



OLIGOCENE AND EARLY MIOCENE RUMINANTS (MAMMALIA, ARTIODACTYLA) FROM PAKISTAN AND UGANDA

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ABSTRACT

Late Oligocene and Early Miocene fossil ruminants from Napak and Moroto in Uganda and the Zinda Pir sequence in Pakistan comprise at least eight taxa, including an indeterminate lophiomerycid, *?Gelocus gajensis*, *Walangania africanus*, *Bugtimeryx pilgrimi*, an indeterminate large cervoid, *Progiraffa exigua*, *Palaeohypsodontus zinen-sis*, and an unnamed bovid. The fossils range in age between 25 and 16 million years old and together with species of tragulids provide evidence for the existence of diverse latest Oligocene and earliest Miocene ruminant faunas in sub-Saharan Africa and southern Asia. The fossils from Pakistan may also document the first appearance and subsequent radiation of giraffes and bovids, two groups that dominate later Neogene and modern herbivore faunas.

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INTRODUCTION

Our friend Will Downs liked to travel; both within the natural and cultural geographies of this

world and within the abstract geographies of the past and future. He wanted to go everywhere and pretty much did. Precambrian river gorges, Triassic

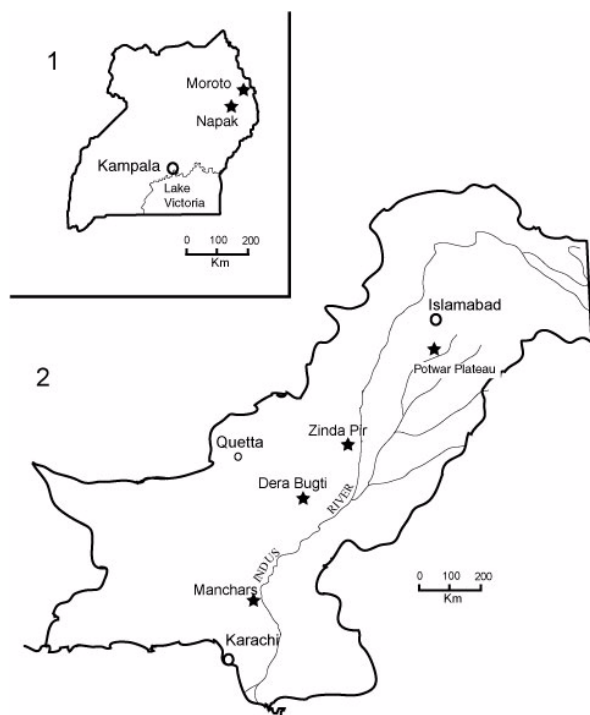


Figure 1. Geographic positions of localities: 1) fossil sites in Uganda; 2) fossil sites in Pakistan.

tribal deserts, Miocene tropical volcanoes, and even densely urban, modern civilizations were all Will's habitats.

This paper uses our memories of Will as an opportunity to bring together descriptions of fossil material from just three of the places where he worked: Uganda and the Potwar Plateau and Sulaiman Ranges of Pakistan. While these fossils would ordinarily not have been described together, they do have a commonality. They are early representatives of one of the great mammalian radiations, the Oligocene to Early Miocene radiation of the ruminants. The ruminant radiation gave rise to six modern families with nearly 200 extant species, and it also produced an abundance of extinct species and higher level taxa. However, most of what we know of this radiation is based on taxa from the temperate Oligocene and Miocene of North America, Europe, and central Asia, with little being known of contemporaneous ruminants from tropical southern Asia or Africa, which are now the sites of the greatest species diversity. In this paper we describe fossil material from the Early Miocene of Uganda and the Oligocene through Early Miocene of southern Asia, and, particularly in the case of Pakistan, this adds a new element to our understanding of the evolutionary history of early ruminants.

The material we discuss was collected during fieldwork by several of us during the past 15 years,

and in most cases represents species that are poorly known. The fossils represent at least eight species belonging to six major groups. Seven species come from Pakistan and one from Uganda. The scope of the study is limited in two ways. First, we only discuss new material and do not attempt to reanalyze older collections, which in East Africa are quite extensive. Such an undertaking would be too much for the limited time available and is only significant in the case of the East African record. Secondly, with the exception of one species, the taxa discussed in this paper are all members of the Pecora. Tragulids are also very well represented in these collections, perhaps with as many as seven additional species in two genera from the Oligocene and Early Miocene. The material, however, requires a thorough study of the very large and species rich Middle and Late Miocene collections of tragulids from the Potwar Plateau and East Africa. Tragulids are thus not considered here.

METHODS

Molar and premolar terminology in this paper follows that of Janis and Scott (1987) and Gentry (1994), although we use "prehypocristid" to refer to what is otherwise called the cristid obliqua. Other modifications are noted in the text. Measurements are in millimeters or centimeters, with lengths being the maximum dimension parallel to the mesiodistal axis of the tooth, trigonid width the maximum through the protoconid and metaconid perpendicular to the mesiodistal axis, and talonid width the maximum through the hypoconid and entoconid perpendicular to the mesiodistal axis.

General locations for the fossil sites are shown in Figure 1.1-1.2. The ages of the sites are based on the published literature in the cases of Uganda and the Potwar Plateau, and the accompanying paper by Lindsay et al. (this issue) for the Zinda Pir sites in the Sulaiman ranges. The age estimates for East African sites are primarily radiometric, while those for the Potwar Plateau are based on paleomagnetic sequences. The Lindsay et al. (this issue) paper presents new interpretations of the stratigraphy and paleomagnetic record of the Zinda Pir Dome area. In citing ages from it we have used their second interpretation (see figure 6b in Lindsay et al. this issue), which suggests a Late Oligocene through Early Miocene age for all of the Chitarwata Formation. The alternative, Interpretation A (Lindsay et al. this issue, Figure 6A), suggests an Early Oligocene age for the lower part of the Chitarwata Formation, and a Late Oligocene to Early Miocene age for the upper part. Both interpretations favor an Early Miocene age for the lower

Table 1. Length and Widths of Lower Teeth.

		p3 (mm)	p4 (mm)	dp4 (mm)	m1 (mm)	m2 (mm)	m3 (mm)	indet. m (mm)
Lophiomerycidae, gen. et sp. indet.								
Z 2278	Length:				8.4			
	Width:				4.7			
<i>?Gelocus gajensis</i>								
Z 271	Length:						--	
	Width:						9.1	
Z 2298	Length:						22.7	
	Width:						10.0	
<i>Walangania africanus</i>								
BUMP 721	Length:		9.8		9.9	11.1		
	Width:		5.5		6.8	7.7		
BUMP 722	Length:	8.7	8.6		9.9			
	Width:	4.5	5.3		6.4			
BUMP 584	Length:					10.8		
	Width:					7.2		
BUMP 552	Length:						16.0	
	Width:						6.9	
BUMP 450	Length:	9.1						
	Width:	4.5						
<i>Bugtimeryx pilgrimi</i>								
Z 269	Length:			8.7	11.0			
	Width:			6.1	7.5			
Z 270	Length:						18.0	
	Width:						8.1	
Z 2024	Length:					12.2		
	Width:					7.8		
Z 2030	Length:				12.2			
	Width:				8.2			
Z 2032	Length:						--	
	Width:						8.0	
Z 2068	Length:		8.1		--			
	Width:		4.9		5.9			
<i>?Cervoidea, gen. et sp. indet.</i>								
Z 2031	Length:				17.8			
	Width:				11.2			

Vihowa Formation. Interpretation A of Lindsay et al. (this issue) is the same as an age correlation suggested by Welcomme et al. (2001) for the Chitarwata Formation in Bugti Hills 300 km south of the Zinda Pir area.

Measurements for the lower and upper teeth and astragalus are in Tables 1, 2, and 3.

Abbreviations

BUMP: Boston University Uganda Museum
Makerere University Paleontology Expedition;
GSP-H: Geological Survey of Pakistan - Howard

University Project; GSP-Y: Geological Survey of Pakistan - Harvard University Project; GSP-DGK: Geological Survey of Pakistan - D.G. Khan collection; GSP-S: Geological Survey of Pakistan - Sind collection; PMNH-Z: Pakistan Museum of Natural History - Zinda Pir collection.

SYSTEMATIC PALEONTOLOGY

Order Artiodactyla
Suborder Ruminantia
Infraorder Tragulina

Table 1. (continued).

		p3 (mm)	p4 (mm)	dp4 (mm)	m1 (mm)	m2 (mm)	m3 (mm)	indet. m (mm)
<i>Progiraffa exigua</i>								
S 88	Length:							18.6
	Width:							14.3
S 412	Length:	17.7						
	Width:	9.2						
S 305	Length:							21.3
	Width:							13.9
H 208	Length:						32.1	
	Width:						14.5	
Y 31676	Length:							20.2
	Width:							14.8
Y 41662	Length:					21.2		
	Width:					14.4		
<i>Palaeohypsodontus zinensis</i>								
Z 241	Length:				12.0			
	Width:				7.2			
Z 2075	Length:		9.6		12.1	13.8		
	Width:		--		--	--		

Table 2. Length and Widths of Upper Teeth.

		P3 (mm)	P4 (mm)	dP4 (mm)	M1 (mm)	M2 (mm)	M3 (mm)	Indet. M (mm)
<i>Walangania africanus</i>								
BUMP 23	Length:						10.0	
	Width:						12.0	
BUMP 274	Length:	9.0		9.1	10.9	11.2	11.5	
	Width:	7.8		9.8	11.5	12.1	11.9	
BUMP 390	Length:				10.1			
	Width:				12.1			
<i>Bugtimeryx pilgrimi</i>								
Z 2027	Length:				9.7			
	Width:				10.0			
Z 2028	Length:					10.3		
	Width:					--		
Z 2029	Length:							9.7
	Width:							11.6
<i>Progiraffa exigua</i>								
H 664	Length:						26.7	
	Width:						29.1	
H 312	Length:	18.5		10.8	22.3	24.0	24.3	
	Width:	15.1		17.5	21.7	25.9	23.7	

Lophiomerycidae Janis, 1987
Genus and Species Indeterminate

Material

Locality Z 108: Z 760, fragment of a left P3; Z 761, fragment of a very worn upper right molar; Z 2277,

fragment of a right p3; Z 2278, left mandible with m1-m2; Z 2299, right astragalus.

Locality and Age

Known from only one Zinda Pir site, Locality Z 108 in the lower part of the Chitarwata Formation. Late

Table 3. Length and Width of astragalus.

	Medial Length (cm)	Distal Width (cm)
Lophiomerycidae, gen. et sp. indet.		
Z 2299	1.90	0.91
<i>Bugtimeryx pilgrimi</i>		
Z 228	2.95	1.61
Z 2021	2.41	1.37
Z 2034	2.56	1.41
<i>Progiraffa exigua</i>		
DGK 23	5.17	3.18
DGK 188	4.91	2.88
Z 2276	4.92	2.83
Y 40808		2.90

Oligocene and approximately 25 Ma (Lindsay et al. this issue).

Description

The mandible, Z 2278 (Figure 2.1-2.4) is the only identifiable specimen. It has the broken posterior root of dp4, intact crown of m1, and anterior half of a newly erupted m2. Identification of the position of the teeth is based on the shape of the jaw margin posterior to the m2.

The lower molars are brachyodont, with smooth enamel, distinctly selenodont protoconid and hypoconid, and a cuspidate metaconid. On the m2 the unworn protoconid is much taller than the metaconid, but the slightly worn hypoconid of the m1 appears to have originally been about the same height as the entoconid. The trigonid is distinctly narrower than the talonid (trigonid: talonid = 0.89), giving the molars a slightly trapezoidal aspect in occlusal view. The anterior face of the metaconid is

rounded and lacks any hint of a premetacristid. The antero-lingual face of the protoconid is also rounded, with the preprotocristid sharply differentiated. After first descending at a steep angle, the preprotocristid turns abruptly lingually and extends around the anterior of the tooth as a low crest (“paralophid”), reaching the lingual margin and having a barely discernable twinned cusplule at its anterior. The large anterior fossette has a broad lingual opening. The entoconid is slightly anterior to the hypoconid, and its posterior face is rounded, without a postentocristid. The antero-lingual face of the entoconid is flat, without an entoconid groove (“*Zhailimeryx*-fold”). The hypoconid has a broad and shallow vertical groove on its posterior face. The posthypocristid extends to the lingual margin of the tooth, leaving a narrow opening to the posterior fosset, but without forming a distal tubercle (variously interpreted in closely related forms as an entostylid or hypoconulid).

