PALÆO VERTEBRATA

ARTICLE

Miocene Bovidae (Mammalia) of the Siwaliks, Part 1: Hypsodontinae and Bovinae

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Abstract: The fluvial sediments of the Siwaliks in northern Pakistan preserve an exceptional geologic and paleontological record encompassing parts of the Oligocene and all of the Miocene and Pliocene. The sediments, which can be thousands of meters thick, have abundant vertebrate and invertebrate fossils from hundreds of different levels. Fossils were first discovered in the Siwaliks in 1832 and there are important collections of them in the Museum of the Geological Survey of India as well as in various European, British, and American museums. Renewed collecting has now added over 10,000 bovid fossils to a new collection held by the Geological Survey of Pakistan. The fossils include rare skulls and many isolated horn cores, as well as teeth and postcranials. Here we discuss material belonging to the Hypsodontinae, Boselaphini, and Bovini. We recognize four hypsodontine and twenty-two bovine species, plus one species of uncertain subfamilial placement. Nineteen of the twenty-seven have previously been named, while another five have cranial material suitable for defining a new species. Two species, referred to as ?Hypsodontinae sp. and Bovidae sp. 1, are distinctive but left unnamed. We are also uncertain about how distinctive what we refer to as *Selenoportax* aff. *vexillarius* is from *Selenoportax vexillarius*. Boselaphinines predominate in the fossil collections, both in terms of number of species and number of specimens. Most of the boselaphine genera are endemic to the Siwaliks, as are the hypsodontine *Palaeohypsodontus* and the possible bovin *Pachyportax*. The predominance of boselaphines together with the number of endemic taxa gives the Siwalik bovid fauna a distinctive aspect and collectively comprise the best-known Miocene record of the subfamily.

Keywords: Bovidae, new species, new genus, Miocene, Siwaliks, horn cores

Submitted 11 June 2025, Accepted 19 May 2026
Published Online 30 July 2026, doi: 10.18563/pv.49.1.e1

INTRODUCTION

The Siwalik formations of northern India and Pakistan comprise a thick sequence of Neogene fluvial sediments containing abundant remains of fossil mammals. According to Pilgrim (1939) the earliest fossil bovids from the region to come under scientific notice were limb bones from the Hundes plain in Tibet, sold by traders to Captain W.S. Webb in 1819 (Webb, 1820). Discovery of fossil bovids continued with the travels and collecting of British officials in the 19th century and the later projects of academic institutions. The opening pages of Pilgrim (1939) summarised these activities up to the middle of the 20th century. They reveal an assemblage of extinct species, especially boselaphines and bovins, documenting many aspects of morphology but leaving much to be sought about phylogeny and ages of the fossils (Gentry *et al*., 2025).

Earlier collections of Siwalik bovids include those now in the Natural History Museum, London, and the Museum of the Geological Survey of India (Kolkata: formerly Calcutta), as well as those made by American and European museums between 1922 and 1967 which are now deposited in the American Museum of Natural History (New York, USA), the Yale Peabody Museum (New Haven, USA), the Bavarian State Museum for Palaeontology and Historical Geology (Munich, Germany), and the Geological Institute, State University of Utrecht (Utrecht, Netherlands). More recently collecting by Pakistani institutions and geological research and collecting in collaboration with various American university groups has produced many new specimens, some of which represent new taxa. Among these new collections are those made under the aegis of the Geological Survey of Pakistan and the Pakistan Museum of Natural History, together with Harvard University and the University of Arizona. The Harvard-GSP database holds more than 10,000 records for bovids. The repository for the material is the Vertebrate Palaeontology Collection & Research Center, Geological Survey of Pakistan in Islmabad.

Chronological framework

In this paper we discuss fossils from the Potwar Plateau in northern Pakistan and from the Zindir Pir area in the Sulaiman Ranges east of Dera Ghazi Khan and southwest of the Potwar Plateau. Our chronological framework is based on paleomagnetic correlations of more than 65 stratigraphic sections to the Geomagnetic Polarity Time Scale. Sections included are from the Kamlial, Chinji, Nagri, and Dhok Pathan Formations on the Potwar Plateau (Barndt *et al*., 1978; Opdyke *et al*., 1979; Behrensmeyer and Tauxe, 1982; Johnson *et al*., 1982; Tauxe and Opdyke, 1982; Sheikh, 1984; Johnson *et al*., 1985, 1988; Badgley and Tauxe, 1990; McRae, 1990; Kappelman *et al*., 1991), as well as from the Chitarwata, Vihowa and Litra Formations of the Sulaiman Ranges (Friedman *et al*., 1992; Lindsay and Downs, 2000; Raza *et al*., 2002; Lindsay

et al., 2005; Lindsay and Flynn, 2016). These latter three formations continue into the Bugti Hills about 300 km south of the Zinda Pir area were the Chitarwata Formation goes well back into the Oligocene (Antoine *et al*., 2013). Fragmentary fossil bovids, including a horn core of *Sivoreas eremita*, are also known from the Lower Indus Basin, where the Miocene is represented by the Gaj and Manchar Formations (Khan, M.J. *et al*., 1984; Raza *et al*., 1984; Thomas, 1984a).

Because exposures are continuous over large areas, the stratigraphic sections can be correlated locally using lithological marker horizons believed to be isochronous (Behrensmeyer and Tauxe, 1982) as well as by magnetic-polarity, but no sections are correlated on the basis of biostratigraphy. Details of our procedures for determining ages are discussed in Barry *et al*. (2002, 2013) and Barry and Behrensmeyer (2025). All age estimates are based on the Gradstein *et al*. (2012) Geomagnetic Polarity Time Scale. More details of stratigraphy and dating for some critical localities are given in Appendix 1 in the Supplementary Online Materials.

Our localities are spatially and temporally limited collecting areas (Barry *et al*., 2002; Barry and Behrensmeyer, 2025: figures 3.1, 3.4, and 3.5;). We also use a survey block or collecting level for documenting isolated fossils of biostratigraphic interest. These survey blocks differ from localities in that they are more extensive in area, span a greater stratigraphic thickness, and may include fossils from multiple sedimentary layers, while localities typically are from single depositional settings (Behrensmeyer, *et al*., 2005; Behrensmeyer and Barry, 2025). Survey blocks are prefixed with two letters combined with a number. The Geological Survey of Pakistan and Pakistan Museum of Natural History localities and specimens are prefixed with an H, S, Y, Z, or DGK. The age estimates for most referenced localities are within 200,000 years and the age is given in the text as a single point estimate of the midpoint. The ages for localities with less precise estimates are given as a range between the minimum and maximum possible dates. Some Middle Miocene localities have many more bovid fossils than others, for example Y 76 (11.4 Ma with 462 bovid fossils), while in the Late Miocene there is one super rich locality Y 311 (10.1 Ma with 1838 bovid specimens). More typically a locality has only 10 to 20 bovids, but often with important specimens. For example our Locality Y 439 (9.3 Ma) has only 3 bovids, but one is the holotype of a new genus and species.

A small number of localities and their contained fossils collected by Barnum Brown in 1922 and G. Edward Lewis in 1932 and now in the American Museum of Natural History (Colbert, 1935a,b; Pilgrim, 1937) and Yale Peabody Museum (Jukur and Brinkman, 2021) are well enough documented as to provenience and stratigraphic horizon to include in this study. Unfortunately other Brown and Lewis localities, as well as the extensive collections made during the British era by the Geological Survey of India and its predecessors cannot be included, because the geographic and stratigraphic data are inadequate. This means that type specimens and other Siwalik fossils described by Falconer, Rütimeyer, Lydekker, and Pilgrim usually cannot be incorporated in our chronological framework with any precision. In some cases, however, it is possible to constrain the ages of the localities more narrowly. A few such especially critical Brown localities are listed in Appendix 1, together with comments on their likely age. Table 1 shows the approximate ages of the Potwar and Suliaman terrestrial formations.

In comparing Siwaliks bovids with those of western Eurasia, we refer often to the land mammal biochronological units Astaracian (Middle Miocene), Vallesian, and Turolian (successive Late Miocene units), and to the numbered European Neogene mammal units MN3-7/8 (Middle Miocene) and MN9-10 and 11-13 (Vallesian and Turolian respectively). Despite being initially called biostratigraphic zones, MN units were set up in 1974 (Mein, 1999) as a temporal succession of mammal faunas recognised by characteristic species, immigrant or newly evolved species, and species associations. Each unit has a reference faunal locality to ensure stability of the scheme. Later studies sought to place the units according to magnetostratigraphic, biostratigraphic, and geochronological scales (Steininger, 1999; Agusti *et al*., 2001; Gradstein *et al*., 2012), but sometimes without agreement on their dates. Eronen *et al*. (2009) summarized the likely climatic and environmental history of the Late Miocene western Eurasian fauna (the Pikermian chronofauna). Woodburne *et al*. (2013) present a "Chinese Standard" for the Neogene of Northern Asia.

