formation (Fig. 2) has yielded a rich and diversified fauna including selachians, reptiles and mammals. Rodents, creodonts and artiodactyls are strongly similar to those of Oligocene Eurasian faunas (Marivaux et al. 1999, 2002; this paper). The overlying Oligocene levels are represented by fluvial sands intercalated with three main fossiliferous ferruginous crusts. The fossils described here come from the uppermost Oligocene crust (J2, Welcomme et al. 2001), which has also yielded numerous remains of the giant rhinocerotoid *Paraceratherium bugtiense*, the anthracothere *Anthracotherium bugtiense* and an entelodont (*Paraentelodon* sp.). The overlying fossiliferous levels having yielded a typical Miocene fauna (e.g., *Prodeinotherium*, *Dorcatherium*, *Eotragus*), we consider the crust (J2) where the specimens described here were found as late Oligocene (Fig. 2).

Among the numerous fossil mammals collected in the vicinity of Dera Bugti, Pilgrim (1912) described two new ruminant species ultimately based on very scarce material and doubtfully assigned to *Gelocus gajensis* and *Prodremo-*

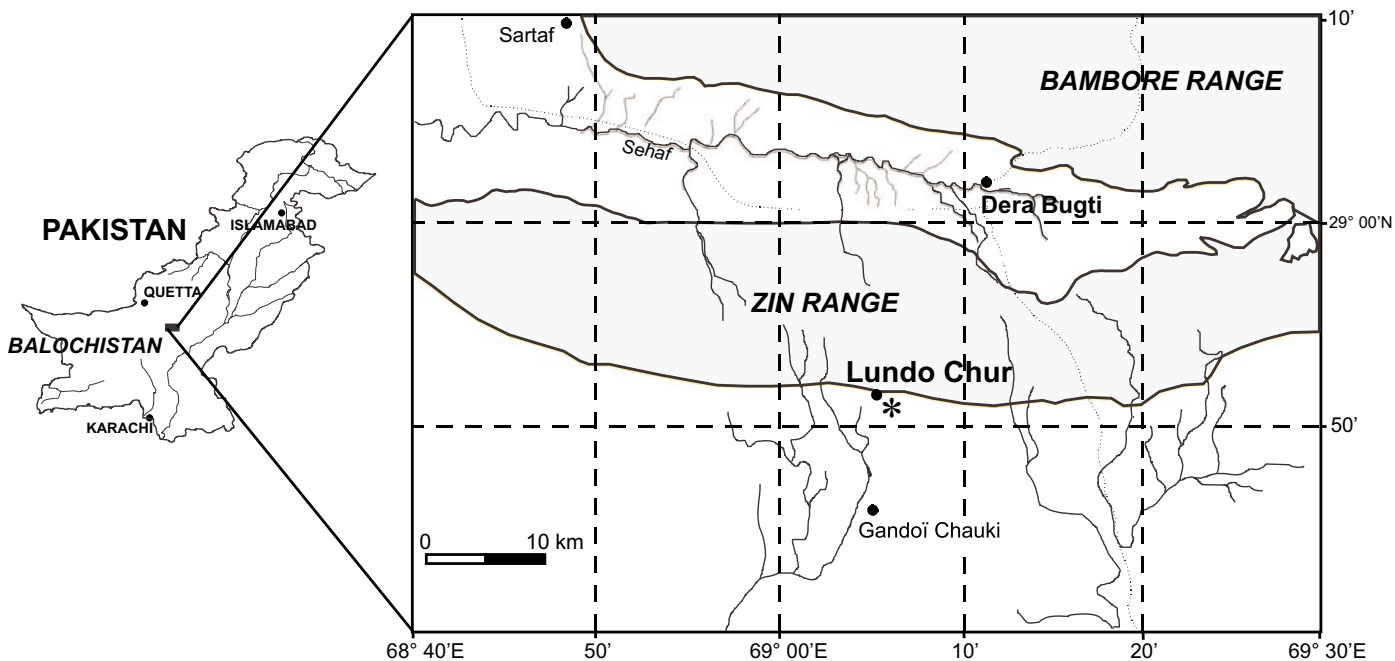


Fig. 1. Map of Pakistan with an enlargement of the Bugti area, and the location of Lundo Chur where the described material has been found. Present-day latitudes and longitudes are also shown.

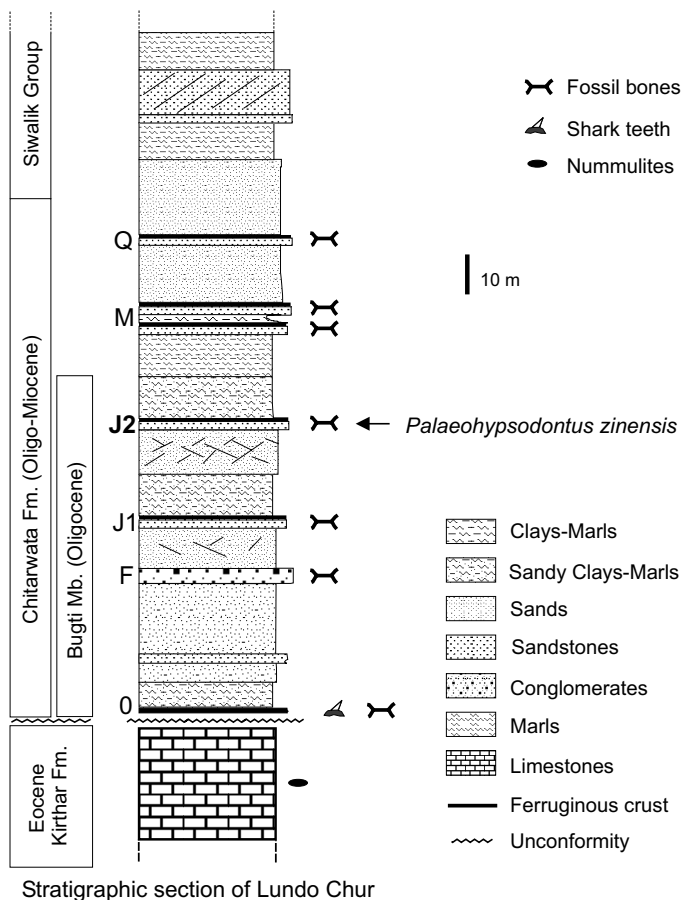


Fig. 2. Synthetic lithostratigraphic section of the Bugti Member (adapted from Welcomme et al. 2001) with the accurate stratigraphic setting of *P. zinensis* sp. nov.