There is a distinct “M” shaped structure (“*Dorcatherium*-fold” in the broad sense) on the posterior of the trigonid of both the m1 and m2 (Figure 2.4). The metaconid leg of the “M” (“*Dorcatherium*-fold” in the sense of Janis 1987) is formed from a deep cleft with the resulting lingual fold reflected labially to form a thickened pillar-like structure. The cleft starts at the unworn tip of the metaconid and closes before reaching the base of the cusp. The labial leg on the protoconid (the “*Tragulid*-fold”) is formed from an equally deep groove with a reflected and thickened labial margin forming a ridge connecting to the prehypocristid. The longer postprotocristid and shorter postmetacristid (the two cross connections of the “M”) are subhorizontal, coming together at a very shallow angle and joining ventrally with a vertical crest that con-

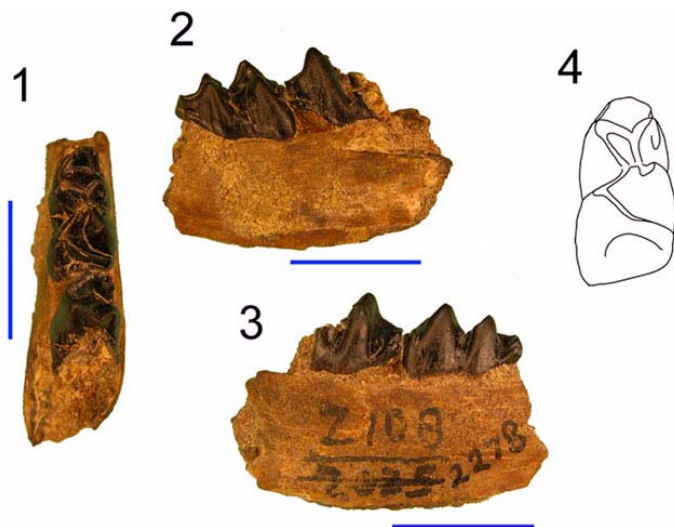


Figure 2. Mandible of indeterminate lophiomerycid (Z 2278): 1) occlusal view; 2) lateral view; 3) medial view; 4) diagrammatic sketch of m1, oblique view from rear. Scale bar = 1 cm.

nects with the preentocristid. The postprotocristid, postmetacristid, and vertical crest together form a “Y” shaped structure on the posterior of the trigonid, with the vertical stem being as long as the diverging arms. At the base of this structure where it contacts the preentocristid there is a very small vertical fold in the entoflexid and another on the labial side making a connection to the “*Tragulus*-fold”-prehypocristid complex. Finally, there is a strong anterior basal cingulum that arises at the base of the preprotocristid and then passes around the front of the tooth to form a lingual tubercle, a very strong and high posterior basal cingulum that extends labially, and a low bulbous “ectostylid” that is probably a vestige of a labial cingulum.

The upper molar (Z 761) is very worn and possibly is an m1. It preserves a faint lingual cingulum, extending around the protocone. The two premolars are fragments of the anterior of a P3 (Z 760) and posterior of a p3 (Z 2277). The three specimens preserve little by way of distinctive morphology and are assigned to this taxon on the basis of size.

Comparisons

This taxon differs from both extant and extinct tragulids (including *Dorcabune* Pilgrim 1910) in the development of the preprotocristid and absence of the premetacristid, as well as in the length of the common stem of the postmeta- and postprotocristid complex and the closing of the “*Dorcatherium*-fold” before it reaches the base of the metaconid.

Archaeotragulus krabiensis Métais, Chaimanee, Jaeger, and Ducrocq 2001, was described as a tragulid, but shares some similarities with the Zinda Pir mandible not otherwise seen in tragulids. These principally involve the formation of the trigonid, in that the preprotocristid of *Archaeotragulus krabiensis* is developed as a substantial antero-lingually directed loph that, in combination with the absence of a premetacristid, leaves the trigonid open lingually. In addition, the postprotocristid and postmetacristid join at a shallow angle to form a short vertical stem that passes down the rear of the trigonid to connect to the preentocristid. There are, however, differences that in our opinion preclude assigning the Zinda Pir specimen to *Archaeotragulus*. By comparison to the Zinda Pir mandible, the lingual cusps of *Archaeotragulus krabiensis* are more bulbous, and the unworn trigonid cusps are more equal in height; the preprotocristid is more lingually directed, and the anterior fossa is less open; the “*Dorcatherium*-fold” extends to the base of the metaconid and the postprotocristid and postmetacristid join at a more acute, steeper angle with

a shorter vertical stem; and there is no sign of a “*Zhailimeryx*-fold” on the entoconid nor a distal swelling on the posthypoconid.

The absence of the postentocristid and premetacristid (producing a “figure-8” morphology), together with strong anterior and posterior cingula and a wide, lingually open anterior fossette are characters of taxa placed in the Lophiomerycidae by Janis (1987) and others (Guo et al. 2000; Métais et al. 2001). To this character list we would add 1) the “Y” shaped configuration of the postprotocristid and postmetacristid, with a long common stem connecting to the preentocristid; 2) the relative heights of the protoconid and metaconid and the relative lengths of the postprotocristid and postmetacristid; and 3) the distinctive form of the “*Dorcatherium*-fold,” which is confined to the tip of the metaconid cusp and does not extend to its base. The presence of these characters in the lower molars of the Zinda Pir form indicate it is a lophiomerycid.

Of currently recognized lophiomerycids, *Zhailimeryx* Guo, Dawson, and Beard 2000 and *Krabimeryx* Métais, Chaimanee, Jaeger, and Ducrocq 2001 are similar to the Zinda Pir specimen in possession of the typical lophiomerycid features, but differ in many details. Most notably, differences include the presence of a well defined “*Zhailimeryx*-fold” on the anterior face of the entoconid, the apparent absence of a well defined “*Tragulus*-fold” connected to the prehypocristid, and the weakness or absence of a bulbous ectostylid. In addition, in neither of these two taxa does the preprotocristid extend as far lingually as in the Zinda Pir tooth, although in *Zhailimeryx* there is an anterior cusp described by Guo et al. (2000) as a “rudimentary paraconid” that might correspond to the “twinned cuspule” observed on Z 2278.

Both *Lophiomeryx* Pomel 1853 and *Iberomeryx* Gabunia 1964 (including *Cryptomeryx* Schlosser, 1886) share the characteristic lophiomerycid trigonid features, and both lack the “*Zhailimeryx*-fold” on the entoconid, a similarity shared with Z 2278. Nevertheless, *Iberomeryx* and especially *Lophiomeryx* differ substantially from the Zinda Pir specimen. European and perhaps Asian species of *Lophiomeryx* are more hypsodont and lack any vestiges of a “*Tragulus*-fold” or of basal tubercles on the labial side of the tooth, while having a more open posterior fossette, a distinct cuspule terminating the posthypocristid, and an incomplete postentocristid that extends from the unworn tip of the entoconid partway down the cusp, leaving the entoconid base rounded. In addition, in *Lophiomeryx* the antero-lingually directed prehypocristid joins the preentocristid-postmetac-

ristid complex, rather than being more medially terminated.

Species of *Iberomeryx* have bulbous basal tubercles on the labial side of the tooth (interpreted as ectosylids, but possibly a labial cingulum remnant), a weak “*Tragulus*-fold” variably developed on anterior molars, and, also variably, the prehypocristid connected directly to the trigonid rather than to the preentocristid-postmetacristid complex (Nanda and Sahni 1990; Métais et al. 2001). These are similarities shared with the Zinda Pir mandible and suggest *Iberomeryx* is the mostly closely related of known taxa. The Zinda Pir specimen, however, differs from the better-known species of *Iberomeryx* such as *I. minus* and *I. parvus* in the strength of the “*Tragulus*-fold,” which on both its m1 and m2 is very well formed with a thickened labial margin contacting the anterior end of the prehypocristid. The Zinda Pir mandible also has the terminal end of the prehypocristid more lingually directed, and there is no trace of a cuspule on the lingual termination of the posthypocristid.

The enigmatic *Iberomeryx savagei* Nanda and Sahni 1990 is known from a few specimens of Late Oligocene age from the Kargil Formation of northern India. While too small to be the same species, it appears to also have had a well-formed “*Tragulus*-fold” contacting the prehypocristid and a lingually extended preprotocristid.

Discussion

The Tragulina are regarded by most current workers as a paraphyletic assemblage, and the lophiomerycids may also be paraphyletic, with some genera having closer relationships to the Tragulidae (Métais et al. 2001). As currently recognized, the family contains Middle Eocene to Late Oligocene species.

Métais et al. (2001) suggested the Kargil species represented a new genus, and it is likely the Zinda Pir specimens are a closely related species. Forster-Cooper (1915) based *Gelocus indicus* from Dera Bugti on a single upper molar. His specimen, which is taken to be a third molar, has a strong lingual cingulum and very small metaconule. It is of appropriate size for an upper molar matching Z 2278 and might be the same species.

The “M” structure (or “*Tragulus*-fold”) is thought to be a uniquely derived character of tragulids (Métais et al. 2001) or tragulids and leptomerycids (Geraads et al. 1987). The clear presence of the structure in combination with a lingually extended preprotocristid and absence of a premetacristid suggests it may be a primitive feature shared by both early tragulids and lophiomerycids.

Infraorder Pecora
Superfamily *Incertae sedis*
Family Gelocidae Schlosser 1886
Genus *Gelocus* Aymard 1855

Characters of lower dentition

Fourth lower premolar slender, with small metaconid. Lower molars with cusps brachyodont; bunoselenodont protoconid and hypoconid; metaconid and entoconid conical and slightly compressed laterally; rudiment of paraconid present. Metaconid and entoconid crowded. Metastylid absent; trace of “*Dorcatherium*-fold” present. Prehypocristid joins posterior of protoconid, postmetacristid joins postprotocristid and preentocristid at center of tooth. (Modified from Viret 1961)

?*Gelocus gajensis* Pilgrim 1912

Diagnosis

Small pecoran (m2-m3 length: ~ 3.4 cm). Enamel rugose. Without remnant of paraconid, but with pre- and postcristids of metaconid and entoconid very strongly differentiated. Faint fissure on metaconid with a raised lingual edge (cf. “*Dorcatherium*-fold”) and an antero-lingual groove on the entoconid.

Material

Locality Z 108: Z 271, anterior half of a barely worn m3; Z 2298 very worn right m3.

Locality and Age

Known from only Locality Z 108 in the lower part of the Chitarwata Formation. Late Oligocene and approximately 25 Ma (Lindsay et al. this issue).

Description

Specimen Z 271 (Figure 3.1-3.3) is a lightly worn molar with the trigonid and anterior parts of the talonid cusps intact. Specimen Z 2298 (Figure 3.4) is a very worn, but otherwise intact m3. The following description is based on both teeth.

The molars are brachyodont, with rugose enamel, bunoselenodont protoconid and hypoconid, and cuspidate metaconid and entoconid. In an unworn condition the metaconid was probably slightly taller than the protoconid. On the very worn specimen Z 2298 the trigonid is slightly narrower than the talonid. The metaconid and entoconid are both transversely narrow, with convex labial and lingual faces and long axes parallel to the long axis of the tooth. The anterolingual face of the protoconid is convex as in tragulids, not concave as in pecorans. There is no trace of a metastylid.

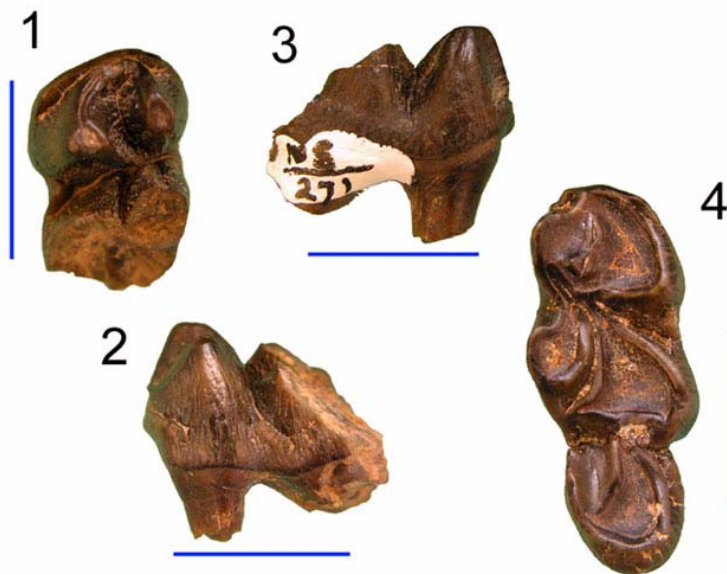


Figure 3. Lower molars of *?Gelocus gajensis*: 1) Z 271, occlusal view; 2) Z 271, lateral view; 3) Z 271, medial view; 4) Z 2298, occlusal view. Scale bar = 1 cm.

A short, distinct premetacristid contacts the short preprotocristid just above the low anterior cingulum, leaving a forward-facing anterior fossette that was probably open until an advanced wear stage. The postmetacristid is a swollen crest, bounded on the lingual side by a fine and indistinct crease. Towards the apex of the metaconid the crease becomes a faint fissure with its lingual edge raised as a barely differentiated crest. This is presumably the vestige of a “*Dorcatherium*-fold.” Similarly, on the posterior of the protoconid, there is a scarcely discernable raised area that could be a vestige of a “*Tragulus*-fold.” The postmetacristid is nearly vertical and the same length as the steeply descending postprotocristid. The two crests join to form a deep “V” that contacts the preentocristid without forming a common stem as in lophiomerycids.

The entoconid is anterior to the hypoconid and crowded against the rear of the metaconid. A very prominent preentocristid passes down its front, slightly labial to the midline of the cusp. This preentocristid is very sharply set off from the antero-lingual surface of the entoconid, producing a suggestion of an entoconid groove. A parallel lingual fold (“*Zhailimeryx*-fold”), however, is not preserved and, if it ever existed, it could not have extended to the base of the entoconid. The prehypocristid is directed anteriorly towards the posterior of the trigonid and does not contact the postmetacristid-preentocristid complex. The posthypocristid extends to the lingual margin of the tooth and the postentocristid is absent, leaving the posterior fossette narrowly open. Only Z 2298 preserves the posterior part of m3. It comprises a very large crescent-shaped hypoconulid, the antero-labial end of

which contacts the posthypocristid at the midline of the tooth. There is a short, low crest that extends anteriorly from the hypoconulid along the lingual edge of the tooth, but fails to reach the posterior of the entoconid, leaving the lingual wall incomplete. A modest anterior basal cingulum arises at the base of the preprotocristid and passes around the front of the tooth to the lingual side. Finally, there is a low ectostylid that is possibly formed from a labial cingulum and a weak antero-labial cingulum on the hypoconulid.