Table 1. Age estimates for the terrestrial formations of the Potwar Plateau and Zinda Pir Dome. The overlap in age estimates between adjacent formations is the result of time transgression of the formation boundaries. [1]See Hussain *et al*. (1992) for discussion of this unit and the problem of Upper Siwalik formation nomenclature. [2]In the Southern Potwar, the Kamlial and Murree Formations are not differentiated. [3]The age estimate for the top of the Vihowa follows Raza *et al.* (2002). [4]The dates cited are based on Interpretation B of Lindsay et al. (2005, Fig 6B, p.13). An alternative correlation to the Geomagnetic Polarity Time Scale (Lindsay *et al.* 2005, fig 6A, p.12) places the base of the Chitarwata Formation at approximately 29.5 Ma and its top at 21.9 Ma. This correlation postulates an over two million year long hiatus between the top of the Chitarwata Formation and the base of the Vihowa Formation, which would be younger than 19.7 Ma. A subsequent third correlation (Lindsay and Flynn 2016) places the bottom of the formation in C11n.1r at approximately 29.5 Ma and the top at the base of C6n at 19.7 Ma. (Age estimates adjusted to the Gradstein *et al*. (2012) Geomagnetic Polarity Time Scale.)

Formation	Age Range (Ma)
Potwar Plateau	
Tatrot	3.5 to 3.3
Samwal[1]	ca. 3.6 to ca. 1.5
Dhok Pathan	9.8 to ca. 3.5
Nagri	11.5 to 9.0
Chinji	14.0 to 11.4
Kamlial/Murree[2]	18.0 to 14.0
Murree	? to 18.0
Zinda Pir Dome	
Litra	Late Miocene
Vihowa[3]	ca. 19.7 to ca. 11
Chitarwata[4]	25.8 to ca. 19.7

Important localities and formations outside the Siwaliks are listed in Table 2. Dates are taken from either the cited references or tabulations in the literature, with African localities from Werdelin (2010) and van Couvering and Delson (2020). The Middle Miocene starts at 15.97 Ma and the Late Miocene at 11.63 Ma The base of the Pliocene is 5.33 Ma (Gradstein *et al*., 2012).

Synopsis of bovid skull and dental characters

Bovidae are pecorans having horns with hollow keratin sheaths mounted on unbranched bony cores (Bibi *et al*., 2009).

Some species have horns in both sexes. Initially the horn cores were stumpy, short, straight and almost upright spikes inserted above the back of the orbits and widely apart. Later horn cores evolved to be longer with increased basal diameters (especially anteroposteriorly), and changed inclination and divergence. In many groups the horn cores acquired backward curvature and torsion, and underwent other changes. These changes, like those in other parts of the skull, teeth and skeleton, are often interlinked. Upper incisors are lacking and only a few early species retain minute upper canines.

The cheek teeth of bovids usually differ from those of cervids and giraffids in their smoother enamel, greater hypsodonty, the selenodont cusps joining to one another earlier in wear, weaker cingula, and the less bulky styles, stylids and ribs. The state of early bovid teeth can be seen in genera like *Eotragus* and *Namacerus*: higher-crowned and occlusally simpler than contemporary cervids but lower crowned than the usually more hypsodont extant bovids. Thereafter bovid teeth evolve into a considerable range of morphologies with two main underlying patterns (Schlosser, 1911: 499, 501; Gentry, 2010: figure 38.4). They may tend towards boödonty with ox-like or crushing molars with a large occlusal area (only in large species and less marked than in grazing horses), large basal pillars, strong labial ribs on the metacone as well as the paracone of upper molars, a more complicated outline of the central fossettes in uppers, and the lingual lobes of upper molars narrowing at their tips by a localised "pinching" of their sides. Lower molars show outbowed lingual walls and central fossettes with a central constriction. In contrast aegodont bovids have goat-like cutting teeth with occlusal simplicity, no or reduced basal pillars, prominent styles (linked with absence of ribs) on upper molars, and flat lingual walls on lower molars. These two patterns are not rigidly adhered to, so diversity prevails.

Metapodials on either side of the main cannon bone are absent or splint-like and more reduced than in cervids. The metatarsal has an open groove distally on its anterior surface. Many bovids show cursorial characters in their limb bones.

In Eurasia tiny bovid-like dental remains are known from the early Oligocene of Mongolia onwards (Dmitrieva, 2002), but the first definite Bovidae with horns only appear in Eurasia and Africa around 19-18 Ma, just before the Early to Middle

Table 2. Important localities and formations outside the Siwaliks.

Locality	Country	Stage / MN Unit	Age (Ma)	References and Comments
Beglia Formation	Tunisia	?Middle - Late Miocene.	?14 - 11	
Belometchetstkaja	Russia	Middle Miocene MN 5 or 6	15	
Çandir	Turkey	Middle Miocene MN 5 and 6	16.4 - 13.4	
Fort Ternan	Kenya	Middle Miocene	13.8 - 13.7	
Langebaanweg (Varswater Formation)	South Africa	Early Pliocene	5.2-5.1	Baard's Quarry contains fossils of varying date many of them younger than the Varswater Formation.
Lothagam (Nawata Formation to Kaiyumung Member of the Nachukui Formation)	Kenya	Late Miocene - Middle Pliocene	7.4 - ~ 4.2	
Maboko	Kenya	Middle Miocene	15,3	
Namurungule Formation	Kenya	Late Miocene	~ 8.5	
Ngorora Formation	Kenya	Middle - Late Miocene	13.1 - 10.5	Deino et al., 1990. Equids are from younger exposures at Ngeringerowa.
Pikermi	Greece	Late Miocene MN12	7.4 - 7.1	Bohme et al., 2017
Sahabi (Upper)	Libya	Late Miocene	6.5 - ~ 5.5	
Samos	Greece	Late Miocene MN11-13	8.0- 6.7	Koufos et al. 2009
Sansan	France	Middle Miocene MN6	~14.2 - 12.85	Reference locality for European mammal zone MN6 15.2-15.0 Ma in Sen and Ginsburg (2000)
Sevastopol (= Sebastopol)	Ukraine	Late Miocene MN9	11 - 9.88	

Miocene transition (Gentry, 2010; Antoine *et al*., 2013). Prior to the era of cladistically organised molecular taxonomy, Bovidae were understood as a series of subfamilies and tribes, many of them (Bibi, 2013, 2014) corresponding with ecological guilds. Molecular research on extant bovids indicated that the African tribe Neotragini is not a unitary group, that some taxonomically puzzling species are indeed long isolated, and that some relationships are unexpected. Adding fossil groups to the analysis of Hassanin *et al*. (2012) produces a partly conjectural arrangement of bovids (Table 3).

A simplified version of the relationships between what was left of the tribes in Hassanin *et al*. (2012) is shown in Figure 1A along with a simplified phylogeny based on Bibi (2013, 2014) in Figure 1B. In the expectation that molecular rates of evolution will have varied in the past, Bibi took 16 dated divergence points from the fossil record to convert the bovid part of the Hassanin *et al*. (2012) cladogram into a phylogeny. He discovered that if his results were to be relied upon, classificatory changes would be needed, but a stable scheme of relationships that includes extinct species has yet to be agreed upon (Calamari, 2021). Miocene Siwalik Hypsodontines and Bovines are listed in Table 4. Many of the Siwalik species belong to the Boselaphini and a guide to boselaphine generic names is given in Appendix 2 (in Supplementary Online Material), while Appendix 3 (in Supplementary Online Material) is a synopsis of some bovid skull and dental characters. It mainly covers the Boselaphini because of their prominence in the Miocene Siwaliks record.

The main focus of interest for the Siwalik Miocene bovids starts with those of the Chinji Formation from about 14.0 Ma onwards. However earlier ones do occur. Barry *et al*. (2005) described and reviewed the oldest ruminants in the post-Eocene of Pakistan including the possible bovid *Palaeohypsodontus zinensis* and an unnamed bovid. We therefore begin by briefly considering the poorly known Hypsodontinae of the late Early Miocene Vihowa Formation in the Sulaiman Range and the Early-Middle Miocene Kamlial Formation of the Potwar Plateau. The Vihowa bovids are from near the base of that formation, conformably overlying the fluvial sediments of the uppermost Chitarwata Formation and date from ~18.7 Ma (Downing and Lindsay, 2005; Lindsay *et al*., 2005; Métais *et al*., 2009; Antoine *et al*., 2013). The Kamlial bovids from the base of the terrestrial sequence, overlying Eocene marine rocks, are estimated to be 17.9 Ma. The oldest bovids from either formation comprise horncores, dental, and postcranial fossils. Horncores, however, only become common in the Middle Miocene uppermost Kamlial or lowermost Chinji Formations, at which time our new collections indicate at least seven species are represented. The Early and Middle Miocene bovids are all small (body weight of 8 to 55 kg), and species over 60 kg only appear at the beginning of the Late Miocene. The ages given for species in the text and Table 4 are based on the more secure identifications of the material, with horn cores given preference.

In the Systematic Paleontology section only a limited number of the more notable specimens are listed under "***Material***" for each taxon in the Harvard-GSP and other collections, while the lists in Appendices 4 through 7 (in Supplementary Online Material) are complete for all studied and referred specimens and include measurements. Within each taxon, the listings are ordered by age and locality. Appendix 4 has the cranial material, Appendix 5 dental, Appendix 6 astragali that are complete enough to measure the distal width (including Antilopinae**)**, and Appendix 7 other postcranial elements. Skulls with teeth are listed in both Appendices 4 and 5. Several localities have very large numbers of specimens and for them we have compiled even more selective lists of specimens. For a novel taxon the lists in Appendices 4 through 7 constitute the hypodigm.