therium beatrix. According to Pilgrim (1912), both specimens come from the “Upper Gaj” Formation which was then and subsequently considered as early Miocene. The “Upper Gaj” Formation is now considered as equivalent in age to the Lower Chitarwata Formation (Downing et al. 1993) and thus probably Oligocene in age, at least in the Dera Bugti area (Welcomme et al. 2001). Since the beginning of the last century, no new material of ruminants has been recovered in this area. We report here the occurrence of a dentally highly-specialized ruminant, which provides a glimpse into the evolutionary history of bovid-like artiodactyls in South Asia during the late Paleogene. There is actually no real consensus about the interrelationships of living ruminants with the exception of the major dichotomy that separates Pecora and Tragulina, evidenced by both molecular (e.g., Miyamoto et al. 1993) and morphological (Webb and Taylor 1980) data. Pecoran ruminants include all the modern ruminants bearing cranial appendage (i.e., Cervidae, Bovidae, Giraffidae, and Antilocapridae, except the cervid *Hydropotes*, that illustrates a case of secondary loss of antlers as evidenced by Randi et al. 1998) plus the hornless Moschidae. The modern tragulids (chevrotains) unambiguously represent the most plesiomorphic living ruminants, and are the only extant representatives of “Tragulina”, a wide paraphyletic assemblage including numerous extinct families of Paleogene ruminants (Webb and Taylor 1980). Pecora underwent a rapid radiation and different families evolved in parallel involving the acquisition of similar morphological characters that make the phylogenetic relationships between the different families still obscure. The current morphological consensus for the phylogeny of ruminants is summarized in Fig. 3. This largely

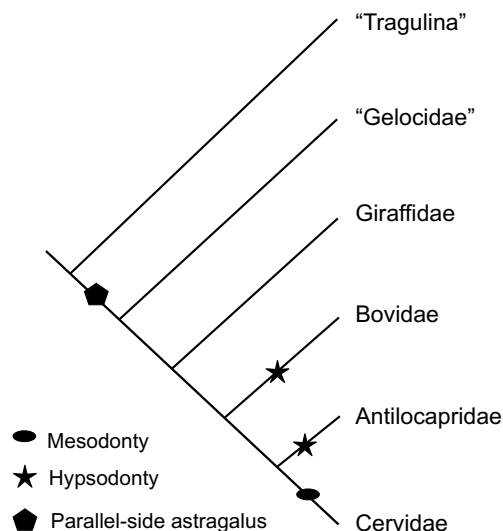


Fig. 3. Simplified cladogram illustrating the interrelationships between different families of ruminants (modified from Janis and Scott 1987). The term "Gelocidae" designates a heterogeneous assemblage of extinct hornless pre-pecoran ruminants. The distribution of the characters discussed in the text are indicated by symbols.

simplified phylogeny is extracted from Janis and Scott (1987), and the main dental and postcranial features discussed in the paper have been added.

Fossils described herein are temporarily housed in the collections of the Institut des Sciences de l'Evolution, Université de Montpellier II.

Abbreviations used.—ISEM, Institut des Sciences de l'Evolution, Université de Montpellier II, Montpellier, France; DBJ2, Dera Bugti locus J2 (Lundo Chur), Bugti Hills; ages of the Mongolian localities are in agreement with Meng and McKenna (1998). L, W, H, for length, width and height respectively; TD, transversal diameter; APD, antero-posterior diameter.

Systematic paleontology

Order Artiodactyla Owen, 1848

Suborder Ruminantia Scopoli, 1777

Family indet.

Palaeohypsodontus Trofimov, 1958

Type species: *Palaeohypsodontus asiaticus* Trofimov, 1958.

Palaeohypsodontus zinensis sp. nov. Métais

Figs. 4, 5; Tables 1, 2.

Holotype: ISEM DBJ2-A1, fragmentary right mandible with d4-m1 (only the third lobe of d4 is preserved, Fig. 4).

Etymology: Named in reference of the Zin range which forms a prominent dome in the Bugti Hills' landscape, especially from the locus where the specimens have been found.

Referred material.—Left astragalus (ISEM DBJ2-A2) and right fragmentary metatarsal bone (ISEM DBJ2-A3) cautiously referred to *P. zinensis* sp. nov (Fig. 5).

Locality.—The material was collected in Lundo Chur (Quarry, J2), 30 kilometers southwest of Dera Bugti, Balochistan, Pakistan (Fig. 1).

Horizon.—Fossiliferous crust J2 in the Bugti lithostratigraphy (Welcomme et al. 2001), late Oligocene (Fig. 2). The crust J2 has also yielded remains of the giant rhinocerotoid *Paraceratherium bugtiense*, the anthracothere *Anthracotherium bugtiense* and the entelodont *Paraentelodon* sp.

Diagnosis.—Large species of *Palaeohypsodontus*, with lower molars clearly hypsodont (the ratio of height to width of the moderately worn m1 is 2.1, almost twice as hypsodont as the type species *P. asiaticus* from Mongolia). Further differs from *P. asiaticus* in having a tiny metastylid forming a narrow vertical rib on the lingual wall of the lower molar, no ectostylid, a well-developed entostylid, and a salient mesial cingulum.