Comparisons

The size and general morphology of the two Zinda Pir molars suggest reference to Pilgrim’s *?Gelocus gajensis*, while its larger size precludes reference to “*Gelocus*” *indicus* Forster-Cooper 1915. Absence of a metastylid precludes reference to a number of small Oligocene pecorans, including *Prodremotherium* Filho, 1877, *Notomeryx* Qiu 1978, and *Gobiomeryx* Trofimov 1957. The absence of a well-formed “*Dorcatherium*-fold” precludes not only tragulids, but also *Bachitherium* Filhol 1882. Absence of a well-defined and deep “*Zhailimeryx*-fold” and a strong paracristid, together with more conical lingual cusps preclude reference to *Indomeryx* Pilgrim 1928 (Métais et al. 2000; Tsubamoto et al. 2003).

Discussion

Pilgrim (1912) based his species on a single specimen, which he very briefly described and questionably referred to *Gelocus*. The type specimen came from deposits near Dera Bugti, at the “base of the Gaj” (Pilgrim 1912, caption to plate XXV). In his use of the “Gaj Formation,” Pilgrim

was referring to what is now called the Chitarwata Formation (Downing et al. 1993). It seems likely that Pilgrim's specimen came from the lowest fossiliferous levels at Dera Bugti and is approximately contemporaneous with the material from Locality Z 108. If so, this material could be as old as Early Oligocene (Welcomme et al. 2001), although we prefer a Late Oligocene age for the site.

The presence of a strong premetacristid on the ?*Gelocus gajensis* type and the Zinda Pir fossils would seem to preclude reference to *Gelocus* (Janis 1987). However, we follow Pilgrim in tentatively making that reference because of the absence of a metastylid combined with relatively conical lingual cusps and faint trace of a "*Dorcatheirium*-fold." It seems likely to us that the Bugti and Zinda Pir species represents an undescribed genus, but because of the fragmentary state of our material we do not think it is advisable to base a new taxon on it.

Superfamily ?Cervoidea Goldfuss 1820
Family *Incertae sedis*

Genus *Walangania* Whitworth 1958

Diagnosis

Small pecoran (m2-m3 length: ~ 2.8 cm). Frontal appendages unknown, likely absent. Enamel of cheek teeth finely rugose. The p1 possibly present, p3 and p4 with strong labial incision, oblique entoconid, and transverse entostylid on p4. Metaconid of p4 variable, with slight development of posterior flange; anterior crest weakly or not bifurcated. Lower molars brachyodont and selenodont. Metaconid and entoconid slightly oblique, compressed, with small metastylid situated lingual to the posterior end of postmetacristid. "*Palaeomeryx*-fold" variably present. P3 with weakly concave lingual wall anterior to the protocone. Upper molars brachyodont, large metaconules on M1 and M2. Paracone with strong labial rib, metacone rib feeble or absent. Strong parastyle, metastyle not distinct. Subsidiary crests present in the anterior fossette and separate from posteriorly directed postprotocrista. Limbs of advanced pecoran type. (Modified from Whitworth 1958).

Walangania africanus (Whitworth 1958)

Diagnosis

As for the genus.

New Material

Napak I: BUMP 390, heavily worn right upper M1 or M2; BUMP 391, left DP3; BUMP 396, astragalus; BUMP 584, left mandible fragment with m2.

Napak IV: BUMP 23, worn left M3(?).

Napak IX: BUMP 721, right mandible fragment with p4-m2; BUMP 722, right mandible fragment with p3-m1.

Napak CC: BUMP 103, left proximal radius and distal humerus; BUMP 105, right proximal radius; BUMP 274, right maxilla with erupting P3, P4 in crypt, and DP4-M3; BUMP 450, left mandible fragment with alveoli for p1 and p2, and crown of p3; BUMP 800, incomplete m1 or m2.

Moroto II: BUMP 178, left proximal metatarsal; BUMP 552, incomplete left m3.

Localities and Age

The type of *Walangania africanus* is from Songhor in western Kenya, and the species is widely distributed throughout the Early Miocene sites of East Africa, with an age range of approximately 17.8 Ma to 21 Ma. Radiometric dating has shown that the Moroto fossil localities are older than 20.6 Ma (Gebo et al. 1997), while the Napak localities are thought to be approximately 19 Ma using radiometric dating and faunal correlations with other sites in East Africa (Bishop et al. 1969; Drake et al. 1988; Pickford 1981).

Description

Whitworth's (1958) initial description and subsequent discussions (Janis and Scott 1987; Pickford 2002) provide a useful account of the morphology of this taxon and the range of variation encompassed within it. Here we describe additional dental material that clarifies some points.

Lower Dentition. Whitworth (1958, p. 20) noted variation in the premolars, which is also seen in the material discussed here. BUMP 450 (Figure 4.1) preserves the alveolus of the posterior root of a more anterior tooth, which in this specimen is not separated by a diastema from the anterior root of p2. The crown of p3 of BUMP 450 has a weak labial incision and a minute cusplet on a posterolingually directed crest that is suggestive of a metaconid. The equivalent crest on the p3 of BUMP 722 (Figure 4.2) is barely discernable, with no hint of the cusplet. The p4 of this latter specimen has a strong labial incision, compressed heel, and an oblique entoconid and large transverse entostylid that together form a basin with a narrow lingual opening. The metaconid is indistinct and the anterior crest (or parastylid) is relatively long and sim-

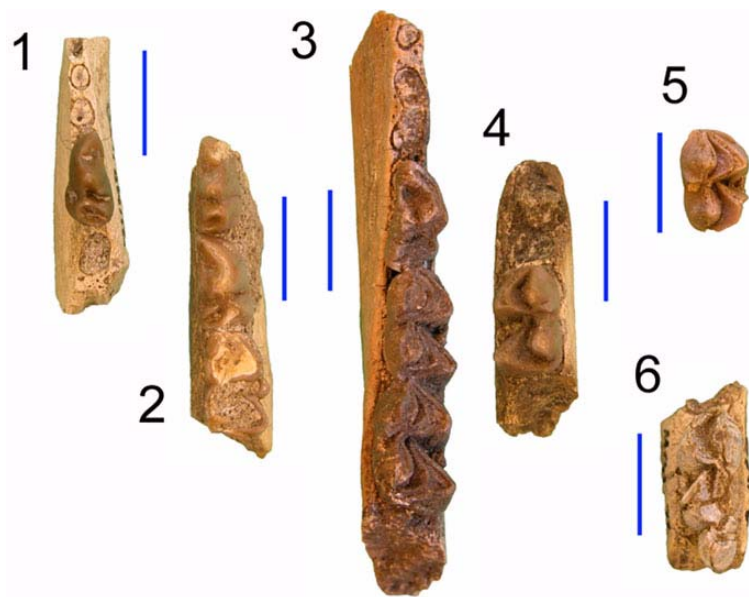


Figure 4. Lower dentitions of *Walangania africanus*: 1) BUMP 450, occlusal view; 2) BUMP 722, occlusal view; 3) BUMP 721, occlusal view; 4) BUMP 584, occlusal view; 5) BUMP 800, occlusal view; 6) BUMP 552, occlusal view. Scale bar = 1 cm.

ple, with no development of a paraconid. The p4 of BUMP 721 (Figure 4.3) conforms closely to that of Whitworth's type from Songhor. It has a marked labial incision and a distinct metaconid that is much lower than the protoconid. There is a low lingual extension of the metaconid that runs forward to connect with the anterior portion of the anterior crest. However, the anterior crest is simple with no suggestion of the bifurcation into a paraconid and parastylid seen in the type. Both BUMP 722 and 721 have a very slight posterior flange on the p4 metaconid.

The lower molars (Figure 4.4-4.6) are brachyodont, with a faint "*Palaeomeryx*-fold" on the unworn or lightly worn teeth (Figure 4.5). On the anterior molars the metastylid is well separated from the metaconid and situated lingual to the posterior end of the postmetacristid. The unworn, but damaged m3 from Moroto II (BUMP 552) (Figure 4.6) appears to have had only a minute metastylid and a large entoconulid.

Upper Dentition. The most significant new specimen is BUMP 274 (Figure 5.1), a well-preserved maxilla with undamaged crowns of P3, DP4, and all the molars. An unerupted P4 is also present, but only the labial face of the tooth is exposed. P3 has a tall, anteriorly situated paracone with a strong labial rib. The posterior crest of the paracone is an elongate blade and a large parastyle is separated from the paracone by a deep vertical groove. The protocone is situated slightly anterior to the center of the tooth and connected to the parastyle and metastyle by low crests. The lingual crest is weakly concave in front of the protocone. Posterior to the protocone and within the median valley a very low longitudinal spur of enamel is attached to the inner

face of the postprotocrista. This is presumably serially homologous to the P4 structure referred to variously as an "accessory crest" (Hamilton 1973, p. 77) or a "transverse crest" (Gentry 1994, p. 138) and to what Whitworth (1958, p. 22) referred to as "subsidiary crests" on the molars.

The upper molars are low crowned, with large metaconules on M1 and M2 and a reduced metaconule on M3. The parastyles and mesostyles are strong on all the molars. The paracones have very strong labial ribs with deep grooves before them, and the metacones have only faint ribs. On the M1 the postmetconule crista has a distinct bifurcation. There is a suggestion of this structure in a faint swelling of the enamel of M2, but it is lacking on M3. All the molars of BUMP 274 and BUMP 23 (Figure 5.2) have a small and low set of enamel spurs near the junction of the postprotocrista and premetaconule crista. The form varies among the teeth, but in general the spurs have a "Y" shape and presumably correspond to the subsidiary crests noted by Whitworth (1958, p. 22). The spurs wear to form a small enamel island. All three molars of BUMP 274 have minute entostyles but not the protocone cingulum described below for *Bugtimeryx pilgrimi*. In BUMP 23 the entostyle is larger and more pillar-like. In all specimens the entostyle is attached to the anterior base of the metaconule and is possibly a remnant of a lingual cingulum.

Comparisons

Walangania has been shown to differ from the contemporary African *Propalaeoryx* Stromer 1926 and "*Gelocu*" *whitworthi* Hamilton 1973. However, it has not been discussed in the context of Late Oli-

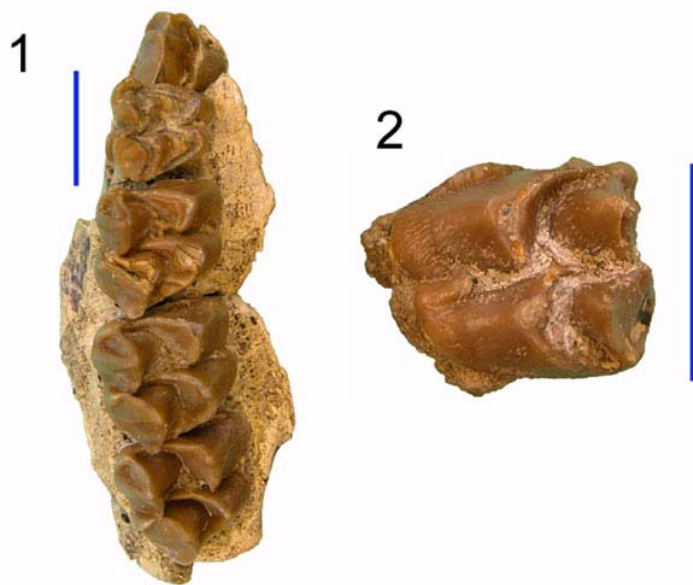


Figure 5. Upper dentitions of *Walangania africanus*: 1) BUMP 274, occlusal view; 2) BUMP 23, occlusal view. Scale bar = 1 cm.

gocene/Early Miocene pecoran ruminants, other than for general reviews such as Janis and Scott (1987) and Gentry (1994). Both noted its close similarity to primitive Early Miocene cervoids from Europe and have suggested its affinities lie with Miocene cervoids. We do not attempt a more detailed comparison to European forms here because we have not reviewed the very extensive East African collections. Comparison to *Bugtimeryx*, based primarily on the new Napak and Moroto specimens as well as published material, follows description of additional material of *Bugtimeryx* in the next section.

Discussion

Whitworth (1958) published descriptions of Early Miocene ruminants from East Africa, naming the species *Walangania gracilis* and *Palaeomeryx africanus*. Ginsburg and Heintz (1966) later suggested that *P. africanus* should be removed from *Palaeomeryx* and placed it in a new genus *Kenyameryx*. Hamilton (1973) reviewed the material and, concluding that the *Walangania gracilis* and *Kenyameryx africanus* material represented the same taxon, combined them under the name *Walangania africanus*. Most researchers agree that both forms belong in *Walangania*, but the question of whether to maintain a specific distinction between *W. gracilis* and *W. africanus* is open. *Walangania* is one of the earliest ruminants in Africa, but its phylogenetic relationships remain controversial. While it traditionally has been viewed as a potential ancestor to the Bovidae, Janis and Scott (1987) and Gentry (1994) have presented evidence for a closer relationship to the Cervoidae.

The presence or absence of p1 in *Walangania* has been debated (Hamilton 1973; Janis and Scott 1987; Gentry 1994). If BUMP 450 is correctly referred to this species, then either p1 or dp1 was present. Similarly a bifurcated postmetconule crista has previously been considered absent from *Walangania* (Janis and Scott 1987, p. 31), suggesting that the Napak maxilla BUMP 274 has been misidentified. Its small size, concave antero-lingual P3 crest, posteriorly directed postprotocrista, and minute entostyles preclude reference of the Napak maxilla to *Propalaeoryx austroafricanus*, but since the upper dentition of the East African species *P. nyanzae* is hardly known, it is possible that BUMP 274 represents it. This seems unlikely, however, given the difference in size.