Table 3. Conjectural phylogenetic arrangement of Bovidae with extinct taxa marked with obelisks. Siwalik Miocene taxa of known affinity in bold type. (A) the early Hypsodontinae, (B) Boselaphini and allied tribes, (C) all remaining bovids.

(A) Subfamily †Hypsodontinae	
†Hypsodontini	Middle Miocene, perhaps diphyletic to other bovids
(B) Subfamily Bovinae	
Boselaphini	nilgai and four-horned antelope
Tragelaphini	kudu, bushbuck group. African
Bovini	cattle, buffalo
(C) Subfamily Antilopinae	
Neotragus	former "Neotragini" is polyphyletic. Small, African
Aepyceros	impala, African
Antilopini	blackbuck, saiga antelope, gazelles
†Olocerini	Late Miocene, includes †*Urmiatherium*
†*Criotherium*	Late Miocene, plus †*Palaeoreas*
Reduncini	waterbuck and reedbuck group plus *Pelea*
Cephalophini	duikers, African
†***Tethytragus***	Middle Miocene, not a boselaphine
Hippotragini	roan, sable antelope, oryx, addax
Alcelaphini	hartebeest and wildebeest group
Pantholops	chiru, Tibet. Linked with Caprini, below
Caprini	the former mainly Eurasian subfamily Caprinae
Ovibovina	muskox, serow, goral
Caprina	takin, chamois, sheep, goats

METHODS

Dental nomenclature follows Gentry *et al*. (1999), Gentry (2010), and Bärmann and Rössner (2011). All measurements are in millimetres or centimetres and were made with digital callipers. Upper case = upper teeth, lower case = lower teeth.

Hypsodonty index (hyp) = height of unworn or very slightly worn m2s or m3s divided by molar length, expressed as a percentage of molar length. Crown height is measured on the protoconid. Premolar/molar index (p/m) = length of premolar row divided by the length of the molar row, expressed as a percentage of the length of the molar row. Basal index of a horn core = transverse or mediolateral basal diameter as a percentage of anteroposterior basal diameter (transverse diameter/anteroposterior diameter). Skull orientations are described with the tooth row visualised as horizontal.

Discussion and analysis of Siwalik species has been plagued by inadequate types as well as the lack of information on the localities they came from and their ages. Bovids are something of an exception, largely because of the quality of the collections made by Barnum Brown (Pilgrim, 1937). There are still, nevertheless, named species which are difficult to characterize and compare, as for example *Ruticeros pugio* which was based on a single horn core from an unknown locality (Pilgrim, 1939). Ideally a new taxon would be based on associated cranial, dental, and skeletal materials of known age, but in the Siwalik such specimens are exceedingly rare.

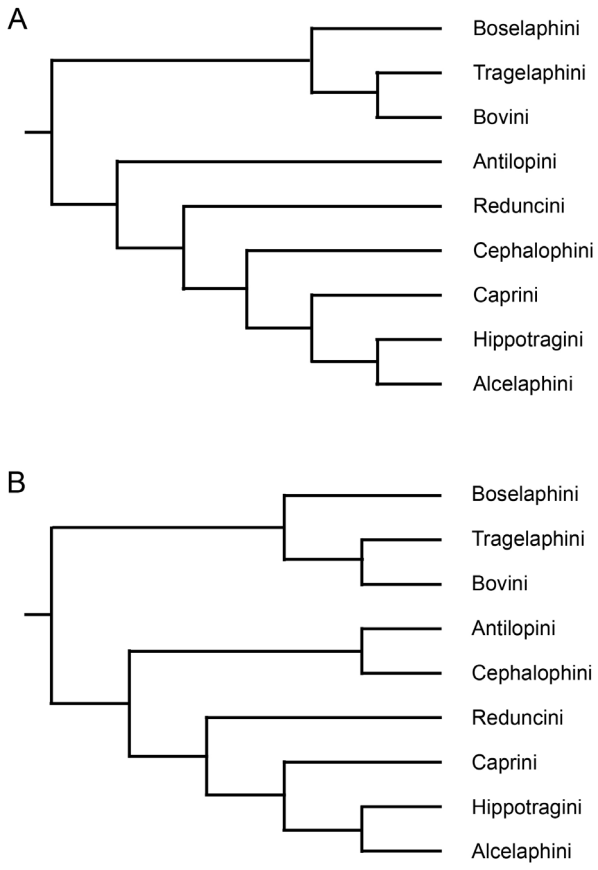

Figure 1. Two simplified classifications of Bovidae. A) from the cladogram of mitochondrial genomes in extant artiodactyls (Hassanin et *al*., 2012) and B) from the bovid phylogeny of Bibi (2013, 2014). Neotragini and some more isolated species have been omitted.

At a minimum, therefore, we believe that in principle bovid taxa should be based on horn cores and the fossil should give an indication of not just the horn core's shape, but how it is inserted on the skull and any features such as the presence of sinuses, demarcations, and keels, as well as the size, position, and shape of supraorbial foramina in pits, the degree of horn core divergence, and the distance between the two insertions. Thus, if possible, a holotype or other specimens should show where the midline and orbit lie as well as the orientation on the skull.

With one exception, we adhere to this standard. In the following we name five new species, but because the material is not adequate for defining a new species, we leave unnamed at least two others that we believe are distinctive. Furthermore, throughout the sequence there are additional specimens in the Harvard-GSP collections that do not belong to any of the approximately twenty-seven species discussed in the following. While likely to represent additional, otherwise unknown species, these are too fragmentary to justify adding further taxa. There may be as many as five such taxa in the Late Miocene.

Institutional Acronyms

AMNH: American Museum of Natural History, New York, New York; GSI: Geological Survey of India; GSP: Geological Survey of Pakistan; ISEM: Institut des Sciences de l'Evolution, Université de Montpellier II, Montpellier; NHML: Natural History Museum, London; PMNH: Pakistan Museum of Natural History, Islamabad; YPM: Yale Peabody Museum, New Haven, Connecticut. Fossil specimens prefixed with H, S, Y, Z, or DGK are deposited in the collections of the Vertebrate Palaeontology Collection & Research Center, Geological Survey of Pakistan, or in the Pakistan Museum of Natural History, both in Islamabad. The Brown collection is in the American Museum of Natural History and the Lewis collection is in the Yale Peabody Museum. In the following we frequently refer to the collections made by the Harvard-GSP project simply as the "GSP collections."

SYSTEMATIC PALEONTOLOGY

Family ?BOVIDAE Gray, 1821

Subfamily HYPSODONTINAE Köhler, 1987

The subfamily Hypsodontinae was created for a widespread group of Middle Miocene horned pecorans, often taken to be Bovidae. They also appear to be present in the Early Miocene of China (Chen, 1988; Jin *et al*., 2025) and perhaps Arabia (Thomas *et al*., 1982; Whybrow *et al*., 1982; Gentry, 1987), and with the exception of *Hypsodontus sinensis* Jin, Jiangzuo, and Wang (2025) at that stage are without demonstrable horns. Bovid-like teeth extend well back into the Oligocene of eastern Asia (Wang, 1992; Dmitrieva, 2002), and we take these as possible hypsodontines. However, doubts have been expressed about the bovid relationships of the subfamily (Bibi *et al*., 2009; Gentry, 2010), or at least any possible Oligocene members (Métais *et al*., 2003), and it looks as if Hypsodontinae as a whole might have been separate at the family level. Janis and Manning (1998) noted a possible connection from the Asian teeth to the early Miocene Antilocapridae (Merycodontinae) of North America, which could lead to removing the Hypsodontinae from the Bovidae. For the present we use *Hypsodontus* and *Kubanotragus* for the horned

Table 4. List and classification of Siwalik bovid species other than Antilopinae, with estimated ages of first and last appearances in the Siwaliks. Dates in parentheses are endpoints with imprecise estimates and are given as a range between the minimum and maximum dates. Bracketed species = lineages.

?Family Bovidae	
Subfamily Hypsodontinae	
Palaeohypsodontus zinensis Métais et al., 2003	?28.3 - 18.2 Ma
?Hypsodontinae sp.	15.2 Ma
Kubanotragus sokolovi Gabunia, 1973	14.1- 12.1 Ma
Hypsodontus pronaticornis Köhler, 1987	13.7 - 12.8 Ma
Family Bovidae	
Subfamily indet.	
?Bovidae sp. 1	16.0 - 15.1 Ma
Subfamily Bovinae	
Tribe Boselaphini	
Eotragus noyei Solounias et al., 1995	17.9 - 16.8 Ma
Carina meryx lindsayi genus and species nov.	(18.3 - 17.9 Ma)
Elachistoceras khauristanensis Thomas, 1977	14.1 - 8.5 Ma
┌*Strepsiportax meyeri* species nov.	14.1 - 12.4 Ma
└*Strepsiportax gluten* Pilgrim, 1937	12.4 - (11.2 - 10.8) Ma
┌*Sivaceros antecedens* species nov.	14.1 - 13.4 Ma
└*Sivaceros gradiens* Pilgrim, 1937	13.0 - (11.3 - 11.0) Ma
?(Sivaceros) vedicus Pilgrim, 1939	9.8 Ma
Sivoreas eremita Pilgrim, 1939	14.1 - 12.1 Ma
Helicoportax praecox Pilgrim, 1937	13.4 - (11.2 - 10.8) Ma
┌*Selenoportax vexillarius* Pilgrim, 1937	(11.2 - 10.8) Ma
└*Selenoportax* aff. *vexillarius*	10.2 - 9.8 Ma
┌*Miotragocerus pilgrimi* (Kretzoi, 1941)	?10.5 - 8.8 Ma
└*Miotragocerus punjabicus* (Pilgrim, 1910)	8.7 - 6.4 Ma
Tragoportax salmontanus Pilgrim, 1937	8.4 - 7.2 Ma
Punjabameryx inflata genus and species nov.	?9.4 - 7.3 Ma
Ruticeros pugio Pilgrim, 1939	?
Tribe ?Bovini	
┌*Pachyportax latidens* (Lydekker, 1876)	?
│*Pachyportax falconeri* (Lydekker, 1886)	9.8 - 8.9 Ma
│*Pachyportax dhokpathanensis* Pilgrim, 1937	9.0 - 7.2 Ma
└*Pachyportax giganteus* (Akhtar, 1995)	?
Subfamily ?Bovinae	
Rectacornis mirabilis genus and species nov.	9.6 - 9.0 Ma

representatives of the subfamily Hypsodontinae in the Middle Miocene (Gentry, 2010) (Tables 3 and 4).