Description.—Dental material: The labial side of the mandible is more convex at the level of m1 than that of d4, whereas the lingual side appears to become slightly concave below the molars. The height of the mandible is 15 mm below m1 and d4. The teeth are rectangular in occlusal view, markedly compressed transversely, and noticeably hypsodont with respect to the contemporaneous ruminants (the ratio height/length of the crown is 0.9). The teeth are obliquely implanted in the jaw, so that they are forwardly tilted in lateral view. The lingual cusps are strongly compressed transversely and higher than the labial ones, which are crescentic. The crown of d4 is broken except for the third lobe. In contrast to the condition seen in the m1, the neck is apparent and the lacteal

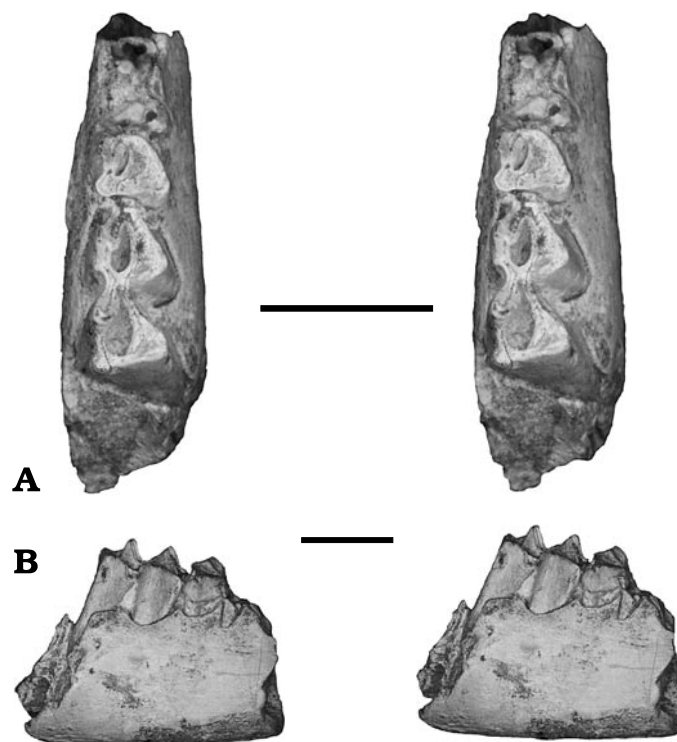


Fig. 4. *Palaeohypsodontus zinensis* sp. nov., late Oligocene (Chattian), Lundo J2, Bugti Hills, Balochistan, Pakistan. Holotype (ISEM DBJ2-A1). **A.** Stereophoto of occlusal view. **B.** Stereophoto of labial view. Scale bars 1 cm.

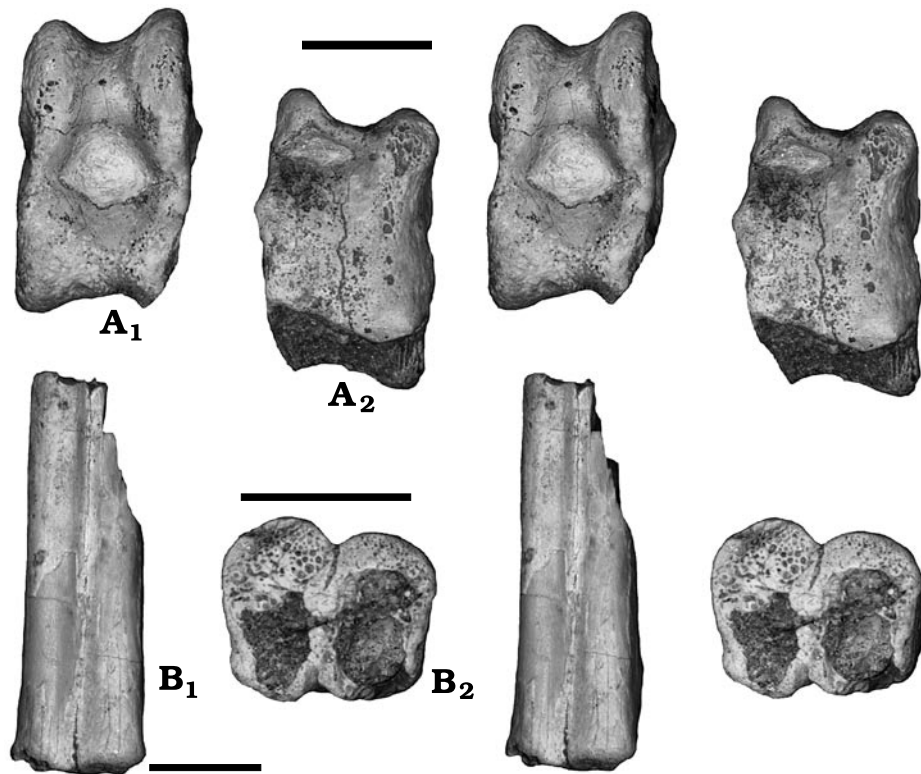


Fig. 5. *Palaeohypsodontus zinensis* sp. nov., late Oligocene (Chattian), Lundo J2, Bugti Hills, Balochistan, Pakistan. A. Left astragalus (ISEM DBJ2-A2) in anterior (A₁) and posterior (A₂) views. B. Shaft of right metatarsal (ISEM DBJ2-A3) in anterior (B₁) and distal (B₂) views. All stereo-photographs. Scale bars 1 cm.

tooth, and despite its advanced wear, it seems to be more brachyodont than the first molar. The enamel is thin and the posthypocristid is transversally oriented. The distal extremity of the posthypocristid consists of a bulky structure which forms a distinct pillar in the postero-lingual corner of the tooth. Although the second lobe is broken, a weak ectostylid seems to occur between the latter and the third lobe. As in Miocene pecoran ruminants, the cusps join up in early wear stages, isolating a central cavity between both distal cusps. No cingulum can be distinguished on the rear of d4.