Genus *Bugtimeryx* Ginsburg, Morales, Soria, 2001

Diagnosis

Small pecoran (m2-m3 length: ~ 2.5 to 3.4 cm depending on species). Frontal appendages unknown. Molars brachyodont with finely rugose enamel. Anterior crest of p4 bifurcated with paracoid and parastylid turned lingually, strong labial incision, oblique entoconid, and transverse entostylid. Metaconid of p4 tall, rounded posteriorly. Lower molars with protoconid and hypoconid slightly oblique and compressed. Posterior median valley open until late in wear, diminutive metastylid situated lingual to the posterior end of the postmetacrista, “*Palaeomeryx*-fold” very faint. Upper molars with large metaconules. Paracone with strong labial rib, metacone with weak rib. Parastyle large, metastyle distinct. Subsidiary crests present in the anterior fossette and separate from labially

directed postprotocrista and premetaconule crista. Postmetaconule crista with bifurcation. Minute entostyle and low lingual cingulum on posterior of protocone. Limbs of advanced pecoran type.

Bugtimeryx pilgrimi Ginsburg, Morales, Soria, 2001

Diagnosis

Smallest species of *Bugtimeryx* (m2-m3 length: ~ 2.5 to 3.0 cm); “*Palaeomeryx*-fold” moderate, stronger on m2 than on m3 (modified from Ginsburg et al. 2001).

New Material

Locality Z 127: Z 269, left mandible with dp4-m1; Z 270, right mandible with m3; Z 2021, complete right astragalus; Z 2022, distal right metacarpal; Z 2023, right distal tibia; Z 2024, right mandible fragment with m2 and anterior of erupting m3; Z 2026, right mandible fragment with m1 and erupting m2; Z 2027, right maxilla fragment with DP4, M1, and erupting M2; Z 2028, left maxilla fragment with M1, M2, and a fragment of M3 in crypt; Z 2029, left maxilla fragment with indeterminate molar; Z 2030, left mandible with m1; Z 2032, right mandible with anterior of m3; Z 2034, right slightly damaged astragalus; Z 2035, left damaged astragalus; Z 2038, right complete magnum-trapezoid; Z 2084, right complete scaphoid; Z 2086, incomplete distal phalanx; Z 2087, incomplete epiphysis of a proximal phalanx.

Locality Z 129: Z 228, right astragalus.

Locality Z 133: Z 175, incomplete and very battered left calcaneum.

Locality Z 151: Z 2057, distal metapodial (probably a metacarpal); Z 2068, right mandible with p4 and anterior of m1.

Locality Z 155: Z 2081, damaged left astragalus.

There are at least four and perhaps as many as five different individuals represented among the dental remains from Locality Z 127. Only two are fully adult, with erupted and worn m3s. The three astragali appear to come from three different but fully grown individuals, suggesting that at least three adults and either three or four juveniles are represented.

Localities and Age

Localities Z 127, Z 151, and Z 155 are all in the upper part of the Chitarwata Formation, with estimated ages of 24 to 23 Ma (Lindsay et al. this issue).

Description

Lower Dentition. The p4 appears to have been about the same length as the m1, although in the only specimen with both teeth preserved (Z 2068) (Figure 6.1-6.2) the m1 is broken at the rear, making its length unmeasurable. The worn and fractured p4 of Z 2068 has a strong labial incision separating a large, centrally situated protoconid from a compressed heel. The laterally directed metaconid is as tall as the protoconid and terminates in a large distinct cusp with an anteroposteriorly elongated oval wear figure and rounded posterior. The short anterior crest curves sharply lingually and has a bifurcated end with both the paraconid and parastylid being directed lingually. The entoconid is set at an oblique angle to the long axis of the tooth, while the large entostylid is transverse. The basin between these two cusps is closed lingually.

The lower molars are brachyodont (Figure 6.3-6.7), with fine vertical striations in the enamel. The metaconid and entoconid are situated slightly oblique to the long axis of the tooth and, while flattened labially, retain a more convex lingual face. The protoconid and hypoconid are distinctly selenodont. The premetacristid contacts the anterolabial end of the preprotocristid, but posteriorly the median valley is narrowly open until late in wear. With slight wear the postmetacristid connects with the postprotocristid, and these subsequently connect with the preentocristid. The prehypocristid, however, remains separate even after considerable wear (Z 270, Z 2032). The lightly worn teeth (Z 269, Z 2024, Z 2030) have very faint vestiges of a “*Palaeomeryx*-fold,” whereas the more worn teeth appear to lack them. Where preserved, the metastylid is distinct but very small. It is closely appressed to the metaconid and situated just lingual to the descending trace of the postmetacristid. The m3's have a small entostylid. All the molars have strong, low ectostylids and anterior and posterior basal cingula.

Only Z 270 preserves the posterior part of m3. It comprises a large crescent-shaped hypoconulid the antero-labial end of which contacts the postero-lingual end of the posthypocristid. There is a small, separate entoconulid (seen also on the broken m3 of Z 2032) with a posterior extension that together with the entostylid fills the gap between the postentocristid and lingual end of the hypoconulid crescent, making the lingual wall complete.

The broken dp4 of Z 269 is molariform in appearance.

Upper Dentition. The three maxillary fragments (Figure 7.1-7.3) are poorly preserved, with much of

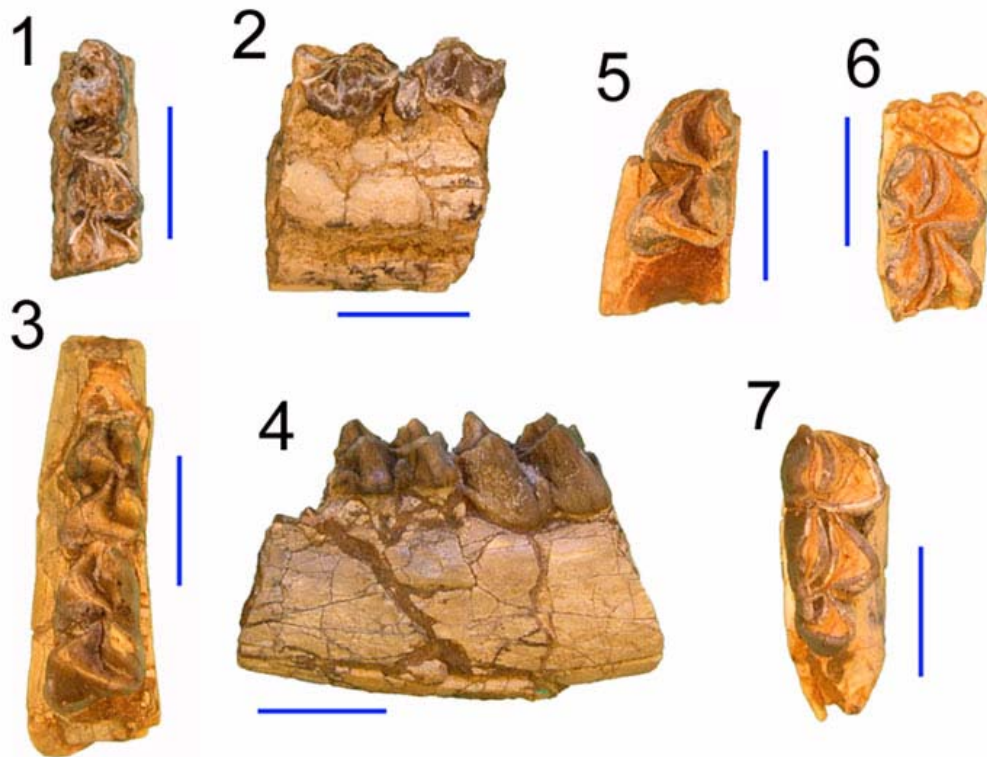


Figure 6. Lower dentitions of *Bugtimeryx pilgrimi*: 1) Z 2068, occlusal view; 2) Z 2068, lateral view; 3) Z 269, occlusal view; 4) Z 269, lateral view; 5) Z 2030, occlusal view; 6) Z 2032, occlusal view; 7) Z 270, occlusal view. Scale bar = 1 cm.

the enamel spalled from the crowns of the teeth, especially labially. One maxilla (Z 2027) has what we interpret as DP4, M1, and an erupting M2; a second (Z 2028) has the M1 and M2 preserved with a very small piece of the M3 in crypt; while the third (Z 2029) has a worn indeterminate molar or dP4. The teeth are all low crowned with large metaconules that produce a quadrate outline in occlusal view. Where preserved, the parastyle and mesostyle are strong and the paracone has a strong labial rib with a deep groove just before it. The metacone has a much weaker rib. The postprotocrista is directed labially, as is the much longer premetaconule crista. At the apex of the metaconule, the postmetaconule crista is posteriorly directed, but the crista then turns sharply and runs labially to reach a much reduced metastyle. On the indeterminate molar of Z 2029 and the M2 of Z 2027, the postmetaconule crista has a distinct bifurcation, giving rise to a large internal enamel spur. There is in addition a small structure filling the space between the lingual face of the paracone and the junction of the postprotocrista and premetaconule crista. In the unworn condition (M2 of Z 2028) the structure is a low cross of enamel that connects the anterior face of the taller premetaconule crista to the paracone and is clearly

separate from the terminal end of the labially directed postprotocrista. In the worn condition (M1 of Z 2028 and Z 2029) it merges with the wear traces of the postprotocrista and premetaconule crista to form one or more small enamel fossettes, giving a bifurcated appearance to the postprotocrista. Although heavily damaged in this area, all the



Figure 7. Upper dentitions of *Bugtimeryx pilgrimi*: 1) Z 2027, occlusal view; 2) Z 2028, occlusal view; 3) Z 2029, occlusal view. Scale bar = 1 cm.

preserved molars have this structure. Finally there appears to be a minute entostyle on the M2 of Z 2027 and, more clearly, a low cingulum that originates between the protocone and metacone and runs along the posterior face of the protocone.

The wear and pattern of tooth eruption of the maxillas indicate they represent the remains of three different individuals.

Postcranial Remains. Tibia: Z 2023 is a poorly preserved distal portion of a tibia, in which fusion of the epiphysis to the diaphysis is incomplete. The articulation for the fibular malleolus is divided into a larger posterior portion separated from a smaller anterior one by a well-defined sulcus for the fibular spine of the malleolus. Both articular surfaces are damaged, but the posterior one is clearly concave.

Astragalus: The best preserved astragali are Z 228 and Z 2021, while the others are to varying degrees damaged. As noted by Ginsburg et al. (2001) the astragalus of *Dorcabune* is parallel sided as are those of advanced pecorans, making identification of either difficult. In contrast to *Dorcabune*, the distolateral calcaneal facet is confined to the distal edge of the astragalus, and separated from the raised lateral rim of the sustentacular facet by a roughened sulcus, while the proximal lateral calcaneal facet is confined to the edge of the sustentacular facet and does not extend dorsally. The cuboid condyle extends laterally, creating a distinct notch on the lateral side of the astragalus similar to what is seen in tragulids. The condyle, however, is cylindrical rather than conical as in small species of *Dorcabune*. The astragalus is narrow, with an approximate width to length ratio of 1:1.8.

Scaphoid: Although the color is slightly different, it is possible that Z 2084 came from the same individual as the magnum-trapezoid Z 2038. The specimen is slender when viewed from a proximal aspect and proximally-distally short for the dorsal-ventral diameter.

Magnum-trapezoid: Z 2038 is well preserved with a rectangular outline, a tall proximal keel, and a narrow lunar facet that does not expand laterally. The inferior posterior unciform facet is widely separated from the anterior unciform facet.

Metacarpals: Z 2022 is well preserved, while Z 2057 is somewhat broken and crushed, with matrix obscuring some features. In both specimens the third and fourth metacarpals are fused, with the medullary cavities separate at the level of the nutrient foramen. On the distal articular surfaces the keels extend dorsally, but are not as well developed there as they are ventrally. Consequently, in lateral view the keels are strongly asymmetrical.

On each metacarpal the tubercle for the collateral ligament has a lipped rim ventrally, but the lip does not extend dorsally. As a result the dorsal external articular surface of the condyle is incomplete. In contrast, the internal articular surface extends dorsally, terminating in a small pit at the end of the shaft.

Comparisons

Ginsburg et al. (2001) placed *Bugtimeryx* in the Giraffidae without comment. However, both the type and our material shows the taxon to have a faint "*Palaeomeryx*-fold." We have, therefore, tentatively placed it in the Cervioidea.

While the low-crowned molars of *Bugtimeryx* can easily be distinguished from even the earliest bovids, the p4 described here is surprisingly bovid-like. Similarities include the short, compressed heel set off from the protoconid by a strong labial incision, the short, sharply turned anterior crest, and the height and distinctiveness of the metaconid. However, in early bovids (as documented by material from the Kamlial Formation of northern Pakistan) the p4 paraconid is smaller, the metaconid is separated from the protoconid by a narrow isthmus of enamel, and the entoconid is more nearly transverse. Postcranially there are also similarities and differences. Bovid s have a less distinctive notch above the distolateral calcaneal facet of the astragalus, their scaphoid tends to be wider and deeper relative to the dorsal-ventral dimension, and the magnum-trapezoid has a wider articulation for the scaphoid and a lower proximal keel. Finally, while the distal metapodial keels of early bovids are asymmetrical, the external articular surface of the condyle is complete on the dorsal aspect.

Bugtimeryx differs from *Namibiomeryx* Morales, Soria, Pickford 1995 in being much less hypsodont, lacking precocious fusion of the prehypocristid and trigonid complex, having a bifurcated anterior crest on p4, more distinct metastylids, and a crescent-shaped m3 hypoconulid forming a continuous lingual wall.

Ginsburg et al. (2001) recorded similarities between *Bugtimeryx* and *Andegameryx* Ginsburg 1971, but noted that they differed in the presence of a larger metastylid on the lower molars of *Bugtimeryx*. The material described here shows they also differ greatly in p4 morphologies. *Bugtimeryx* can be distinguished from *Walangania* on the basis of the p4, which in *Walangania* is at best only weakly bifurcated anteriorly. *Walangania* also possesses larger, more distinct metastylids and in the upper molars a shorter, more posteriorly directed postprotocrista and a lingual protoconal cingulum. Many of the same characters distinguish *Bugtim-*

eryx from cervoid-like taxa such as “*Gelocus*” *whitworthi* Hamilton 1973, *Bedenomeryx* Jehenne 1988 or *Pomelomeryx* Ginsburg and Morales 1989, which typically also have a stronger “*Palaeomeryx*-fold” (Ginsburg et al. 1994).