Horned Hypsodontinae, as noted above, became widespread in the Middle Miocene from Mongolia westwards to embrace Eastern Europe, the Siwaliks, north Africa and Kenya. They did not survive past the Middle Miocene (Köhler, 1987; Bonis *et al*., 1998) unless high-crowned teeth in the Beglia Formation in Tunisia (Table 2) at levels with hipparionine horses (Robinson, 1986) were *Hypsodontus*. The torsion of the horn cores led Pilgrim (1934) and many after him to discuss possible relationship to the Late Miocene *Oioceros* group and to Caprini.

Genus *PALAEOHYPSODONTUS* Trofimov, 1958

Type species. *Palaeohypsodontus asiaticus* Trofimov, 1958

Species *Palaeohypsodontus zinensis*

Métais, Antoine, Marivaux, Welcomme, and Ducrocq, 2003

Palaeohypsodontus zinensis Métais *et al*., 2003: 377, figs 4-5.

Palaeohypsodontus zinensis Barry *et al*., 2005: 24, figure 14.

Holotype. ISEM DBJ2−A1, fragmentary right mandible with dp4 and m1. From Lundo Chur (Quarry, J2), in Baluchistan, Pakistan (Late Oligocene).

Diagnosis. Large species of *Palaeohypsodontus*, with lower molars clearly hypsodont (the ratio of height to width of the

moderately worn m1 is 2.1, almost twice as hypsodont as the type species *P. asiaticus* from Mongolia). Further differs from *P. asiaticus* in having a tiny metastylid forming a narrow vertical rib on the lingual wall of the lower molar, no ectostylid, a well−developed entostylid, and a salient mesial cingulum. (From Métais *et al*., 2003: 377.)

Métais *et al*. (2003) expressed doubts about the classification of *Palaeohypsodontus zinensis*, seeing it as only questionably pecoran.

Estimated age. 28.3? - 18.2 Ma.

Material.

Locality Z 121 (18.2 Ma)

Z 65 Lingual fragment of a right upper molar.

Z 241 Right mandible fragment with molar, probably m1.

Discussion. The holotype mandible and some postcranials of *Palaeohypsodontus zinensis* came from the Late Oligocene of the Chitarwata Formation near Dera Bugti. Barry *et al*. (2005) added two bovid-like teeth from Locality Z 121 in the Early Miocene lower Vihowa Formation and a damaged mandible (Z 2075) from the mid-Oligocene Chitarwata Formation, Locality Z 142, which at approximately 28.3 Ma (see Appendix 1 in Supplementary Online Material) would be older than other fossils of the species. However, the latter specimen is very poorly preserved and *P. zinensis* is mentioned in this account only because of the two Vihowa teeth. The molar on Z 241 shows restrained outbowing of the walls of the lingual lobes, posterior openings of the two central fossettes, an incipient metastylid, no basal pillar, and a trace of an anterior cingulum. It shows a degree of hypsodonty in lingual view. The m2 might have been a substantially longer tooth. Some pecoran postcranial material from Locality Y 747 in the Kamlial Formation would fit *P. zinensis* in size (Barry *et al*., 2005).

?Hypsodontinae sp.

Estimated age. 15.2 Ma.

Material.

Locality Y 642 (15.2 Ma)

Y 30947 Left m3.

Discussion. Hypsodontinae are the most likely group to have reached in the Middle Miocene the size and degree of hypsodonty shown in specimen Y 30947. The tooth is bigger than would be expected in *Palaeohypsodontus zinensis* and might be as big as a large example of the Chinji *Kubanotragus sokolovi*.

Genus *HYPSODONTUS* Sokolov, 1949.

Type species. *Hypsodontus miocenicus* Sokolov 1949: From Belometchetskaja, Russia

Diagnosis. Robust and rather short horn cores without keels and having little compression, insertions quite close together and perpendicular on the frontal, horn core with marked homonymous torsion, and curving slightly forward distally, dorsal orbital rims wide and perhaps at a slightly higher level than the frontal medial to the horn core, sagittal crest present, premolar rows short, lower molar lingual walls almost planar, and molars hypsodont especially in larger species, basal pillars on molars very weak or non-existent.

Species *Hypsodontus pronaticornis* Köhler, 1987

Hypsodontus pronaticornis Köhler, 1987: 147, figure 14.

Holotype. Right horn core with part of frontal from Çandir, Turkey (Middle Miocene).

Diagnosis. A larger species of *Hypsodontus*. Horn cores moderately long, curving outwards and forwards, little divergent overall, with homonymous torsion, sinuses in the frontals and horn pedicels, premolar rows short, molars hypsodont. The central cavities of the molars are separate and the lingual basal pillar is on the protocone.

Estimated age. 13.7 - 12.8 Ma.

Material.

Locality Y 59 (13.7 Ma)

Y 23735 Right horn core.

Locality Y 824 (13.1 Ma)

Y 40789 Right upper molar, probably an M2, middle wear

Locality Y 795 (12.8 Ma)

Y 32872 Left partial m3 in early wear.

Discussion. This species is represented in the Siwaliks with certainty by only the few fossils listed in Appendices 4 and 5 (Supplementary Online Materials), but other fragmentary bovid teeth and skeletal elements of similar size might belong to it and would extend its range to as young as 12.3 Ma. The large tooth Y 40789 is the best evidence for the presence of *H. pronaticornis*. It is in middle wear and shows no signs of excessive use. It is high crowned, has slightly rugose enamel, strong styles and no basal pillar.

The horn core Y 23735 (Figure 2) is larger than *H. sokolovi* and is definitely not that species. It could be held to fit a rather small *H. pronaticornis*. The inclination is moderately upright, divergence increases from base to preserved tip, homonymous torsion is clearly present, and there is no backward curvature. A keel starts centrally on the anterior side, swings round medially, but rapidly fades away. The pedicel is quite high and the dorsal orbital rim is sloping but fairly wide. There is a small supraorbital pit medially at the foot of the pedicel and some minor internal sinuses anteromedially to the pit. The frontals are not high above the level of the dorsal orbital rims.

Genus *KUBANOTRAGUS* Gabunia, 1973

Type species. *Kubanotragus sokolovi* Gabunia, 1973: Belometchetskaja, Russia.

Diagnosis. A small Hypsodontinae with protruding large orbits, long, slender, and remarkably straight horn cores inserted vertically above the middle of the orbits, horncores almost parallel but slightly curved and diverging outwards, with slight transverse compression and oval to circular cross section, with at most incipient homonymous torsion, no keels, relatively long pedicle with frontal sinuses, presence of fairly wide and deep postcornual grooves. Molars very hypsodont.

Species *Kubanotragus sokolovi* Gabunia, 1973

Kubanotragus sokolovi Gabunia, 1973: 112, figure 34, plate 8 figure 6.

Kubanotragus sokolovi Thomas, 1984a: 47, figures 19-20, plate 4 figures 2-3.

Holotype. A right horn core P.I.N. 428/10 from Belometchetskaja, Russia (Middle Miocene).

Diagnosis. A smaller species of *Kubanotragus*. Horn cores moderately long, with rather small cross-sectional diameters relative to their length, without keels but tending to develop

blunt corners anteriorly, posteromedially, and laterally in their distal parts, nearly straight in anterior view, little divergence and very slightly concave forwards in side view. The insertions are moderately wide apart partly because of the slenderness of the horn cores. The postcornual fossa is shallow, but large in relation to the size of the horn core. The molars are hypsodont. The central cavities are separate and the enamel is rather thin. The mesostyle is thin.

Estimated age. 14.1 - 12.1 Ma.

Material.

Locality Y 478 (14.1 Ma)

Y 25419 Left horn core on part of frontal.

Y 28076 Left m1-m3.