The molar (m1) is rectangular in occlusal outline and twice as long as it is wide. Lingual cusps are strongly compressed transversely and clearly higher than the labial ones, which are much more worn. The lingual wall of the tooth is rather flat. Only a narrow vertical groove occurs between the two lobes. The trigonid and talonid are equal in length but the trigonid is slightly narrower. No ectostylid occurs between the labial and strongly crescent cusps (protoconid and hypoconid). The stylids are not very bulbous, except for the relatively prominent entostylid which forms a postero-lingual pillar on the tooth. There is no trace of a *Palaeomeryx* fold on the protoconid or *Dorcatherium* fold, but a distinct metastylid occurs on the postmetacristid. This minute cusp extends on the lingual side of the teeth until the base forming a weak pillar. A strong mesial cingulum occurs in front of the tooth. The enamel is smooth. Measurements are provided in Table 1.

Postcranial material: two fragmentary postcranial remains (an eroded astragalus ISEM DBJ2-A2, and a fragmentary right metatarsal ISEM DBJ2-A3) were found in the same spot

than the type specimen and they are thus tentatively referred to *Palaeohypsodontus zinensis*. The particular morphology of the astragalus is a key-apomorphy of the order Artiodactyla: in addition to the proximal trochlea, which articulates with the tibia, the astragalus also develops a distal trochlea articulating with tarsal bones. ISEM DBJ2-A2 seems to correspond to the size estimate range of the animal predicted from the dental remains (Table 3). The body mass of both species of *Palaeohypsodontus* has been estimated from the area of the m1 (Legendre 1989), and compared with estimates of body mass provided from the size of the astragalus (Martinez and Sudre 1995; Table 3). We obtained body mass values significantly close enough (about 17.5 kg by using both methods) for considering dental remains and astragalus as belonging to the same species. The trochleas of the astragalus are not aligned, the distal one is shallower and slightly rotated medially with respect to the proximal one. Unfortunately, it is not possible to see if there was a ridge separating the articular surfaces of the cuboid and navicular, because the distal trochlea is badly broken. The sustentacular facet is mediolaterally convex and it occurs on the whole width of the plantar face. A weak ridge medially borders the sustentacular facet as in the astragali of Pecora (Martinez and Sudre 1995). In lateral view, the fibular facet extends along the anterior part of proximal trochlea, but it is limited by an attenuated and longitudinal ridge near the apex of the trochlea.

The shaft of a right metatarsal is broken proximally and the section led to the conclusion that it probably belonged to a juvenile individual, because it lacks the distal epiphysis. The digit III and IV are not completely fused in sectional

Table 1. Measurements of the holotype and referred dentaries of *Palaeohypsodontus asiaticus* from Tatal Gol (Mongolia), *P. cf. asiaticus* from Ulan Tatal (China), *P. zinensis* sp. nov. from the Bugti Hills (Pakistan), and the holotype of *Hanhaicerus qii* from Ulan Tatal (China). Abbreviations: L, length; W(tr), width of trigonid; W(ta), width of talonid; H, height. All measurements are in mm. Asterisks indicate estimates from the figures of the type specimens.

	<i>P. asiaticus</i> (type) Tatal Gol (Mongolia) Trofimov, 1958	<i>P. cf.</i> <i>asiaticus</i> Ulan Tatal (China) Huang, 1985	<i>P. zinensis</i> sp. nov. Bugti Hills (Pakistan) this paper	<i>Hanhaicerus</i> <i>qii</i> Ulan Tatal (China) Huang, 1985
Lp2	–	6	–	–
Wp2	–	2	–	–
Lp3	–	7	–	–
Wp3	–	–	–	–
Lp4	–	7	–	–
W(tr)p4	–	4	–	–
W(ta)p4	–	5	–	–
Lm1	–	7.4	10.6	–
W(tr)m1	–	5.1	5.1	–
W(ta)m1	–	6.2	5.6	–
Hm1	–	6.1*	10.8	–
Lm2	6.5	8.5	–	9.7
W(tr)m2	4.5	6.3	–	6.1
W(ta)m2	4.5	7.8	–	6.2
Hm2	5.5	6.7*	–	6.5*
Lm3	9	–	–	13.5
W(tr)m3	5	5.8	–	6.2
W(ta)m3	5	8.3	–	7.2
Hm3	12	7.8*	–	6.8*

* indicate estimated values.

Table 2. Dimensions of the postcranial elements referred to *Palaeohypsodontus zinensis* sp. nov. L, length; TD, transverse width; APD, dorso-plantar height. All measurements are in mm.

	L	TD	APD
ISEM DBJ2-A2	24	14	13
ISEM DBJ2-A3	37	12	9

Table 3. Comparison of weight estimations of *P. zinensis* sp. nov. and *P. asiaticus* using the astragalus size ($W_{\text{astragalus}}$) from the method developed in Martinez and Sudre (1995), and those obtained using the m1 area (W_{m1}) from Legendre (1989).

	W_{m1} (kg)	$W_{\text{astragalus}}$ (kg)
<i>Palaeohypsodontus zinensis</i> sp. nov.	17.8	17.5
<i>Palaeohypsodontus asiaticus</i>	12	–

view. Unfortunately, the state of preservation of the metatarsal gully does not allow us to see if it was open along its entire length, as living in bovids and giraffids, or closed at its distal end by a thin bridge, as in living cervids and moschids (Heintz 1963). Measurements are provided in Table 2.