Small, primitive giraffoids such as *Propalaeoryx* bear a general resemblance to *Bugtimeryx* but are about 20 to 30% larger. In *Propalaeoryx* the p4 is relatively long, with an oblique entostylid and an elongated metaconid. In addition, its lower molars have more separated and lingual metastylids, while the medial valley is open posteriorly (Janis and Scott 1987; Morales et al. 1999).

Dremotherium Geoffroy Saint-Hilaire 1833 and *Amphitragulus* Pomel 1846 are dentally very similar to *Bugtimeryx*, particularly in the structure of the p4 with a bifurcated anterior crest bent sharply to the lingual side combined with a short heel, oblique entoconid, and large metaconid (Janis and Scott 1987; Ginsburg et al. 1994). *Amphitragulus* has, in addition, an m3 with a strong connection between the posthypocristid and entoconid and a posteriorly extended entoconid. *Amphitragulus* and *Dremotherium*, however, have a well-developed “*Palaeomeryx*-fold” and in the upper molars a more posteriorly directed postprotocrista, salient cingulae on the upper molars, and in the case of *Amphitragulus* a simple postmetaconule crista.

Discussion

Ginsburg et al. (2001) based *Bugtimeryx pilgrimi* on a mandible with m2 and m3, and referred an upper molar (PAK 2490) and several postcranial elements to the species. The cruciate protocone and lingual cingulum of the upper molar suggest to us that the referred upper molar belongs to a species of *Dorcabune*, mostly likely *Dorcabune sindiense* Pilgrim 1915.

As envisaged by Ginsburg et al. (2001) *Bugtimeryx* had three species: 1) the genotype *Bugtimeryx pilgrimi*; 2) *Bugtimeryx beatrix* (Pilgrim 1912), founded on a single mandible with m2-m3 and questionably referred to *Prodremotherium* by Pilgrim (1912); and 3) *Bugtimeryx gajensis* (Pilgrim 1912), also based on a single mandible with m1-m2 and initially questionably referred to *Gelocus* (Pilgrim 1912). The three species were diagnosed by Ginsburg et al. (2001) as being different in size. Only *B. gajensis* has distinctive morphological features. The type and referred material of *B. pilgrimi* came from what are thought to be Early Miocene levels of the Chitarwata Formation at Dera Bugti (Welcomme et al. 2001). Both of Pilgrim’s specimens also came from deposits near Dera Bugti, from what he called the “base of the Gaj” (Pilgrim 1912, caption to plate XXV). In his use of “Gaj,” Pil-

grim was referring to what is now called the Chitarwata Formation (Downing et al. 1993), and it seems likely that Pilgrim’s specimens came from the lowest fossiliferous levels at Dera Bugti. If so, they could be as old as Early Oligocene (Welcomme et al. 2001).

B. pilgrimi and *B. beatrix* differ solely in size. The material described here is intermediate in size between the two, and we strongly suspect the fossils all belong to a single species. However, we have chosen to refer our material to *B. pilgrimi* because of the possible great differences in age between the types of *B. pilgrimi* and *B. beatrix*, and because as a taxon, *B. pilgrimi* is currently better known. “*Bugtimeryx gajensis*” is a significantly larger species, and if material recently collected from the lower unit of the Chitarwata Formation at Zinda Pir and described in the preceding belongs to the same species, then it represents a different genus.

Our concept of *Bugtimeryx* relies greatly on the morphology of the p4 from locality Z 151, and thus our reference of that material to the taxon is critical to many of the conclusions we reach. However, the fossils from locality Z 151 are considerably older stratigraphically than the other Zinda Pir material described here and could belong to a different taxon. If so, then the distinctions we make between *Bugtimeryx* and other taxa are more problematic.

Genus and Species Indeterminate

Material

Locality Z 127: Z 2031, fragment of a right mandible with m1(?); Z 2033, lingual half of a very worn left upper molar.

Locality and Age

Known from only one site, Locality Z 127 in the upper part of the Chitarwata Formation. It is approximately 23 Ma in age (Lindsay et al. this issue).

Description

The mandible (Figure 8.1-8.2) has a single, moderately worn tooth, which because of the dentary’s shape we believe to be an m1. The tooth is brachyodont, with metaconid and entoconid slightly oblique to the long axis of the tooth, flattened labially, and convex lingually. Both protoconid and hypoconid are selenodont. The premetacristid contacts the anterolabial end of the preprotocristid, while the posthypocristid contacts a small entostylid to close the posterolingual end of the median valley. The prehyoconid is isolated, but a small

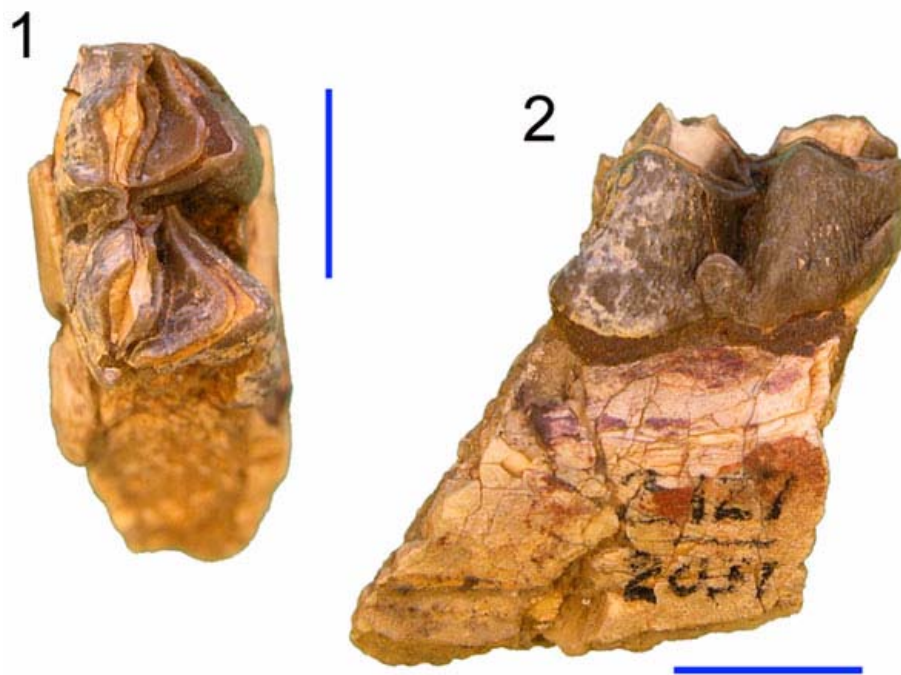


Figure 8. Mandible of an indeterminate large cervoid (Z 2031); 1) occlusal view; 2) lateral view. Scale bar = 1 cm.

secondary spur of the preentocristid contacts its anterior tip. There is a very subdued “*Palaeomeryx*-fold.” The metastylid is small and situated well forward of the descending trace of the premetacristid. The molar has a low ectostylid as well as anterior and posterior basal cingula.

The upper molar is a very heavily worn lingual half of a tooth. It has a minute entostyle on the anterior face of the metaconule and a low cingulum along the posterior face of the protocone.

Comparisons and Discussion

The teeth of this taxon are too small to belong to *Progiraffa exigua* and too large for ?*Gelocus gagensis* or any species of *Bugtimeryx*. They are, in addition, appreciably older than the material referred to *Progiraffa exigua*. The presence of an accessory connection between the preentocristid and prehypocristid is unusual but has been reported in *Oriomeryx* Ginsburg 1985 (Ginsburg et al. 1994). That taxon, however, has a strong “*Palaeomeryx*-fold” and upper molars without a lingual cingulum.

Superfamily Giraffoidea Gray 1821
Family ?Giraffidae Gray 1821

Genus *Progiraffa* Pilgrim 1908

Diagnosis

Moderate-sized pecoran (m2-m3 length: ~ 5.3 cm). Ossicones present. Brachyodont teeth with rugose enamel. Lower molars with prominent

metastylid well separated from the metaconid, lingual face of metaconid and entoconid convex, m3 with robust entoconulid filling the lingual wall. “*Palaeomeryx*-fold” absent. Upper molars with subsidiary spurs separate from labially directed post-protocrista and premetaconule crista. Postmetaconule crista with bifurcation. Low lingual cingulum on posterior of protocone.

Progiraffa exigua Pilgrim 1908

Diagnosis

As for the genus.

New Material

Locality Z 117: 2376, medial phalanx.

Locality Z 120: Z 593, fragment of a right p2 or p3; Z 2276, left astragalus; Z 2392, right lower molar fragment.

Locality Z 121: Z 2274, right distal metatarsal.

Locality Z 124: Z 162, posterior portion of skull.

Locality Z 126: Z 2391, distal left humerus.

Locality Z 137: Z 202, right cuboid-navicular; Z 210, proximal left femur.

Locality Z 203: DGK 15, left astragalus.

Locality Z 205: DGK 23, right astragalus; DGK 45, left proximal femur; DGK 148, fragment of an ossicone; Y 41662, left mandible with incomplete m2 and m3.

Locality Z 211: DGK 145, left unciform; DGK 204, astragalus; DGK 215, right m1 or m2; DGK 291, right magnum-trapezoid.

Locality Z 212: DGK 188, right astragalus; DGK 200, right distal metacarpal.

Locality H 8115: H 208, left m3; H 664, right M3(?).

Locality H 8125; H 312, right maxilla with erupting P3 and DP4-M3.

Locality S 2: S 88, very worn left m1 or m2; S 412, left p3.

Locality S 4: S 48, incomplete left m3; S 495, fragment of a right m1 or m2.

Locality S 6: S 154, right m1 or m2.

Locality S 15: S 305, right mandible fragment with m1 or m2.

Locality Y 591: Y 24013, broken left cuneiform; Y 24020, distal metapodial; Y 24021, fragment of a left P4; Y 31676, left m1 or m2.

Locality Y 592: Y 17554, incomplete left astragalus; Y 31204, fragment of a left calcaneum; Y 31206, right P4; Y 47224, medial phalanx; Y 47225, right fibula.

Locality Y 652: Y 23429, left cuneiform.

Locality Y 687: Y 47366, proximal phalanx.

Locality Y 721: Y 26598, incomplete right astragalus; Y 26599, fragments of a right calcaneum.

Locality Y 738: Y 31148, fragment of a very worn left upper molar.

Locality Y 744: Y 40808, incomplete right astragalus.

Locality Y 747: Y 31733, left cuboid-navicular; Y 31735, left unciform; Y 31736, left cuneiform; Y 31739, left cuneiform; Y 31743, incomplete right astragalus; Y 31745, fragment of a right astragalus; Y 31748, left astragalus; Y 31760, medial phalanx; Y 31764, proximal portion of a proximal phalanx; Y 31766, medial phalanx; Y 31768, distal metapodial; Y 31771, distal portion of a medial phalanx; Y 31772, distal fragment of a proximal phalanx; Y 31773, medial phalanx; Y 31774, medial phalanx; Y 31775, distal metapodial; Y 31776, distal metacarpal; Y 31784, right distal femur; Y 31787, proximal left tibial epiphysis; Y 31789, fragment of a proximal right tibial epiphysis; Y 31794, fragment of a left distal radius; Y 31797, lower left p3; Y 41455, distal metapodial; Y 46276, distal metapodial; Y 46277, left cuneiform; Y 46284, fragment of a left astragalus; Y 47475, proximal portion of a proximal phalanx; Y 47476, proximal phalanx; Y 47477, fragment of left m1 or m2; Y 47478, distal

portion of a proximal phalanx; Y 47479, distal metapodial epiphysis.

Locality Y 780: Y 32920, small fragment of a right astragalus.

Locality Y 802: Y 46236, right fibula; Y 46237, left lunar.

Locality Y 843: Y 41451, distal portion of a proximal phalanx.

The presence of three left cuneiforms at Locality Y 747 indicates there are at least three individuals at that site.

Localities and Age

Pilgrim's type specimen is from the equivalent of the Chitarwata Formation at Dera Bugti, but its age is not known with any certainty. The Zinda Pir sites are in the upper unit of the Chitarwata Formation and the overlying Vihowa Formation, with an age range of approximately 20 to 17 Ma (Lindsay et al. this issue). The Manchar sites (GSP-H and GSP-S) are in the lower part of the sequence (Raza et al. 1984; Hussain, personal commun., 1986) and are of Lower and Middle Miocene age. The oldest Potwar sites (GSP-Y 747 and Y 721) are at the base of the terrestrial sequence in the Salt Range and are estimated to be about 18.3 Ma, while the youngest (GSP-Y 591 and Y 592) are estimated to be about 16.0 Ma (Johnson et al. 1985). Ginsburg et al. (2001) have reported additional specimens from level 6 of Welcome et al. (2001) in the Chitarwata Formation at Dera Bugti, to which the latter authors assign an Early Miocene age.

Description

Lower Dentition. The available specimens are all isolated premolars and molars, except for Y 41662, a mandible with broken but otherwise well-preserved m1 and m2. The presumed p3's (S 412 and Y 31797) (Figure 9.1-9.2) are low and long, with faint labial incisions, a large posterolingually directed metaconid that runs parallel to the equally strong, oblique entoconid. The latter converges on a large, more transverse entostylid to define a basin with a narrow lingual opening. The long anterior crest is bifurcated, with a robust, lingually directed paraconid. In both specimens there is a low cingulum just behind the base of the paraconid.