Discussion. In the Siwaliks this species comes mostly from Locality Y 478 but there are also teeth from Localities Y 518 and Y 758 and two astragali from Localities Y 761 and Y 59. Y 25419 (Figure 3) is a horn core of fairly typical appearance for this species. It is of rather small diameter relative to its length as also seen in the holotype of *Kubanotragus sokolovi* (Gabunia, 1973: figure 34) and the *Hypsodontus* cf. *gaopense* of Bonis *et al*. (1998: figure 1) and it shows the characters of the species diagnosis. Y 25419 doesn't show torsion, but torsion is just detectable in at least two other horn cores. The postcornual fossa is shallow but large in relation to the size of the horn core. The frontals contain sinuses and in the horn cores Y 15804 and Y 25164 they rise to the top of the pedicel. The frontal appears to carry on horizontally in the same plane in front of the horn insertion as it had behind it and not to dip downwards. The basicranium Y 25423 has very small anterior tuberosities on the basioccipital hardly distinguishable at the front of longitudinal ridges which flank and define a central longitudinal groove. The posterior tuberosities project a good deal sideways.

Figure 2. *Hypsodontus pronaticornis*. Y 23735, right horn core in A) anterior, B) lateral, and C) medial views. Scale 20 mm.

The lower molars of Y 28076 (Figure 4) show a high degree of hypsodonty with the m3 index at 157%, no basal pillars, slight goat folds, no metastylids, slightly curved central fossettes, labial lobes pointed not rounded, and the lingual wall of the 3rd lobe of m3 offset labialwards. They are of a size to be expected in this species.

Fossils of this or similar species under many names have been found in China, Turkey, Greece, and north and east Africa. Interestingly a hypsodontine cranium (NHML M15543) from Maboko, Kenya (Morales *et al*., 2003), which is the holotype of *Nyanzameryx pickfordi* Thomas 1984c and was referred to as *Kubanotragus pickfordi* by Geraads *et al*. (2024), has horn cores like *Hypsodontus sokolovi*, no sinuses visible in its broken right pedicel, and on the basioccipital a short central longitudinal ridge is flanked by hollows behind the ill-defined anterior tuberosities. Maboko is more than one million years older than Locality Y 478. A comprehensive review of Middle Miocene Hypsodontinae would now be helpful.

Family BOVIDAE Gray, 1821

Subfamily INDET.

Bovidae sp. 1

Estimated age. 16.0 - 15.1 Ma.

Material.

Locality Y 591 (16.0 Ma)

Y 24018 Left mandible with broken m3.

Locality Y 642 (15.2 Ma)

Y 20424a,b Separated right p4 and m2-m3.

Y 31678 Right mandible with damaged p3-m3.

Locality Y 742 (15.2 Ma)

Y 26401 Base of a left horn core.

Locality Y 678 (15.1 Ma)

Y 41270 Left mandible with intact p2 and p3, a fragment of p4, and m2-m3.

Y 24196 Base of a left horn core.

Discussion. A species considerably larger than *Eotragus noyei* is represented by sparse dental remains and possibly two horn cores, all from the Kamlial Formation. It is close in size to species of the Middle Miocene Chinji Formation and marks the appearance of larger bovids in the Siwaliks by 16.0 Ma. The molars of Y 20424 have small-moderate basal pillars, slightly rounded lingual lobes, broadly pointed labial lobes, and a goat fold on m2. On the m3 a flange (?entostylid) from the back of the entoconid passes into the shallow hollow lingually on the hypoconulid lobe, while the partial m3 Y 24018 appears to have a hypoconulid lobe with a closed lingual wall, as does Y 41270. The lightly worn m3 of Y 20424 would have had a hypsodonty index of over 73%. The p4 of Y 20424 and that of the damaged right mandible Y 31678 have three transverse ridges of the metaconid, entoconid and entostylid that are quite long, parallel and directed slightly posterolingually. The ridges are almost as large as those of *Hypsodontus sokolovi*, but the basal pillars on the molars are a difference. Y 20563 and Y 31678 are slightly smaller than the other specimens and are only tentatively placed in this species.

Two additional Kamlial horn core pieces may be linked with this species. One is Y 24196 from Locality Y 678 (15.1 Ma) and the second is Y 26401 from Locality Y 742 (15.2 Ma). In both horn cores the medial face is flatter than the lateral, and the horn cores are more compressed (66% and 69%) than in *Eotragus (E. minus* 82%, *E. noyei* 85%, *E. clavatus* 76% , the latter with

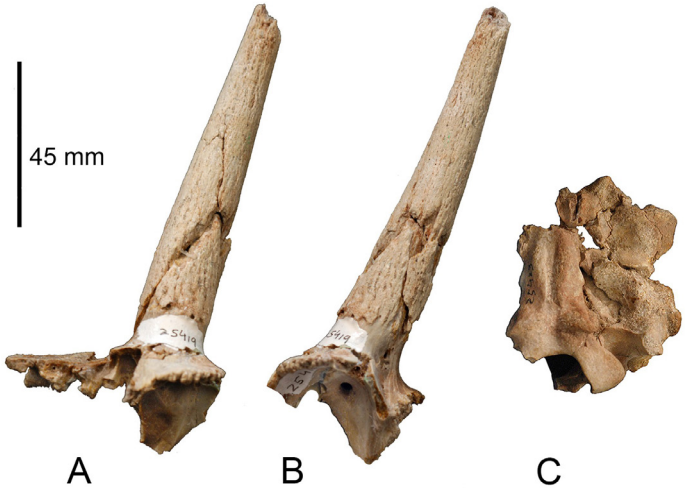

Figure 3. *Kubanotragus sokolovi*. Y 25419, left horn core in A) anterior and B) lateral views; Y 25423 basioccipital in C) ventral view. Scale 45 mm.

N = 5 and range 68-84%). At both ends of Y 24196 the cortex is wide and little spongiose, while the more spongiose medulla is of small extent. In later bovids the spongiose texture reaches close to the outer edges and any areas of solid cortex are much less evident. If they belong with the dental material the slightly compressed horn cores suggest this species might be a bovine, but they are not at all adequate for naming a new taxon.

Subfamily BOVINAE Gray, 1821

Tribe BOSELAPHINI Knottnerus-Meyer, 1907

The Boselaphini are by far the most important bovid group in the Siwaliks. Apart from *Eotragus*, they are first known from late in the Early Miocene in the Siwaliks if our new genus and species from the Vihowa Formation has been correctly placed. In East Africa and Russia boselaphines are only known from around the middle of the Middle Miocene, but only from near the end of the Middle Miocene in Europe. They became widespread in the Late Miocene and declined near its end. Only two species survive today, the Indian nilgai, *Boselaphus tragocamelus* and the small Indian four-horned antelope, *Tetracerus quadricornis*.

Fossil Boselaphini have been known since the middle of the 19th century when they were discovered at Sansan in France, Eppelsheim in Germany, and Pikermi in Greece. Subsequent work revealed their dominance in terms of numbers of preserved specimens in the Middle and Late Miocene of the Siwaliks of Pakistan (Pilgrim, 1937, 1939; Thomas, 1984a). The extinct genera may be informally arranged in two groups, both known from the Middle Miocene. (See Appendix 2 in Supplementary Online Materials where the characters of the groups are distinguished.) Group (A) has the appearance of a taxonomic miscellany but may have given rise to Bovini. Group (B) continues as a more coherent unit into the Late Miocene. Its generic names are in much disorder and in this paper we use only *Sivaceros*, *Miotragocerus* and *Tragoportax*. *Boselaphus* itself could be a survivor of either group.

Like other tribes of antelopes, Boselaphini are more easily identified by characters that evolve within the group than by those they all possessed from the beginning. Their horn cores have keels, may show heteronymous torsion, and often develop a sharp diminution in anteroposterior diameter (a demarcation) along their course. They usually show signs of anteriorwards growth or modification of horn core bases or their pedicels (Bohlin, 1935a; Thenius, 1948; Solounias, 1990: figures 12-15). In *Tetracerus* there is even an extra anterior pair of horns. Most species have hornless females. The pericel is often very short to absent. Strong temporal ridges on the cranial roof may have started as a means of bracing widely inserted and enlarging horn cores, and then persisted. Many boselaphines develop a rugose surface on the cranial roof behind the horn cores and between the temporal ridges.

Boselaphini retain numbers of primitive characters: the braincase roof does not become inclined on the face axis; the horn cores often remain inserted widely apart and above the back of the orbits; supraorbital pits are small; the preorbital fossa is large; the infraorbital foramen is situated low and anteriorly; the median indent at the back of the palate lies behind the lateral ones. The advances in tooth characters from what seems likely to have been the initial bovid condition are less far-reaching than those of Bovini, Tragelaphini, or Antilopinae and this hinders identification.

Genera long recognised as Bovini seem to have evolved from Boselaphini (Rütimeyer, 1878: 117, 160, 167; Pilgrim, 1939: 133, 136, plate 8; Bibi *et al*., 2009), perhaps from those of Group (A). Bovini gradually became large and heavy animals, which often have horned females, low and wide skulls with horn cores emerging transversely from postorbital insertions, sinuses extending far up the horn cores, shortened braincases, and occlusally complicated, hypsodont teeth. They may have evolved on several occasions and this plus Tragelaphini also being in the Bovinae cladistically (Hassanin *et al*., 2012) mean the Boselaphini are likely to be paraphyletic.

Genus *EOTRAGUS* Pilgrim, 1939.

Type species. *Eotragus clavatus* (Gervais, 1850 [In: Gervais, 1848-52]: 78). Sansan, France. Middle Miocene.