Discussion

ISEM DBJ2-A1 shares several synapomorphies (pronounced hypsodonty, lack of both *Dorcatherium* fold and *Palaeomeryx* fold; although those are probably correlated with hypsodonty) with dubious bovid-like taxa known in the Oligocene and early Miocene of Asia. The form of the Bugti Hills differs from *Hanhaicerus qii* from the Oligocene of Ulan Tatal (China, Inner Mongolia, Nei Mongol of Chinese authors, Hsandagolian LMA, Huang, 1985) in its overall morphology and its prominent hypsodonty, although the m1 of *Hanhaicerus* is hitherto unknown. In addition, and contrary to the condition observed in the specimen from the Bugti Hills, the metaconid somewhat overlaps the entoconid in *Hanhaicerus* and the prehypocristid does not join the metastylid. Among other Oligocene hypsodont ruminants that might be related to ISEM DBJ2-A1, *Pseudomeryx hypertalonidus* from the Oligocene of Tatal Gol (Mongolia, Hsandagolian LMA) is an unfortunately poorly-known small ruminant. It is represented only by a lower jaw with m1–m3 and mainly characterized by the trilobed talonid of its m3 (Trofimov 1957). The lower molars of *Pseudomeryx* further display an advanced selenodont condition, but the teeth are obviously brachydont and wider than those of the fossil from the Bugti Hills. *Gobiomeryx dubius* from the late Eocene of Erguil Obo (Mongolia, Ergilian LMA, Trofimov, 1957) may be easily distinguished from ISEM DBJ2-A1 by its smaller size and in having a more brachydont pattern and a well-developed metastylid on lower molars. All other Oligocene ruminants hitherto reported in Asia are as brachydont as *Gobiomeryx* and display a noticeably less advanced stage of selenodonty, with the exception of the genus *Palaeohypsodontus*, a small form geographically restricted to the Mongolian Plateau.

Despite of the scarcity of the material, ISEM DBJ2-A1 is strikingly reminiscent to *Palaeohypsodontus asiaticus*, from the Oligocene of Tatal Gol (Mongolia, Hsandagolian LMA), the type species of *Palaeohypsodontus* initially described by Trofimov (1958) on the basis of a fragmentary lower jaw with m2–3 and an isolated m3. The lower molar from Pakistan shares several affinities with *P. asiaticus*, in particular the marked hypsodonty (significantly stronger than in *P. asiaticus*), the lack of *Palaeomeryx* fold and *Dorcatherium* fold on lower molars, the absence of cingula and any ectostylid. We are aware that these dental features cannot be considered as exclusive derived features of the genus *Palaeohypsodontus* since they are obviously linked to hypsodonty. Nevertheless, given the paucity of the dental material currently available for these presumed early bovids, pertaining the Pakistani form to *Palaeohypsodontus* remains the most relevant solution. Further dental characters such as the presence of a metastylid and an advanced stage of selenodonty with respect to other Oligocene Asian ruminants are also typical of the genus *Palaeohypsodontus*. ISEM DBJ2-A1 is distinguished from *P. asiaticus* by its longer (30%) and slightly narrower m1, its more pronounced molar hypsodonty, and

the well-developed disto-lingual pillar (entostylid) on m1. As pointed out by Huang (1985), and according to the figuration of the type specimen, it appears that Trofimov (1957, 1958) over-estimated the height of the tooth crown on the type. Consequently, the molars of the specimen from the Bugti Hills are nearly twice as high as the specimens from Mongolia (Trofimov 1957, 1958; Huang 1982, 1985). According to its peculiar features, the Pakistani form is unambiguously identified as a new species of *Palaeohypsodontus*.

Is *Palaeohypsodontus* a bovid?—Based on the absence of *Palaeomeryx* fold and cingula, the short premolar row and the hypsodonty of molars, Trofimov (1958) referred *Palaeohypsodontus* to the Bovidae, but he did not exclude it from being an archaic representative of an early specialized branch of “Tragulina”. Additional putative bovid remains were reported in the lower Oligocene Chaganbulage Formation (Mongolia) by Jiang et al. (1976), but the paucity of specimens and the lack of associated horn cores prevented all conclusive familial assignments. Huang (1985) reported further dental remains of *P. asiaticus*, together with a new brachyodont genus, *Hanhaicerus qii* from Ulan Tatal (Hsandagolian LMA), and he confirmed the bovid status of both taxa, suggesting that bovids probably originated in Central Asia. More recently, Vislobokova et al. (1996), Vislobokova and Daxner-Höck (2002), and Dmitrieva (2002) pointed out additional dental remains (including possible upper dentition) of early bovids from the Oligocene of Mongolia. All attempts to attribute *Paleohypsodontus* to the Bovidae are based on the marked hypsodonty of its lower molars. However, and as noted above, convincing familial assignment cannot be based on such a character, since it obviously appeared several times during the evolutionary history of ruminants (Janis and Scott 1987). In that respect, *Palaeohypsodontus* might equally represent the earliest representative of the Antilocapridae, as suggested by Janis and Manning (1998), although such an hypothesis is for now as weakly supported as the bovids affinities of *Palaeohypsodontus*. In that context, the morphology of the astragalus ISEM DBJ2-A2 of *P. zinensis* provides new elements for discussing the bovid status of *Palaeohypsodontus*. Indeed, the slight displacement of the distal pulley with respect to the proximal one clearly indicates a plesiomorphic condition within ruminants, and thus cannot be referred to any group of Pecora, including bovids. The non-alignment of the trochleas as well as the prominence of the metastylid on m1 would rather suggest affinities with the “Tragulina”, although this hypothesis needs further morphological evidence. The familial status of *Palaeohypsodontus* cannot be definitively solved on the basis of the available material from Pakistan, but its likely non-pecoran affinities are supported in this work.