The lower molars (Figure 10.1-10.4) are brachyodont, with fine striations in the enamel. The obliquely situated metaconid and entoconid have flattened labial faces but retain convex lingual faces with weak development of lingual ribs in some cases. The premetacristid contacts the anterolabial end of the preprotocristid, while the



Figure 9. Lower premolars of *Progiraffa exigua*: 1) S 412, occlusal view; 2) Y 31797, occlusal view. Scale bar = 1 cm.

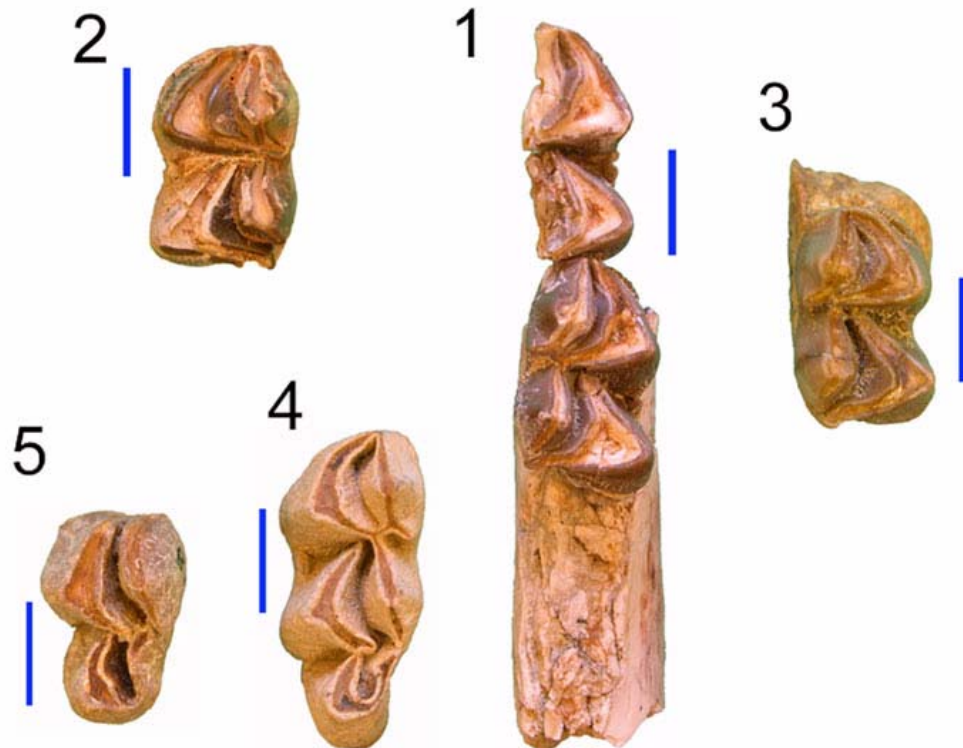


Figure 10. Lower dentitions of *Progiraffa exigua*: 1) Y 41662, occlusal view; 2) Y 31676, occlusal view; 3) S 305, occlusal view; 4) H 208, occlusal view; 5) S 48, occlusal view. Scale bar = 1 cm.

posthypocristid reaches the labial side of the tooth, ending in a tubercle and nearly closing off the posterolingual end of the median valley. In all specimens the prehypocristid is separate from the preentocristid and trigonid cusps, even in very advanced wear. None of the molars have even a vestige of a “*Palaeomeryx*-fold,” but all have large

lingually displaced metastylids that are separated from the metaconid by a strong vertical groove. The metastylid typically lies lingual to the anterior end of the preentocristid. In two of the molars (S 305 and Y 31676) (Figure 10.1-10.2) there is a small entostylid terminating the postentocristid. This entostylid is distinct from the tubercle on the

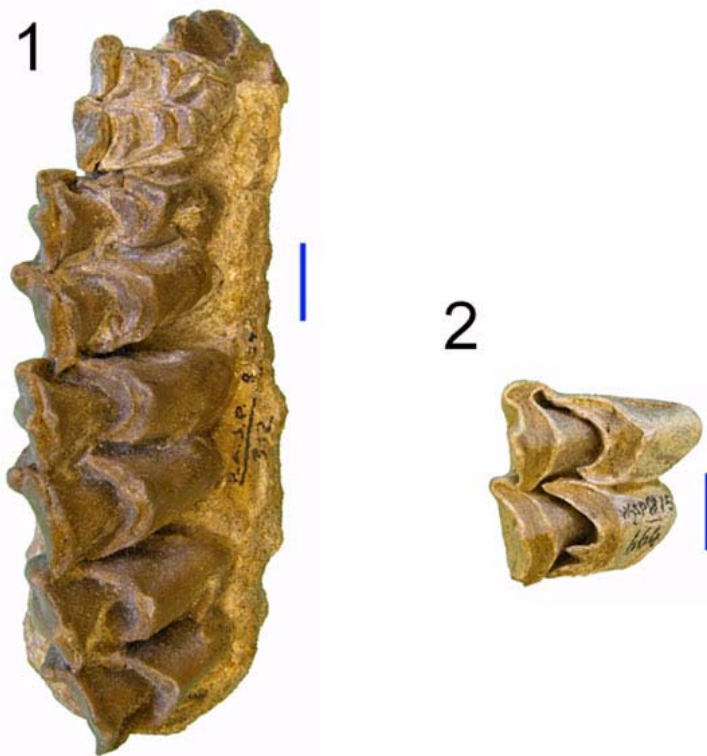


Figure 11. Upper dentitions of *Progiraffa exigua*: 1) H 312, occlusal view; 2) H 664, occlusal view. Scale bar = 1 cm.

posthypocristid. All the molars have low ectostylids and anterior and posterior basal cingula.

Both of the more complete m3's (H 208 and S 48) (Figure 10.3-10.4) have simple, crescent-shaped hypoconulids and a large entoconulid that fills the space between the entoconid and hypoconulid, making the lingual wall of the hypoconulid loop continuous. In S 48 the posthypocristid contacts the entoconulid.

Upper Dentition. H 312 (Figure 11.1) is a well-preserved maxilla with undamaged crowns of all the molars, a worn dP4, and P3 exposed but still in its crypt. An unerupted P4 is also present, but only the forming roots are visible and the crown is hidden within the maxilla. P3 has a tall, anteriorly situated paracone with a strong labial rib and foreshortened anterior crest. The posterior crest of the paracone is, in contrast, elongated and blade-like. A large parastyle is separated from the paracone by a deep vertical groove. The anteriorly situated protocone is connected to the parastyle by a low crest forming a convex lingual wall. Within the posterior fossette of the median valley there is a complicated, low spur of enamel connecting to the inner wall of the postprotocrista and running anteriorly.

The upper molars are low crowned, with large metaconules on M1 and M2. On M3 the metaconule is smaller than the protocone. The parastyles and mesostyles are prominent on all the molars, the paracones have very strong labial ribs and the metacones flat labial faces. On the M1 the

postmetaconule crista has a distinct bifurcation, and there are faint traces of this condition on M2 and M3. The three molars of H 312 have a complex of low enamel spurs near the junction of the postprotocrista and premetaconule crista. On M2 and M3 these appear as a bifurcation of the worn premetaconule crista, but on M1 it has a more complex shape. These spurs clearly have formed as structures separate from the postprotocone and premetaconule crista, although with wear they appear to merge with the centrally directed crista. Both M2 and M3 have a low cingulum on the posterior face of the protocone. This cingulum originates between the protocone and metaconule. At the base of the metaconule there is an entostyle-like structure.

H 664 (Figure 11.2) is judged to be an M3 because, although in advanced wear, it has no posterior interdental facet. In addition, the metaconule is smaller than the protocone, as is typical of an M3. The molar has a bifurcated postmetaconule crista, but it does not have the small spurs, entostyle, nor protocone cingulum seen in the other specimens.

Cranial Remains. Ossicones: DGK 148 (Figure 12.1-12.3) is a small section of an ossicone (here used broadly to include the branched structures of *Climacoceras*). The specimen is associated with a mandible (Y 41662) and postcranials referred to *Progiraffa exigua*. We assume, therefore, it also belongs to *Progiraffa exigua*. The ossicone is pos-

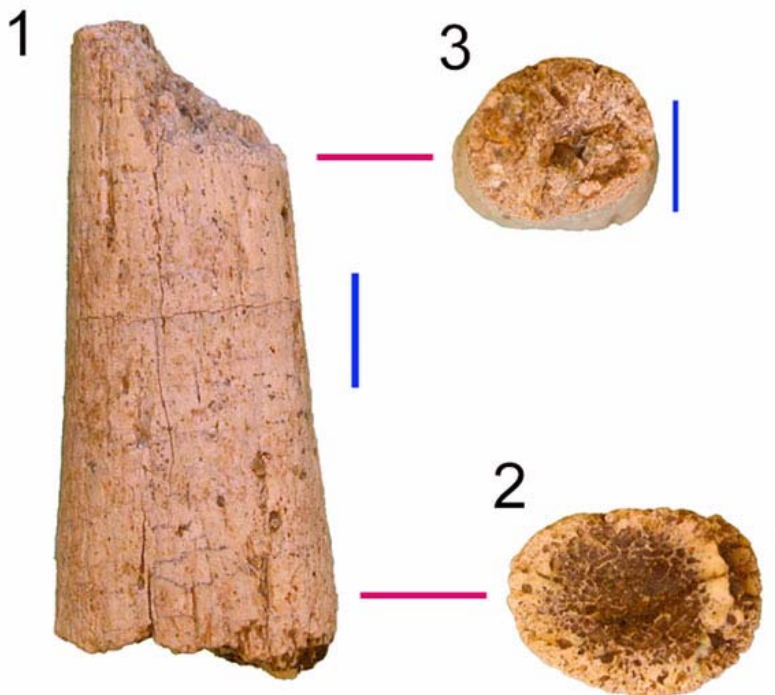


Figure 12. Ossicone fragment of *Progiraffa exigua* (DGK 148): 1) lateral view; 2) proximal view; 3) distal view. Scale bar = 1 cm.

sibly a midbeam segment, approximately 57.3 mm long. It is straight and tapers toward the presumed distal end, with cross-section dimensions of 24.6 x 18.6 mm at the craniad end and 19.0 x 14.9 mm distally. In cross section it has an oval shape, flattened on one side and with the greatest minor dimension slightly off center. In cross section there is a gradual transition between a very thin (3-6 mm at proximal end) outer zone of dense cortical bone and the largely cancellous interior. The surface has many fine grooves originating from nutrient foramina at their proximal ends. These structures are scattered uniformly about the surface and spiral counterclockwise about the long axis of the bone when viewed from the distal end.

Skull: Z 162 (Figure 13.1-13.4) is the rear of a broken skull. The specimen represents a medium-sized ruminant and, as *Progiraffa* is the only known appropriate sized ruminant at this level, we refer it to that species.

The specimen comprises the posterior of a damaged cranium, lacking teeth and ossicones. Except for the nuchal crest and a small remnant of the most dorsal part of the supraoccipital, the dorsal surface of the cranium has been broken away, exposing a natural endocast of the brain. The ventral surface has suffered only minor damage, while the supraoccipital region is more or less intact. Although the frontals and skull roof have been destroyed, the great thickness of the dorsal-lateral part of the lambdoidal crest and orientation of the

dorsal part of the supraoccipital suggest that the skull roof was domed or that there may have been large posterior cranial appendages. The supraoccipital is posteriorly projecting and laterally expanded as it contacts the lambdoidal crest, with shallow pits for the semispinalis capitis. Above the foramen magnum, the supraoccipital is slightly swollen, while ventrally the paired occipital condyles are completely fused into a ring-like structure, with the intercondyloid notch (*incisura intercondyloidea* of Hamilton [1973]) obliterated. The mastoid is narrowly exposed. On the ventral side of the skull, the styloid process is posterolateral to and well separated from the auditory bulla. The bulla is inflated and hollow, with an oval outline in ventral view. It is well separated from the basioccipital and is not anteriorly elongated. Consequently the middle lacerate foramen is left uncovered. The basioccipital is posteriorly wide, narrowing anteriorly. It has well-developed, laterally projecting condylar flexion stops (posterior tuberosities). A pair of very subdued basilar tubercles is located posteriorly at about the level of the posterior lacerate foramen, while anteriorly at the level of the foramen ovale there is a second pair of very faint swellings. A median keel originates between these latter swellings, running anteriorly onto the broken sphenoid. Anterior and lateral to the posterior pair of basilar tubercles and just medial to the auditory bulla there are paired irregular pits.