Diagnosis. Small to moderate sized bovids, with fairly short and not very thickset horn cores, level of maximum mediolateral width is positioned centrally along the anteroposterior cross section of the horn core, sometimes with a rudimentary anterior keel and some mediolateral compression, little divergence, moderately inclined to fairly upright insertions with a hint of distal forward curvature in side view, insertions wide apart and above the back of the orbits. Very restricted frontals sinuses near the supraorbital pits and at the base of the pedicel. Females hornless. Cranial roof strongly curved downwards posteriorly.

Teeth show the characters of early bovids: rugose enamel, rather low crowns, the four selenodont crests on the molars connecting centrally only in early middle wear, basal pillars on lower molars and usually on upper ones, remnants of

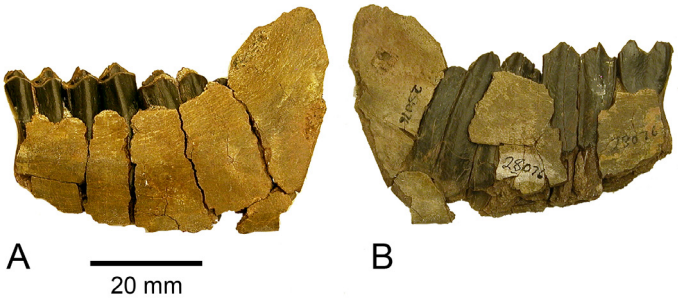

Figure 4. *Hypsodontus sokolovi*. Y 28076, part of left mandible with m1 to m3 in A) labial and B) lingual views. Scale 20 mm.

anterior and posterior cingula, and long premolar rows relative to molar rows. On upper molars styles persist into later wear, the paracone has a labial rib, central fossettes have a simple outline, and posterior part of M3s often noticeably small in early wear. Outbowings of the lingual walls of the lower molars are slight, metastylids lie centrally at the back of the metaconid and extend to the base of the crown, central fossettes have shallow V-shapes, labial lobes are pointed, and hypoconulid lobe of m3 are offset labialwards and usually curved with a concave lingual edge and a convex labial one. Labial ribs and central fossettes on upper premolars are forwardly placed and P2s and P3s often have a vertical groove in their lingual walls. Anterolabial walls of p3-p4 do not turn transversely, parastylid and paraconid of p3 and often p4 not differentiated, metaconid ridge directed diagonally backwards on p3s and sometimes on p4s, lingual end of this metaconid ridge sometimes with small anterior and posterior expansions on p4 and more rarely on p3, entostylid ridge on p3-p4 often as long as the entoconid ridge.

Comments. *Eotragus* is an early bovid best known from Europe. Made (2012) gave a comprehensive account of the type species at Sansan and designated a lectotype. Some specimens show a keel on the horn cores and there may be an approach to a roughened surface on the frontals, features of a boselaphine. Hornlessness of females has been asserted by Thomas (1977), Solounias and Moelleken (1992) and Made (2012). Solounias and Moelleken (1994) considered *E. clavatus* to be a browser. It flourished within the broad date range 15.0-13.0 Ma. *"Antilope" cristata* Biedermann (1873) from Veltheim, Switzerland constitutes another and smaller *Eotragus* within this time span (Made, 1989, 2012). An older small species is *E. artenensis* at 17.0-15.5 Ma (Ginsburg and Heintz, 1968; Alferez *et al*., 1981: plate 1 figures 1,2; Moyà Solà, 1983: plate 1 figures 1,2). *Eotragus halamagaiensis* and *E. lampangensis* come from the Middle Miocene of Asia (Ye, 1989; Suraprasit *et al*., 2015).

Species *Eotragus noyei* Solounias, Barry, Bernor, Lindsay, and Raza, 1995

Eotragus noyei Solounias *et al*., 1995a: 807, figures 2-3.

Holotype. GSP Y 31616, left horn core with superior orbital margin, from Locality Y 747 (17.9 Ma).

Diagnosis. E. *noyei* is smaller than most other species of *Eotragus* and has a horn core profile which, in lateral view, is less concave anteriorly and less convex posteriorly.The horn core is situated more vertically (46°) than any of the other *Eotragus* species (usually 40°). An incipient anterior keel is restricted to the apical region, unlike the continuous faint keel in *E. sansaniensis.* The horn core is short, whereas it is longer in *E. artenensis* and *E. cristatus*. Upper molars are most similar to those of *E. sansaniensis,* although much smaller. The buccal walls of the upper molars, especially of the metacone, are more inclined than in other *Eotragus.* Because of this metaconal inclination, the metastyle is rotated in relation to the anteroposterior tooth axis and thus situated more lingually. The M3 metaconule is notably smaller than the protocone, whereas in other *Eotragus* species it is relatively larger. The entostyles are small and the postmetacrista is short.

Estimated age. 17.9 - 16.8 Ma.

Material.

Locality Y 747 (17.9 Ma)

Y 31616 left horn core. Holotype (Solounias *et al*., 1995a: figure 2).

Y 41459 right maxilla with P2 and M1-M2 (Solounias *et al*., 1995a: figure 3).

Discussion. The holotype horn core, Y 31616, has an incipient anterior keel apically. Its index is 86% and it is smaller than nearly all other *Eotragus* species (Suraprasit *et al*., 2015: figure 5). Dental and other remains from Locality Y 747 and elsewhere were also referred to *E. noyei*. The assigned upper teeth (Solounias *et al*., 1995a: figure 3) were about the size of *E. artenensis*. The occlusal length of M3 at 10.4 is slightly less than that of M2 at 10.7 and the metaconule (posterolingual) crest of the M3 is rather small (Appendix 3, character 39). This is a species smaller than *Palaeohypsodontus zinensis*.

Eotragus minus Ginsburg, Morales, and Soria (2001: 166, figures 9 [4A-D] – 11) was based on a holotype horn core from Dera Bugti level 6 and other pieces. The horn core has a basal index of 12.3×10.1 (82%) and is even smaller than the *E. noyei* holotype, but the very slight compression and the appearance on the illustration of a distal anterior keel are resemblances to *E. noyei*. *E. minus* may be as old as ca. 22 – 20 Ma (Antoine *et al*., 2013: figure 16.4B). Both *E. minus* and *E. noyei* appear to be slightly older than *E. artenensis* in Europe (e.g. Made, 2012: figure 122).

Namacerus gariepensis Morales, Soria, Pickford, and Nieto 2003 from Arrisdrift, Namibia, is an African bovid of late Early Miocene age, approximately 17.5 Ma (Pickford and Senut, 2003). It differs from *E. noyei* by its slightly smaller size and shorter horn cores. The horn cores (only just bigger than in *E. minus*) have few or no characters differing from *Eotragus*, but the species is claimed to be generically separate on its tooth characters. The best characters for this purpose might be greater hypsodonty, crescents less well joined up, lower molars with a weaker metastylid, linear disposition of metaconid-entoconid, and m3 hypoconulid lobe with a central fossettte and lingual wall not offset labialwards. Small size in itself, however, may have imposed neotragine-like features on the teeth.

Khan, A.M. *et al*. (2021) reported this species from the Late Miocene Dhok Pathan Formation, which would be a very large chronostratigraphic range extension. However, their small sample consisted only of teeth, which can easily be confused with other small boselaphines.

CARINAMERYX genus nov.

Type and only included species. *Carinameryx lindsayi* species nov.

Diagnosis. A very small species (9 -11 kg). Horn core differs from those of other small taxa such as *Eotragus, Namacerus,* and *Elachistoceras* in that it has a salient anteromedially descending keel which continues distally to the tip, while the posterior face is rounded and without keels. At the base maximum mediolateral width is positioned anteriorly along the anteroposterior cross section. Horn core without demarcation, mediolaterally compressed (69%) with some flattening of the medial surface, little or not at all curved backwards in side view, shaft straight. Horn core without internal sinuses, surface texture relatively smooth. Skull high and narrow with occipital narrowing upwards and backward-projecting as in *Sivaceros*, but the occipital surface not as flat as in *Sivaceros*. The skull roof gently curved in profile throughout its length as in duikers, occipital condyles relatively large, posterior basioccipital tuberosities distinct and sharp. Dentition brachyodont.

The generic name refers to the horn core keel.

Carinameryx lindsayi species nov.

Genus and species indet. Solounias *et al*., 1995a: 811, figures 5, 6.

Unnamed Genus and Species Barry *et al*., 2005: 26.

Holotype. GSP Y 46299, left horncore (Figure 5). From Locality Z 120 (18.3 – 18.1 Ma) at 30° 3.99'N , 70° 21.71'E. Corrleated to Section C and 117 meters above the base (Lindsay *et al*., 2005).

Diagnosis. As for the genus.

The trivial name is for our late mentor and friend, Professor Everett Lindsay, who initiated collecting and stratigraphic studies in the Zinda Pir Dome where the holotype was found.

Estimated age. (18.3 - 17.9 Ma).

Material.

Locality Z 120 (18.3 - 17.9 Ma)

Y 46299 Left horn core. Holotype, (Solounias *et al*., 1995a: figures 5A-C).

Y 46302 Crushed braincase (Solounias *et al*., 1995a: figures 5D-E). Probably the same individual as the holotype horn core.

Z 219 Right maxilla, P3-M3.