The main defining feature of modern Bovidae is the possession of horns usually recovered by keratin sheaths. Because of their organic nature, the latter are not preserved in the fossil record, but the bony horn cores which sustain the keratin sheaths are usually preserved and constitute the most com-

monly used skeletal element to differentiate fossil bovid species taxonomically (Thomas 1984a). Pecoran ruminants with horn cores indicative of keratinized horn sheaths suddenly appeared in the fossil record (Thomas 1984b). Classically, the earliest bovid known from horn cores is *Eotragus* from the late early Miocene of Europe (Gentry et al. 1999), Pakistan (Solounias et al. 1995), and from the middle Miocene of China (Ye 1989). Other early–middle Miocene bovids occur in Asia: *Gobiocerus mongolicus* from the early Miocene Lou Formation in Mongolia (Sokolov 1952), *Hypsodontus miocenicus* (Sokolov 1949) and *Kubanotragus sokolovi* (Gabunia 1973) both known in the middle Miocene of Northern Caucasus. Most of these early bovids display dental similarities with *Palaeohypsodontus*, although that does not necessarily imply close relationship between these taxa. Indeed, it seems that *Palaeohypsodontus* achieved a fully selenodont grade at the beginning of the Oligocene (MP 21, Vislobokova et al. 1996), and it is thus likely to have derived from an unknown basal Eocene ruminant. None of the ruminants hitherto described in the late Eocene of Asia displays an even incipiently hypsodont dentition, and the real affinities of *Palaeohypsodontus* may lie close to a specialized group of “Tragulina” which might have acquired a fully selenodont and hypsodont dentition. Accordingly, dental similarities between *Palaeohypsodontus* and early true bovids cited by previous authors are most plausibly interpreted as convergences. This hypothesis would imply that the hypselenodont grade appeared independently at least twice in the history of Ruminantia and that it arose iteratively at the beginning of the Miocene in several lineages of Old World and North American ruminants. As stressed by Janis and Scott (1987) the characters regarded by Huang (1985) as typical bovid features (e.g., hypsodonty, loss of *Palaeomeryx* fold and ectostylid) also occurred in early Miocene hypsodont cervoids such as dromomerycids or merycodontine antilocaprids, and therefore cannot be considered as bovid autapomorphies. Likewise, the postcranial elements here tentatively referred to *Palaeohypsodontus* do not allow further investigation about its systematic status (the distal pulley of the astragalus is slightly damaged but it does not seem to be aligned with the proximal pulley as in all known Pecora), but they cast doubt on the current concept of an early differentiation of bovids from the late Eocene–early Oligocene.

Paleoecological inferences.—According to the present fossil record, *Palaeohypsodontus* was a rather rare and geographically restricted taxon during the Oligocene in Asia. It is noteworthy that such a specialized ruminant occurs in two regions which probably belonged to two different biogeographic areas in regard to their distinct latitudinal position during the Oligocene. As a result, it might be expected that such a latitudinal difference induced distinct climatic conditions, and thus clearly distinct habitats. Yet, several large mammals are common to both regions during the Oligocene. For instance, the giant rhinocerotoid *Paraceratherium* as well as entelodontids occurs in both regions, and thus suggest close or similar ecological conditions. The combined oc-

currence of such taxa suggests open but non-grassy habitats, since grasslands are unknown from the Oligocene in the Old World (e.g., Janis et al. 2002), including some elements of fairly abrasive vegetation. Increasing the tooth crown height in order to enhance the durability of the dentition is a frequent process among mammals (Janis and Fortelius 1988). The pronounced hypsodont trend expressed by the dental morphology of *P. zinensis* clearly indicates a fibrous diet based on abrasive food, at least in part. The evidences for inferring the paleoenvironment in which *P. zinensis* lived are still weak for now, but the associated fauna would rather plead for a lush vegetation with substantial food supply for the diversified large mammal fauna which are all brachydont. The numerous complete or fragmentary fossil trunks found at Lundo Chur (associated with the vertebrate remains) suggest a forested environment. However, aside a fairly forested environment, it may be hypothesized the existence of more open habitats in which *Palaeohypsodontus* might have lived. The faunal or floristic fossil evidences are still too poor for proposing a definitive picture of the paleoenvironmental condition, but the preliminary results based on the trunks remains and the fauna associated to *Palaeohypsodontus* suggest a mosaic of both forested and more open landscapes.

Finally, given the scarce material currently available, it is difficult to include *Palaeohypsodontus* within bovids only on the basis of dental characters. Although several authors have soundly suggested that horned ruminants must have obviously evolved from Oligocene and early Miocene hornless ruminants (e.g., Morales et al. 1995), we consider that there are no convincing fossil evidence for claiming that the early radiation of bovids took place at the late Eocene–early Oligocene period in Asia. Moreover, the postcranial elements reported here would rather favor for a dentally highly specialized lineage of “traguloid” ruminants which would acquired the hypsodont grade in response of the more open environment consequent to the climatic deterioration that characterized the Eocene–Oligocene transition (Berggren and Prothero 1992). Several Old World Oligocene and early Miocene hornless ruminants have been assigned to the Bovidae exclusively on the basis of dental remains, although actually no exclusive autapomorphic dental character may be put forward for the Bovidae. Unfortunately, the current classification and phylogeny of the early representatives of extant Pecoran families comes up against the inadequacy of dental features as well as the numerous cases of convergent postcranial characters (Janis and Scott 1987; Gentry 1994). However, the astragalus tentatively referred to *P. zinensis* sp. nov. does not seem to indicate pecoran affinities for *Palaeohypsodontus*, because of its distal trochlea slightly rotated medially (Hussain et al. 1983). Consequently, we consider *Palaeohypsodontus* to be a dentally highly derived traguloid as formerly hypothesized by Trofimov (1957). The occurrence of such hypsodont Oligocene ruminants was until now only recognized from the Hsanda Gol Formation in Mongolia. The presence of this taxon in the late Oligocene of the

Bugti Hills considerably extends its geographical distribution. In addition, this typical Oligocene ruminant provides additional evidence for an Oligocene age for the lower levels of the Bugti continental sequence, and definitively excludes the previous Miocene age ascribed by several authors for these fossiliferous deposits (Raza and Meyer 1984; Flynn et al. 1986; Friedman et al. 1992; Downing et al. 1993). The fauna associated with *Palaeohypsodontus* consists of large mammals such as the giant rhinocerotoid *Paraceratherium*, the entelodontid *Paraentelodon*, or the anthracotheriid *Anthracotherium* which attests to a rather open forested environment, probably similar to that of the contemporaneous Hsandagolian localities in Mongolia and China, despite the great geographical and latitudinal differences between both areas. The preliminary analysis of the slightly older Oligocene ruminant assemblages from the Bugti Hills does not show such dentally highly derived ruminant taxa, and it leaves the question of the origin and familial assignment of *Palaeohypsodontus* open. Further discoveries of postcranial material will undoubtedly help to clarify the taxonomic status of these early bovid-like forms.