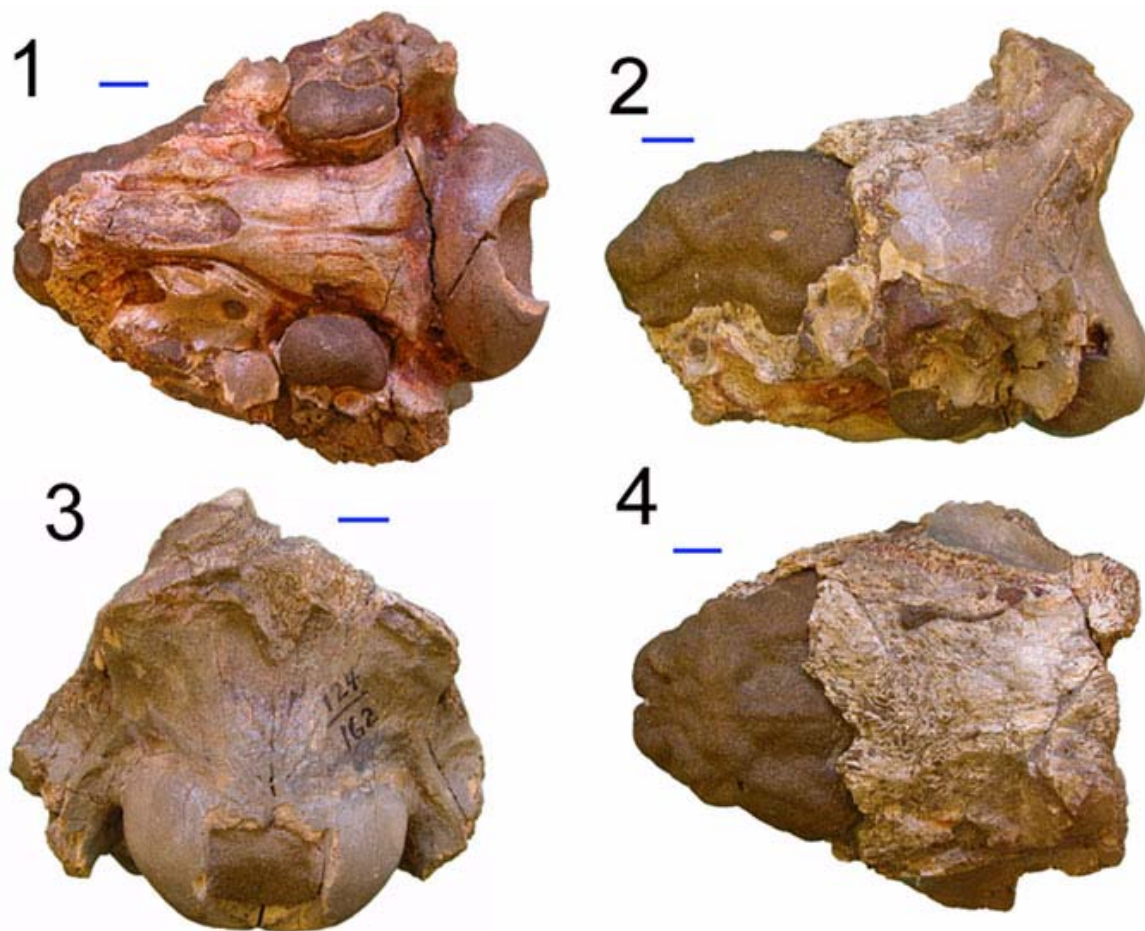


Figure 13. Skull of *Progiraffa exigua* (Z 162): 1) ventral view; 2) left lateral view; 3) nuchal view; 4) dorsal view. Scale bar = 1 cm.

Postcranial Remains. Calcaneum: Y 31204 and Y 26599 both preserve the fibular, cuboid, and much of the astragalar articulations, and in the case of 26599 part of the calcaneal process. The fibular articulation is typically pecoran, with a large convex posterior facet and a smaller concave-convex anterior one. The bulbous posterior fibular articulation has a medially projecting conical process with a distinct posteromedial facet for the proximal lateral facet of the astragalus.

Fibula: Y 47225 is a distal fibula with a small spine indicating it is a reduced remnant. Although damaged, the anterior tibial facet is narrow and flat, and apparently did not curve medially.

Astragalus: The best preserved specimen is DGK 188, while all the others are broken or corroded by weathering. The disto-lateral calcaneal facet is separated from the raised lateral edge of the sustentacular facet by a large sulcus, while the proximal lateral calcaneal facet is confined to the edge of the sustentacular facet and is separated from the dorsal fibular facet. The cuboid condyle extends

laterally, creating a distinct notch on the lateral side of the astragalus, while the cuboid portion of the condyle is cylindrical. The astragalus is narrow, with an approximate width to length ratio of 1:1.7.

Cuboid-navicular: Z 202 is the more complete specimen, but has been cracked and fractured, obscuring some of its features. Y 31723 is very well preserved, except for having lost the postero-ventral portion of the astragalar articulation. In proximal view both are dorso-ventrally narrow compared to the medial-lateral diameter, with the cuboid-astragalar facet being slightly wider than the navicular-astragalar one. The medial plantar process is very prominent and the dorso-medial angle of the navicular-astragalar articulation is retracted. In distal view, the distal process does not extend to the lateral margin of the anterior cuboid-metatarsal facet and the relatively broad posterior metatarsal articulation has a slightly inclined medial part originating near the entocuneiform facet with a more horizontal lateral extension. The facet for the 4th metatarsal lacks a posterior

medial extension bounding the groove for the tendon of the peroneus longus. Consequently the peroneus groove is shallow and broad. The junction between the ectomesocuneiform and endocuneiform articulations rises to form a low prominence, but both facets are on the same level.

Lunar: The sole example (Y 46237) is too poorly preserved to describe.

Cuneiform: With four well-preserved examples and a fifth broken one, the cuneiform is the most common postcranial element. They demonstrate slight morphological and size variation, but the stratigraphically youngest (Y 23429) is typical in all respects. The unciform articulation is relatively short and the disto-ventral process is directed ventrally rather than being inflected distally. The pisiform articulation is narrow at its proximal end, with its lateral margin being continuous rather than angled at the junction with the ulnar articulation.

Magnum-trapezoid: The sole example (DGK 291) is well preserved. Its dorsal-ventral diameter is much larger than its medio-lateral diameter, primarily because the lunar articulation is narrow and not extended laterally. The junction between the lunar and scaphoid articulations forms a high proximal keel. The inferior posterior unciform facet is widely separated from the anterior one.

Unciform: The two referred specimens (DGK 145 and Y 31735) differ somewhat in size and morphology, apparently reflecting individual variation. DGK 145 is the smaller of the two. Its lunar articulation has a flat, rectangular dorsal part that rises ventrally to form an almost cylindrical condyle. The articulation for the cuneiform is relatively narrow, without a marked lateral lip. The junction between the cuneiform and lunar articulations is well differentiated, but low so that the two lie in nearly the same horizontal plane. Y 31735 differs primarily in being about 10% larger and in having a relatively wider posterior lunar articulation and a narrower one for the cuneiform.

Metapodials: The fossils are all distal portions. Three specimens (Z 2274, DGK 200, and Y 31776) preserve both the third and fourth digits, while the remainder have only one side. Z 2274 is a metatarsal, while DGK 200 and Y 31776 are metacarpals. The metatarsal gully appears to be open in Z 2274, but the shaft is not preserved proximally enough to be certain. In all specimens the keels of the distal articular surface extend dorsally but do not project as far as they do ventrally. Consequently, in lateral view the keels are strongly asymmetrical. The external condyle has a lipped rim which, while stronger ventrally, also extends dorsally. The dor-

sal articular surface of the external condyle is thus complete. Both the external and internal articular surfaces terminate in a small pit on the dorsal side of the shaft.

Comparisons

The presence of ossicones leads us to tentatively place *Progiraffa* in the Giraffidae.

Progiraffa exigua differs from middle Miocene giraffids (*sensu* Hamilton 1978) such as *Giraffokeryx punjabiensis* Pilgrim 1911 and *Injanatherium* Heintz, Brunet, and Sen 1981 in numerous ways (Colbert 1933; Morales et al. 1987). These include the presence in *Progiraffa* of a large, well-separated metastylid, a cingulum on the protocone, and an enamel complex connecting the postprotocrista and premetaconule crista. *Progiraffa* also seems to have a more sporadic presence of a bifurcated metaconule and a more primitive basicranium with small basilar tubercles and an oval auditory bulla that is well separated from the basioccipital.

Progiraffa is similar to various primitive giraffoids, such as *Propalaeoryx* Stromer 1926, *Climacoceras* MacInnes 1936, *Teruelia* Moyà-Solà 1987, and *Lorancameryx* Morales, Pickford, and Soria 1993. The first of these, *Propalaeoryx*, is smaller and as far as is known lacks cranial appendages. It also has a more anterior P3 protocone, lacks entostyles on the molars, and the Namibian species *P. austroafricanus* has a "Palaeomeryx-fold" on the lower molars (Morales et al. 1999). The ossicone described here for *Progiraffa exigua* could be a segment of the branched, antler-like ossicone of *Climacoceras*, although it shows no sign of secondary tines and its internal structure has a greater mass of cancellous bone and only a thin outer layer of dense cortical bone. The many fine surface grooves and nutrient foramina on the Zinda Pir specimen are also absent in *Climacoceras africanus*, although Hamilton (1978) noted them in *C. gentryi*. Dentally both species of *Climacoceras* differ from *Progiraffa*. Their rather hypsodont lower molars have more compressed lingual cusps with nearly parallel axes, metastylids that are not separated from the metaconid, and m3 with the hypoconulid lingual wall incomplete. *Climacoceras* also has a more anterior P3 protocone and narrower upper molars. Most of the same dental characters differentiate *Progiraffa* from *Lorancameryx* and *Teruelia*, the latter also lacking the bifurcated paraconid on p3.

The close similarity between *Progiraffa* and *Canthumeryx sirtensis* Hamilton 1973 (including *Zarafa zeltani* Hamilton 1973) has been noted before (Moyà-Solà 1987, Gentry 1994; Ginsburg et al. 2001). *Canthumeryx* is known principally from

the dentition and postcrania, to which a skull may be added if the synonymy of *Zarafa* is accepted (Hamilton 1978, but see Janis and Scott 1987). This taxon is near the size of *Progiraffa* and nearly indistinguishable dentally. Possible points of difference are a slightly stronger and more isolated metastylid in *Progiraffa* and stronger bifurcation of the postmetacrista and greater development of lingual basal structures in *Canthumeryx* (shown principally in material originally attributed to *Zarafa*). The posterior and basicrania of the skull of *Progiraffa* are also very similar to *Canthumeryx*. *Canthumeryx*, however, has a flat skull roof, a large swelling over the foramen magnum, an open intercondyloid notch, and it appears to have a larger, more anterior pair of basilar tubercles. The slender ossicone fragment (DGK 148) described here is also difficult to reconcile with the massive bases seen in the referred skull of *Canthumeryx*, although Churcher (1978; fig. 25.10) choose to reconstruct the specimen with slender, spike-like ossicones.

Nyanzamerix pickfordi Thomas 1984 and *Prolibytherium magnieri* Arambourg 1961 are two additional primitive giraffoids sharing some features of the skull and dentition with *Progiraffa* (Geraads 1986). The isolated ossicone (DGK 148) is especially noteworthy, in that it could be a segment of one of the slender ossicones of *Nyanzamerix*. However, the nuchal area of the East African species is more gracile and less projecting, while the basicrania has more anteriorly positioned basilar tubercles. In addition, *Nyanzamerix* has lower molars with compressed lingual cusps nearly parallel to the axis of the tooth, metastylids that are not well separated from the metaconid, and m3 with the hypoconulid lingual wall incomplete. It is also a much smaller taxon. *Prolibytherium magnieri* shares one very distinctive feature with *Progiraffa* in that it has a reduced intercondyloid notch, while the basilar tubercles are posteriorly situated and very subdued. The great thickness of the skull roof of *Progiraffa* suggests the presence of large and elaborate ossicones as in *Prolibytherium*. The supraoccipital of *Prolibytherium*, however, does not project so strongly posteriorly. There are also dental differences from *Progiraffa*, principally in the possession of compressed lingual cusps that are more parallel to the axis of the tooth, metastylids that are not well separated from the metaconid, and an incomplete hypoconulid on m3.

Discussion

The initial description of *Progiraffa* was very brief and included only one species (Pilgrim, 1908). In his subsequent, more detailed account of *Progiraffa* Pilgrim (1911) referred a second species to

the genus, one which Lydekker (1883) had originally described as *Propaleomeryx sivalensis*. Lydekker's single specimen is an isolated upper molar, with few distinctive characters. It lacks the secondary complex of low enamel spurs near the junction of the postprotocrista and premetaconule crista, and is similar to the molar (H 664) from Sind. Except for its smaller size, the latter specimen is virtually indistinguishable from *Giraffokeryx punjabensis*. The type specimen of *Progiraffa exigua* was until recently all that was known of the taxon, but the new collections show the species is rather common.

The reference of both the ossicone (DGK 148) and skull (Z 162) to one species is somewhat problematic. The construction of the nuchal area of the skull (Z 162) suggests the cranial appendages were probably robust and perhaps even similar to those of *Prolibytherium*. This combination seems incompatible with the more spike-like ossicone DGK 148. The skull fragment is about 19 Ma while the ossicone fragment is between 18 and 16 Ma (Lindsay et al. this issue). Both are from the Vihova Formation.

The oldest specimen we attribute to *Progiraffa exigua* is a poorly preserved distal humerus (Z 2391) from the upper unit of the Chitarwata Formation, at a level we estimate to be 20 Ma. The specimen is clearly a large pecoran, but might belong to the indeterminate large pecoran (Z 2031) from locality Z 127 rather than *Progiraffa exigua*. However, it is appreciably larger than what we expect for a tooth the size of Z 2031 and is an appropriate size for *Progiraffa exigua*.

On the Potwar Plateau *Progiraffa exigua* persists up to at least 16 Ma. There are postcranial remains of a larger form that is morphologically similar from sites between 16 and approximately 14 Ma. While these might belong to another species of *Progiraffa*, we do not describe nor discuss this larger form because it is only known from postcranial elements. The cuneiform (Y 23429) from locality Y 652 is associated with a large distal metapodial, which is likely to represent the larger pecoran, indicating the two probably co-existed. After 14 Ma the still larger but morphologically different remains of *Giraffokeryx* are found.