Discussion. Solounias *et al*. (1995a) recorded skull and dental pieces of a small boselaphine at Locality Z 120 in the Vihowa Formation, some of which could have been of a single individual. The size of the animal is close to that of *Eotragus noyei*, but the holotype horn core (Y 46299), which appears to be almost complete, has an anterior keel descending from the distal end and turning anteromedially at the base. The posterior side is cylindrical with no keels. With an index of 69%, the horn core is more compressed than in *Eotragus noyei*. Its surface is finely striated and internally there are no sinuses. The small crushed braincase Y 46302 (Solounias *et al*., 1995a: figure 5) has a U-shaped occipital as do most bovids, but narrows upwards as in the later and larger *Sivaceros* although the occipital surface is not as flat. The occipital condyles are relatively large and, with the occipital, are strongly backward-projecting. The posterior basioccipital tuberosities are distinct and sharp. In lateral view the skull roof is gently curved in profile throughout its length as in duikers and the temporal ridges probably approached closely posteriorly.

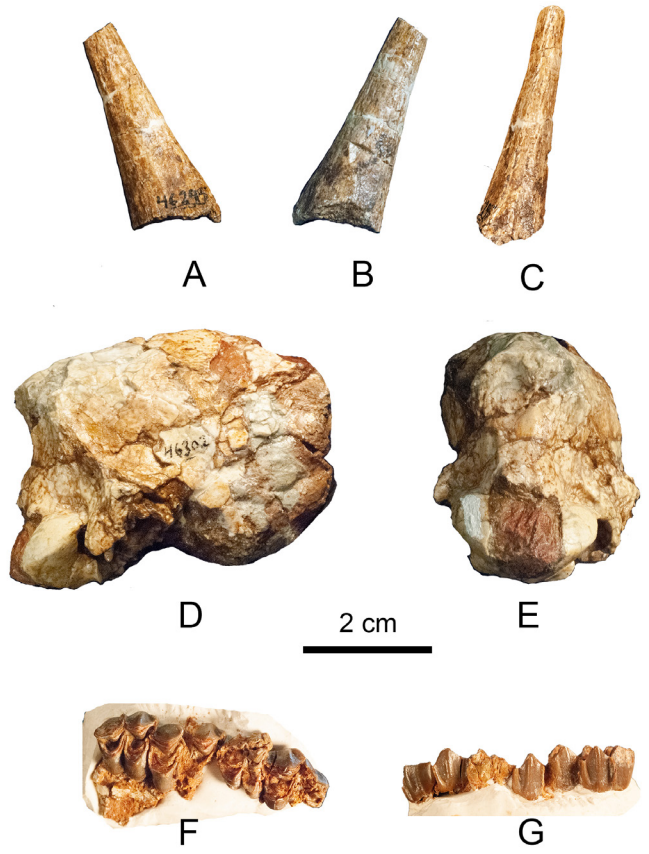

Figure 5. *Carinameryx lindsayi* new genus and species. Y 46299, left horn core, Holotype, in A) medial, B) lateral, and C) anterior views. Y 46302, crushed braincase in D) right lateral and E) posterior views. Z 219 Right maxilla with P3-M3 in F) occlusal and G) lateral views. Scale 2 cm.

The upper teeth of Z 219 (Solounias *et al*., 1995a: figure 6) are about the size of *Eotragus noyei* and too small for *Palaeohypsodontus zinensis*. The molars show smooth enamel, a flat metacone labial wall which is not slanted lingually as in *E. noyei*, the rear crest of the protocone fully curved round labially, and transversely long protocone lobes, both of which fit Bovidae. The M3 has a small posterior part. The P3 of Z 50 is transversely narrow, with the small rear part of the central fossette almost separate from the front part. A right maxilla Z 2460 has a broken M1 and M2 and intact M3. These upper teeth show a large basal pillar on M1 and moderate sized ones on M2 and M3, which is unlike the ?Hypsodontinae sp. described above and nearly all other early or unspecialised bovids. But this is possibly an individual character. The lower molars of Z 2458 also differ from *P. zinensis*. The lobes are better joined up, basal pillars are small and decline in size on posterior molars, the metastylid is obvious in early wear, and the lingual walls have salient ribs especially on the anterior lobe. The m3 has an anterior cingular fold which does not become a goat fold, while its hypoconulid is an unlooped flange. Unlike the horn cores, it is not likely that many or any of these tooth characters will be good differences from *Eotragus* at a generic level. The proximal metatarsal Z 61 has a large naviculocuboid facet and its articular surface is anteroposteriorly shorter than it is wide, reminiscent of modern *Capra*.

Comments. With a first appearance between 18.3 and 17.9 Ma, if the attribution to Boselaphini is correct, this would be the earliest member of that tribe other than *Eotragus*.

Genus *ELACHISTOCERAS* Thomas, 1977

Type species. *Elachistoceras khauristanensis* Thomas, 1977

Diagnosis. Small, close in size to the African grysbok, *Raphicerus melanotis*. Horn cores short, straight, of small dimensions, and with an irregularly oval cross section, inclined backwards and exhibiting a slight anterior curvature (concavity). They were inserted on the cranial vault and not laterally on the dorsal orbital rim as in Neotragini. Teeth rather brachyodont and smaller than in *Eotragus noyei*. The P3 is notably less wide mesially than distally. The P4 is rather triangular.There are no lingual basal pillars. The p4 and p3 are lingually open (no walls). The mandible is deeper below m3 than below the premolars.

Thomas listed paratypes from the type Locality Y 182 and the contemporaneous Locality Y 243 and dealt with other material. He believed (Thomas, 1977: 376) that the position of the horn core insertions in *Elachistoceras khauristanensis* was different from that in the African Neotragini and this presumably was a reason for him to assign the species to the Boselaphini. We have incorporated his opinion into the preceding diagnosis.

Species *Elachistoceras khauristanensis* Thomas, 1977

Elachistoceras khauristanensis Thomas, 1977: 376: plate 15 figure 1a-b. Type species.

Holotype. GSP Y 4262, left horn core, from Locality Y 182 (9.2 Ma).

Diagnosis. As for the genus.

Estimated age. 14.1 - 8.5 Ma.

Material.

Locality Y 650 (13.1 Ma)

Y 31305 Horn core.

Locality Y 243 (9.3 Ma)

Y 7326 Horn core. Paratype (Thomas, 1977: plate 15 figures 3a-b).

Locality Y 182 (9.2 Ma)

Y 4262 Left horn core. Holotype (Thomas, 1977: plate 15 figures 1a-b).

Y 4278 Right mandible with m 1-2 and anterior part of m3. Paratype (Thomas 1977: plate 15 figure 4a-c).

Y 7037 Right horn core. Paratype (Thomas, 1977: plate 15 figure 2).

Y 12528 Right P2. Paratype (Thomas, 1977: plate 15 figure 5).

Y 7047 Right M1. Paratype (Thomas, 1977: plate 15 figure 6).

Discussion. Fossils of small bovids are found through a long interval of Middle and Late Miocene Siwaliks sediments (14.1 Ma to 8.5 Ma) and separation of small Antilopinae from a tiny boselaphine is difficult. It is extremely likely that if *E. khauristanensis* were not a heterogeneous taxon to begin with, then we and other authors have made it so. We have listed in Appendices 4 and 5, fairly arbitrarily, a selection of specimens over a long time range which are too small to be gazelles and do not show any traits by which they might be excluded from *Elachistoceras*. There are 312 specimens of this species in our Siwalik database, of which 63 are older than 10.7 Ma. The oldest horn core, Y 31305, dates from 13.1 Ma. It has one surface flattened and its largest diameter diminishes more quickly than in Thomas's later horn cores. Asim *et al*. (2024) have also reported this species from the Chinji Formation, as have Khan, M. A. *et al*. (2013) and Samiullah *et al*. (2020).

Many tooth characters on the specimens are unremarkable and may be interpreted as inherited from earlier bovids or pecoran ancestors or constrained by the small size of the species, for example: brachyodont or mesodont dentitions; basal pillars moderate to large on m1 and diminishing in size along the lower molar row; premolar rows long in relation to molar rows; labial walls of upper molars with modest styles and with a rib on the paracone and a slighter outbowing on the metacone; rear central fossettes of upper molars sometimes with a spur from the lingual wall; rear lobe of M3 small in relation to front lobe; labial lobes on lower molars pointed but usually not noticeably narrowed; an anterolabial cingulum may be present; p4 transverse metaconid ridge passes slightly backwards; p3 and p4 with long entoconid and entostylid ridges posteriorly; p3 and p4 hypoconids with little labial projection (rather more in Y 25031); metastylids in earlier wear on lower molars may be placed slightly anteriorly to the rear end of the metaconid crest; a fairly shallow horizontal ramus of the mandible.

The spur in the rear central fossettes of some upper molars may have been present in pecoran ancestors but also reappears much later as part of the armoury of boödont teeth. The m3 on Y 28155 has a moderate to large basal pillar and the front of the hypoconid anterior crest is still not joined to the rest of the tooth in middle wear, both of which characters look primitive.

Some characters may be characteristic of the genus or species: basal pillars absent on upper molars; lingual lobes of upper molars slightly turned forwards in later wear; lingual walls of lower molars with two outbowings, more localised in early wear than later on; m3 third lobe with a central fossette at least in early wear and with its lingual wall not slanting labially; p4s sometimes with the anterolabial wall turned transversely at its front; p3s and p4s with some differentiation of parastylid and paraconid; p4 transverse metaconid ridge sometimes with posterior and anterior expansions at its lingual end as in Y 25031.