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References

- Berggren, W.A. and Prothero, D.R. (eds.) 1992. Eocene–Oligocene climatic and biotic evolution. x + 568 pp. Princeton University Press, Princeton.
- Blanford, W.T. 1883. Geological notes on the hills in the neighbourhood of the Sind and Punjab frontier between Quetta and Dera Ghazi Khan. *Indian Geological Survey Records* 20: 1–136.
- Dmitrieva, E.L. [Dmitreva, E.L.] 2002. On the early evolution of bovids [in Russian]. *Paleontologičeskij žurnal* 71: 86–88.
- Downing, K.F., Lindsay, E.H., Downs, W.R., and Speyer, S.E. 1993. Lithostratigraphy and vertebrate biostratigraphy of the early Miocene Himalayan Foreland, Zinda Pir Dome, Pakistan. *Sedimentary Geology* 87: 25–37.
- Flynn, L.J., Jacobs, L.L., and Cheema, I.U. 1986. Baluchimyinae, a new ctenodactyloid rodent subfamily from the Miocene of Balochistan. *American Museum Novitates* 2841: 1–58.

- Forster-Cooper, C. 1924. On the skull and dentition of *Paraceratherium zimensis*, a genus of aberrant rhinoceros from the Lower Miocene deposits of Dera Bugti. *Philosophical Transactions of the Royal Society* 212: 369–394.
- Forster-Cooper, C. 1934. XIII. The extinct rhinoceroses of Balochistan. *Philosophical Transactions of the Royal Society of London, Series B* 223: 569–616.
- Friedman, R., Gee, J., Tauxe, L., Downing, K., and Lindsay, E.H. 1992. The magnetostratigraphy of the Chitarwata and lower Vihowa formations of the Dera Ghazi Khan area, Pakistan. *Sedimentary Geology* 81: 253–268.
- Gabunia, L. 1973. *The Fossil Vertebrate Fauna from Belometchetskaia* [in Georgian]. 136 pp. Metsniereba, Tbilissi.
- Gentry, A.W. 1994. The Miocene differentiation of Old World Pecora (Mammalia). *Historical Biology* 7: 115–158.
- Gentry, A.W., Roessner, G.E., and Heizmann, E.J. 1999. Suborder Ruminantia. In: G.E. Roessner and K. Heissig (eds.), *The Miocene Land Mammals of Europe*, 225–258. Springer Verlag, München.
- Heintz, E. 1963. Les caractères distinctifs entre métatarses de Cervidae et Bovidae actuels et fossiles. *Mammalia* 27: 200–209.
- Hemphill, W.R. and Kidwai, A.H. 1973. Stratigraphy of the Bannu and Dera Ismail Khan areas, Pakistan. *Geological Survey Professional Paper* 716-B: 1–36.
- Huang, X. 1982. Preliminary observations on the Oligocene deposits and mammalian fauna from Alashan Zuoqi, Nei Mongol. *Vertebrata Palasiatica* 20: 341–349.
- Huang, X. 1985. Fossil bovids from the middle Oligocene of Ulanatal, Nei Mongol. *Vertebrata Palasiatica* 23: 153–160.
- Hussain, S.T., Sondaar, P.Y., and Shah, S.M.I. 1983. Fossil mammal bones of Pakistan: a field atlas. *Memoirs of the Geological Survey of Pakistan* 14: 1–15.
- Janis, C.M. and Scott, K.M. 1987. The interrelationships of higher ruminant families with special emphasis on the members of the Cervoidea. *American Museum Novitates* 2893: 1–85.
- Janis, C.M. and Fortelius, M. 1988. On the means whereby mammals achieve increased functional durability of their dentitions, with special reference to limiting factors. *Biological review* 63: 197–230.
- Janis, C.M. and Manning, E. 1998. Antilocapridae. In: C.M. Janis, K.M. Scott and L.L. Jacobs (eds.), *Evolution of Tertiary Mammals of North America, Vol. 1: Terrestrial Carnivores, Ungulates, and Ungulatelike Mammals*, 491–507. Cambridge University Press, Cambridge.
- Janis, C.M., Damuth, J., and Theodor, J.M. 2002. The origins and evolution of the North American grassland biome: the story from the hoofed mammals. *Palaeogeography, Palaeoclimatology, Palaeoecology* 177: 183–198.
- Jiang, Y., Wang, B., and Qi, T. 1976. Stratigraphy of the Early Oligocene Chaganbulage Formation, Haosibuierdu Basin, Ningxia. *Vertebrata Palasiatica* 14: 35–41.
- Legendre, S. 1989. Les communautés de mammifères du Paléogène (Eocène supérieur et Oligocène) d'Europe Occidentale: structures, milieux et évolution. *Münchner Geowissenschaftliche Abhandlungen (A)* 16: 1–100.
- Lydekker, R. 1883. Indian Tertiary and post-Tertiary Vertebrata: Siwalik selenodont Suina, etc. *Memoirs of the Geological Survey of India—Palaeontologica Indica, Series 10*, 5: 143–177.
- Lydekker, R. 1884. Additional Siwalik Perissodactyla and Proboscidea. *Memoirs of the Geological Survey of India—Palaeontologica Indica, Series 10*, 3: 1–34.