? Superfamily Bovoidea Gray 1821
Family *Incertae sedis*

Genus *Palaeohypsodontus* Trofimov 1958

Diagnosis

Hypsodont molars, preentocristid and prehypocristid joining post postmetacristid and postpro-

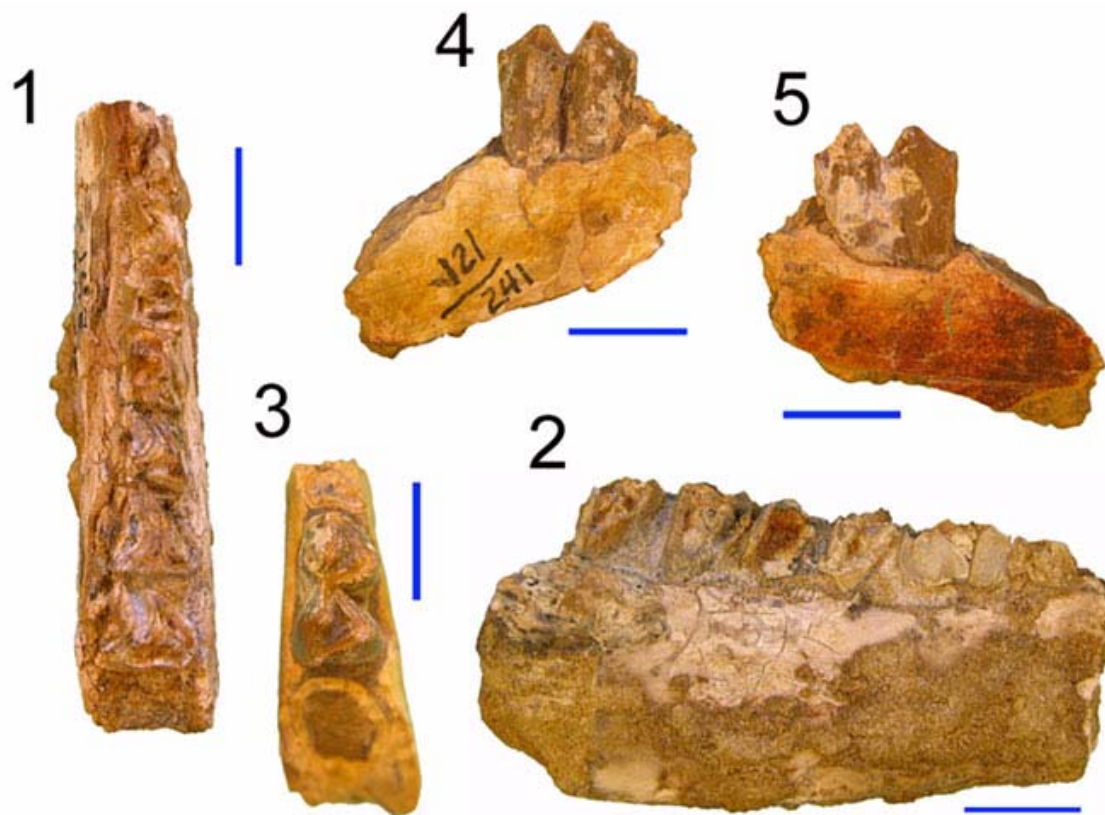


Figure 14. Lower dentitions of *Palaeohypsodontus zinensis*: 1) Z 2075, occlusal view; 2) Z 2075, lateral view; 3) Z 241, occlusal view; 4) Z 241, lateral view; 5) Z 241, medial view. Scale bar = 1 cm.

toecristid very early in wear, small metastylid, strong entostylid, and salient “goat-fold,” metaconid and entoconid slightly oblique with an embayment in the lingual wall between metaconid and entoconid.

Palaeohypsodontus zinensis Métais, Antoine, Marivaux, Welcomme, Ducrocq 2003

Diagnosis

Large (estimated m2-m3 length: 3.5 cm) and hypsodont (height:width ratio at least 2:1 in lower m1) species of genus. With very small metastylid forming vertical rib persisting through early wear; strong, projecting entostylid; preentocristid and prehypocristid joined in early wear by a secondary spur from the preentocristid; very strong “goat-fold” (after Métais et al. 2003).

New Material

Locality Z 121: Z 65, fragment of a right upper molar; Z 241, right mandible with m1;

Locality Z 142: Z 2075, right mandible with heavily damaged crowns of p3-m2.

Localities and Age

Locality Z 142 is in the lower unit of the Chitarwata Formation, while Locality 121 is in the lower part of the Vihowa Formation. The localities have estimated ages of ca. 25 and 18.5 Ma, respectively (Lindsay et al. this issue). The type material of the species is from the J2 level of the “Bugti Member” in the Chitarwata Formation and was assigned a Late Oligocene age (Métais et al. 2003).

Description

Lower Dentition. Z 2075 (Figure 14.1-14.2) is a poorly preserved mandible with most of the enamel spalled from the crowns. The teeth appear to have been in middle wear. Specimen Z 241 (Figure 14.3-14.5) is a right mandible fragment with a well-preserved m1 in early wear, and the posterior root of p4 and anterior root of m2. The p3 of Z 2075 was a relatively long tooth, but crown details are not preserved. The p4 is also relatively long and has a few crown details preserved. It has a weak labial incision, compressed posterior heel, and a long and simple anterior crest with an antero-lingually directed paraconid. The metaconid is broken, but

the preserved base indicates it was a large cusp. The entoconid and entostylid are both transverse, with the basin between them lingually closed.

The m1 of Z 241 is hypsodont with smooth enamel. The labially and lingually flattened metaconid and entoconid are slightly oblique to the long axis of the tooth and separated by a lingual embayment. The protoconid and hypoconid are selenodont. The premetacristid merges with the preprotocristid, while the posthypocristid contacts the postentocristid, closing off the posterolingual end of the median valley and forming a projecting entostylid. The wear traces of the postmetacristid and postprotocristid connect, and both in turn join with the trace of the preentocristid. The preentocristid and prehypocristid are joined by a spur that presumably originated on the anterolabial face of the preentocristid and together with the postmetacristid and postprotocristid form a small chimney-like structure. There is no sign of a “*Palaeomeryx*-fold” nor ectostylid, but there is a very small metastylid closely appressed to the metaconid and just lingual to the descending trace of the postmetacristid. The anterior cingulum (mesial cingulum of Métais et al. 2003) is very tall and strong, forming a “goat-fold” on both labial and lingual sides of the tooth. There is no posterior cingulum.

The badly damaged molars of Z 2075 preserve few details. Both are hypsodont, as evidenced primarily by the deep medial valleys of the trigonid and talonid, and on m2 there is a tall “goat-fold.” (The m1 is too damaged to determine the presence or absence of this feature.) The m2 has a low ectostylid and both molars have vestiges of posterior cingula. The prehypocristid of the m2 is isolated from both the preentocristid and the trigonid cusps, and there is no sign of an accessory spur on the preentocristid.

Upper Dentition. Z 65 is the lingual half of a small pecoran upper molar. It is a close match in size for the associated mandible Z 241 but otherwise has no diagnostic features.

Comparisons

Horncores are not known for this species, but other hypsodontines are known to have horncores and we therefore refer it to the Bovoidea. Because the relationships between hypsodontines and bovids are uncertain, we have not assigned it to a family.

Palaeohypsodontus zinensis differs from other species of *Palaeohypsodontus* in its larger size, greater degree of hypsodonty, and more salient “goat fold.” It differs from *Hanhaicerus qii* Huang 1985 in being much more hypsodont, with a

more reduced metastylid and isolated prehypocristid.

Palaeohypsodontus zinensis differs from advanced hypsodontines such as *Kubanostragus* Gabunia 1973 or *Hypsodontus* Sokolov 1949 in being distinctly less hypsodont, and in having oblique lingual conids, a lingual embayment between metaconid and entoconid, and a connection of the prehypocristid to the preentocristid, rather than directly to the postprotocristid.

Namibiomeryx senuti Morales, Soria, Pickford 1995 is similar to *Palaeohypsodontus zinensis* in its degree of hypsodonty and in having relatively long premolars. However, the lingual wall of the lower molars in *Namibiomeryx senuti* is relatively flatter without a deep embayment, there is no strong development of an anterior basal cingulum, and the hypoconid is separated from the entoconid both anteriorly and posteriorly. Early bovids, as represented by material from the Vihova and Kamliyal formations of Pakistan, are much lower crowned than the nearly contemporary specimen of *Palaeohypsodontus zinensis* and lack strong “goat folds,” as well as the precocious fusion of the prehypocristid to the trigonid complex. Early bovids also have more distinct metastylids and weaker entostylids.

Discussion

The two mandibles referred to this species differ from each other. We have placed them together on the basis of the apparent hypsodonty, salient “goat-folds,” and similarity in size. However, the presence of an ectostylid and posterior cingula on Z 2075, as well as the conformation of the preentocristid, suggests the Z 142 mandible belongs to a different taxon. Z 2075 is considerably older than the other Zinda Pir specimens, and may also be much older than the type specimen of *Palaeohypsodontus zinensis* from near Dera Bugti (Welcomme et al. 2001; Métais et al. 2003; Lindsay et al. this issue).

There are also postcranial remains of a small pecoran from the base of the Potwar sequence at Locality Y 747 (ca. 18.3). While morphologically similar to *Bugtimeryx* and *Progiraffa*, the fossils are larger than *Bugtimeryx pilgrimi* and much smaller than *Progiraffa exigua*. They are an appropriate size for *Palaeohypsodontus zinensis* but are not associated with any hypsodontine dental material, and we therefore do not refer them to this taxon. Whatever the identity of this small pecoran, it clearly represents an additional species in the Kamliyal Formation.

Superfamily Bovoidea Gray 1821
Family Bovidae Gray 1821

Unnamed Genus and Species

Material

Locality Z 110: Z 21, right mandible with m2 hypocond and roots of m3.

Locality Z 120: Y 46299, Fragment of a left horn-core; Y 46300 and Y 46301, horn-core fragments, probably part of Y 46299; Y 46302, edentulous skull, probably part of Y 46299; Z 54, upper molar; Z 60, left distal humerus; Z 61, proximal left metatarsal; Z 219, right maxilla with P3-M3; Z 221, complete left astragalus; Z 226, distal metapodial; Z 246, left M3; Z 247, left m1 or m2; Z 248, left upper molar; Z 249, left P4; Z 250, left P3; Z 251, left I3; Z 253, right p3; Z 254, fragment of upper premolar; Z 593, fragment of p4.

Locality Z 122: Z 108, incomplete right cuboid-navicular; Z 117, proximal epiphysis of a proximal phalanx.

Locality Z 205: DGK 219, right mandible with m1 or m2.

Locality Z 211: DGK 146, left cuboid-navicular.

Localities and Age

Only material from the Zinda Pir Dome area is listed above. The localities span approximately 19.5 to 16 Ma (Lindsay et al. this issue). The identification of some of the material is questionable, especially the mandible from Locality Z 110, which is from the oldest site. However, the skull, horn-core, and dental material from Locality Z 120 are incontestable and, at approximately 18.5 Ma, it is still one of the oldest known bovids. Additional material attributed to the Early Miocene bovid *Eotragus noyi* is from the base of the terrestrial sequence on the Potwar Plateau and is approximately 18.3 Ma (Solounias et al. 1995). Ginsburg et al. (2001) reported *Eotragus* from level 6 at Dera Bugti, attributing an Early Miocene age to it.

Discussion

The Vihowa horncores are illustrated in Solounias et al. (1995, fig. 5), where they are attributed to an unnamed species different from *Eotragus noyi*. Description of the unnamed species will be included in a general revision of Siwalik bovids. It is a small (m2-m3 length: ~ 2.5 cm) species with flattened, keeled horncores.

DISCUSSION

The fossils from Pakistan and Uganda broadly overlap in age, although there are localities in Pakistan that are significantly older than those from East Africa and the Zinda Pir sequence as a whole represents a longer period of time. There are no bovids in the Ugandan sequence, and the family apparently does not appear in sub-Saharan Africa until about 16 Ma. In Pakistan true bovids may appear as early as 19.5 Ma, and the family is certainly present at 18.5 Ma. Since they are not known earlier elsewhere, their appearance in southern Asia may document the beginning of this very important radiation. The density of appropriately sized remains at about 23 Ma strongly suggests that bovids did not occur in Pakistan at that time, but it is possible that they made an as yet undetected appearance between 23 and 19.5 Ma because the remains of medium-sized pecorans are sparse during this interval.

The large bodied *Progiraffa exigua* may be an early representative of the Giraffidae in southern Asia at circa 20 Ma. Other primitive giraffoids that are approximate contemporaries are present in East Africa and Namibia, but they are smaller and as far as known lack ossicones. Large, ossicone-bearing giraffoids are not present in Africa until slightly later at circa 18 Ma.

Other than for the lophiomerycid (and tragulids) the remaining ruminants discussed in this paper represent early pecorans that are not clearly related to the modern families. They are generally similar in both size and morphology to a variety of Late Oligocene and Early Miocene taxa of Europe and central Asia. Nevertheless, none of the East African or southern Asian species is particularly close to the Eurasian taxa. The species of Pakistan in particular give evidence of turnover in the ruminants that is analogous to what is known in the Late Oligocene and Early Miocene of Eurasia.

While we have not treated the tragulids here, they are also diverse and common in both East Africa and Pakistan. In East Africa their record extends to 20 Ma, at which time there are at least three species. While the Pakistani tragulid material is as yet unstudied, the first occurrence is older than in Africa, which is expected because there are older fossiliferous deposits in Southern Asia. In the Zinda Pir area the oldest tragulid is from locality Z 150 at approximately 23 Ma. The slightly younger site Z 127 has three species associated with the primitive pecoran *Bugtimeryx pilgrimi*. In contrast, tragulids apparently do not make an appearance in Europe until MN3 or even MN 4 at about 18 Ma.

The apparent differences between East Africa and southern Asia in ruminant diversity is in part due to the longer period of time represented in the Pakistani fossil sequences and in part due to the lack of a recent systematic treatment of the African Early Miocene ruminants. It is our opinion that revision of the wealth of material collected in Kenya and Uganda during the course of the past 50 years is likely to reveal a much richer record of ruminants, one well worth the effort of studying.

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