- Marivaux, L., Vianey-Liaud, M., and Welcomme, J.-L. 1999. Première découverte de Cricetidae (Rodentia, Mammalia) oligocènes dans le synclinal sud de Gandoi (Bugti Hills, Balouchistan, Pakistan). *Comptes Rendus de l'Académie des Sciences de Paris, série IIA* 329: 839–844.
- Marivaux, L., Vianey-Liaud, M., Welcomme, J.-L., and Jaeger, J.-J. 2002. The role of Asia in the origin and diversification of hystricognathous rodents. *Zoologica Scripta* 31: 225–239.
- Martinez, J.-N. and Sudre, J. 1995. The astragalus of Paleogene artiodactyls: comparative morphology, variability and prediction of body mass. *Lethaia* 28: 197–209.
- Meng, J. and McKenna, M.C. 1998. Faunal turnovers of Palaeogene mammals from the Mongolian Plateau. *Nature* 394: 364–367.
- Miyamoto, M.M., Kraus, F., Laipis, P.J., Tanhauser, S.M., and Webb, S.D. 1993. Mitochondrial DNA phylogenies within Artiodactyla. In: F.S. Szalay, M.J. Novacek, and M.C. McKenna (eds.), *Mammal Phylogeny, Placentals, Vol. 2*, 268–281. Springer-Verlag, New York.
- Morales, J., Soria, D., and Pickford, M. 1995. Sur les origines de la famille des Bovidae (Artiodactyla, Mammalia). *Comptes Rendus de l'Académie des Sciences de Paris, série IIA* 321: 1211–1217.
- Pilgrim, G.E. 1908. The Tertiary and post-Tertiary freshwater deposits of Balochistan and Sind, with notes on new vertebrates. *Records of the Geological Survey of India* 37: 139–66.
- Pilgrim, G.E. 1910. Notices of new mammalian genera and species from the Tertiary of India. *Records of the Geological Survey of India* 40: 63–71.
- Pilgrim, G.E. 1912. The vertebrate fauna of the Gaj Series in the Bugti Hills and the Punjab. *Paleontologia Indica, New Series* 4: 1–83.
- Randi, E., Mucci, N., Pierpaoli, M., and Douzery, E. 1998. New phylogenetic perspectives on the Cervidae (Artiodactyla) are provided by the mitochondrial cytochrome b gene. *Proceedings of the Royal Society of London B* 265: 793–801.
- Raza, S.M. and Meyer, G.E. 1984. Early Miocene geology and paleontology of the Bugti Hills. *Geological Survey of Pakistan* 11: 43–63.
- Solounias, N., Barry, J.C., Bernor, R.L., Lindsay, E.H., and Raza, S.M. 1995. The oldest bovid from the Siwaliks, Pakistan. *Journal of Vertebrate Paleontology* 15: 806–814.
- Sokolov, I.I. 1949. Sur des restes de Cavicornes (Bovidae, Mammalia) trouvés dans le Miocène moyen du Caucase septentrional. *Dokladi Akademii Nauk SSSR* 67: 1101–1104.
- Sokolov, I.I. 1952. Remains of Bovidae, Mammalia, from lower Miocene deposits of Western Gobi [in Russian]. *Trudy Palaeontologičeskogo Instituta Akademii Nauk SSSR* 41: 155–158.
- Thomas, H. 1984a. Les bovidés anté-Hipparions des Siwaliks inférieurs (Plateau du Potwar, Pakistan). *Mémoire de la Société Géologique de France* 145: 1–65.
- Thomas, H. 1984b. Les Bovidae (Artiodactyla : Mammalia) du Miocène du Sous-Continent Indien, de la Péninsule Arabique et de l'Afrique: biostratigraphie, biogéographie et écologie. *Palaeogeography, Palaeoclimatology, Palaeoecology* 45: 251–299.
- Trofimov, B.A. 1957. Nouvelles données sur les Ruminantia les plus anciens d'Asie. *Cursillos y Conferencias del Instituto "Lucas Mallada"* 4: 137–141.
- Trofimov, B.A. 1958. New Bovidae from the Oligocene of Central Asia. *Vertebrata Palasiatica* 2: 243–247.
- Vickary, N. 1846. Geological report on a portion of the Balochistan Hills. *Quarterly Journal of the Geological Society* 2: 260–265.
- Vislobokova, I.A., Dmitrieva, E.L., and Trofimov, B.A. 1996. Ruminants on the Paleogene–Neogene boundary in Mongolia. *Paleontological Journal* 30: 99–108.
- Vislobokova, I.A. and Daxner-Höck, G. 2002. Oligocene–early Miocene ruminants from the Valley of Lakes (Central Mongolia). *Annalen des Naturhistorischen Museums Wien* 103A: 213–235.
- Webb, S.D. and Taylor, B.E. 1980. The phylogeny of hornless ruminants and a description of the cranium of *Archaeomeryx*. *Bulletin of the American Museum of Natural History* 167: 117–158.
- Welcomme, J.-L. and Ginsburg, L. 1997. Mise en évidence de l'Oligocène sur le territoire des Bugti (Balouchistan, Pakistan). *Comptes Rendus de l'Académie des Sciences de Paris, série IIA* 325: 999–1004.
- Welcomme, J.-L., Benammi, M., Crochet, J.-Y., Marivaux, L., Métais, G., Antoine, P.-O., and Baloch, I.S. 2001. Himalayan Forelands: palaeontological evidence for Oligocene detrital deposits in the Bugti Hills (Balochistan, Pakistan). *Geological Magazine* 138: 397–405.
- Ye, J. 1989. Middle Miocene Artiodactyls from the Northern Junggar Basin. *Vertebrata Palasiatica* 27: 37–52.