The metatarsal Y 45979b has less of an anterior longitudinal groove on its shaft than shown in the example of Thomas (1977: plate 15 figure 14).

Comments. The number of species of small antelopes in extant African faunas (Neotragini and some Cephalophini) exceeds that in Old World Miocene faunas generally, but it is not known whether this is an artefact of taphonomy and collecting techniques over the last 170 years or whether it reflects a former rarity of such species. Material in the Hungarian Geological Survey, Budapest, of the *nomen nudum Lagomeryx celer* Kretzoi 1954 from the Late Miocene of Csákvár is of a bovid still smaller than *Elachistoceras khauristanensis*.

Genus *STREPSIPORTAX* Pilgrim, 1937.

Type species. *Strepsiportax gluten* Pilgrim, 1937.

Diagnosis. Small to moderate sized Boselaphini with low and wide skull. Horn cores with strong anterior keel and a posterolateral edge or keel, somewhat compressed mediolaterally, some flattening of the lateral surface, slightly to moderately diverging at the base, inclined backwards, inserted widely apart. A tendency to forward growth of the horn pedicels. Sinuses within parts of frontals and later in front part of pedicels as well. Frontals not raised between horn bases, braincase roof curving downwards posteriorly in side view. Females hornless.

Strepsiportax is found in the Chinji Formation where it co-exists with the similar-sized boselaphine *Sivaceros*, from which it differs in skull architecture. Thenius (1956) sank the genus *Strepsiportax* in the Middle Miocene European *Protragocerus* and was followed by Gentry (1970) and Thomas (1984a), but the view of the present authors is that the type species, *P. chantrei*, is too poorly known to sustain comparisons with other genera, as was noted by Pilgrim (1937: 758).

Strepsiportax meyeri species nov.

Holotype. GSP Y 51471, crushed skull with horn cores and left P2, P4-M3 (Figure 6). From Locality Y 811 (13.4 Ma) at 32° 41.19'N, 72° 24.04'E. Correlated to the K4/KR4 section between 114.5 and 112.0 meters above the base (Sheikh, 1984; McRae, 1990).

Diagnosis. A *Strepsiportax* lacking some of the advanced characters of *S. gluten*. Horn cores not very long, compressed mediolaterally, a variably developed posterolateral keel, the horn cores diverge little, divergence altering little along the course of the horn cores, often a slight backward curvature, poor or no demarcation, sinuses in parts of frontals and just reaching into the front of the pedicels, a large shallow postcornual fossa. The supraorbital pits are small, narrow and wide apart. The

dorsal orbital rims project slightly but are too narrow to form a horizontal shelf. The nasals are long and narrow and look flat on the top rather than transversely curved. The preorbital fossa is very large. The premaxillae rise to a contact with the nasals. The back of the braincase roof may be down turned in profile. The basioccipital is small and the anterior tuberosities localised and close together. The posterior tuberosities are not too wide apart so the basioccipital as a whole is not very triangular in shape. The basioccipital has a short longitudinal groove between the anterior tuberosities but no other grooves or ridges. It has no transverse constriction centrally. The low and wide skull is different from *Sivaceros* and *Helicoportax*, while *Sivoreas* has horncores twisted around a straight axis. Compared to *Eotragus* the horn cores are relatively larger, more inclined and slightly curved backwards in lateral view as well as more transversely compressed with the lateral surface flatter than the medial.

The trivial name is for our late colleague Grant Meyer, who oversaw the collecting and stratigraphic work of the Harvard-GSP project in its early years.

Estimated age. 14.1 - 12.4 Ma.

Material.

Locality Y 478 (14.1 Ma)

Y 25422 Frontlet with both horn cores.

Y 51500 Frontlet with intact horn cores.

Locality Y 640 (13.7 Ma)

Y 20575 Crushed skull, hornless in life. Associated left maxilla with P3, P4, and M2-3, and left mandible with roots of p2-p3 and crowns of p4-m3 and left scapula, distal right tibia, third cervical vertebrae, and fragment of a lumbar vertebrae.

Y 28001 Frontal with complete left horn core.

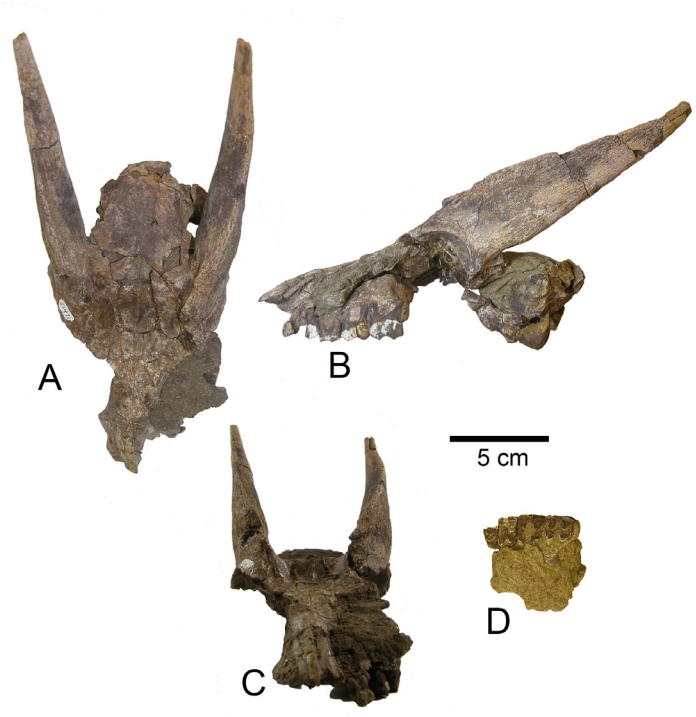

Figure 6. *Strepsiportax meyeri* new species. Y 51471 holotype, crushed skull with horn cores in A) dorsal, B) left lateral, and C) anterior views. D) maxilla (P4-M3 only). Scale 5 cm.

Locality Y 59 (13.7 Ma)

Y 20600 Right horn core.

Locality Y 787 (13.7 Ma)

Y 31882 Skull with dP3-M1, hornless in life.

Locality Y 811 (13.4 Ma)

Y 51471 Crushed skull with nearly complete left and right horncores and P2-M3 (P3 crown missing). Holotype.

Discussion. The crushed holotype skull (Figure 6) allows us to see the size of the teeth and provided much of the information for the diagnosis. Many characters do not differ from *Eotragus*, while others are more advanced but shared with several bovid tribes. Compared to *Eotragus* the horn cores are larger in relation to skull size and often attain a moderate length, they are more compressed transversely, their lateral surface is generally flatter than the medial one although this is not pronounced, and they are more inclined in side view and sometimes slightly curved backwards in side view.

The immature skull Y 31882 was hornless in life. On the left side the nuchal crest outline looks concave upwards like *Sivaceros* and unlike *Strepsiportax gluten*, but distortion makes it difficult to be sure of the overall shape of the occipital. The median indentation at the back of the palate lies behind the level of the lateral ones. The back of the cranial roof was downturned, perhaps quite sharply at the bregma. Y 20575, a dorsoventrally crushed skull, was also hornless in life.

In Y 26846, a partial cranium with the left horn core pedicel, the top of the frontals behind the horn cores could have been rugose which favours *Sivaceros* as an identification, but it cannot be established that the temporal lines approach so closely posteriorly as they would in a *Sivaceros*.

Teeth are present on three specimens in this species but not in the other species of *Strepsiportax* or in *Sivaceros*. Middle Miocene Siwaliks boselaphine teeth will be discussed later.

Characters vary greatly in this species but do suggest, over time, a gradual approach towards *Strepsiportax gluten*. The horn core Y 20600 (13.7 Ma) (Figure 7B, C) appears transitional towards *S. gluten* in that there are signs of the diminution of the anteroposterior diameter concentrated in the centre of its course. It is definitely not a *Sivaceros* despite its compression. Y 28001 is an interesting horn core (Figure 7F). It is long (149 mm) and slender. Its degree of divergence diminishes distally, and its anteroposterior diameter gradually diminishes (an incipient demarcation) in the middle of its length. It also suggests a transition from *S. meyeri* to *S. gluten* despite its age of 13.7 Ma. It is also like the contemporaneous *Kipsigicerus labidotus* Gentry 1970 at Fort Ternan in East Africa.

Comments. Some of the characters of *Strepsiportax meyeri* which differ from *S. gluten* are resemblances to *Sivaceros antecedens* new species: more compressed horn cores, less divergence, and perhaps a weaker demarcation. The crushed hornless (female) skull Y 20575 also suggests that the occipital edges may not have been so smoothly convex upwards as in the *Strepsiportax gluten* holotype (Pilgrim, 1937: figure 14). All this is to be expected and does help to close the striking morphological gap between the two more advanced species *Strepsiportax gluten* and *Sivaceros gradiens*. Judged from the teeth on the holotype *S. meyeri* (in late wear it should be remembered), the premolars are shorter than in *Eotragus* at Sansan although the molars are of equal or greater length (Figure 8).

Species *Strepsiportax gluten* Pilgrim, 1937

Strepsiportax gluten Pilgrim, 1937: 758, figures 12-15.

Strepsiportax chinjiensis Pilgrim, 1937: 764, figures 16-17.

Holotype. AMNH 19746, cranium with horn cores, from Locality B 11, 4½ miles (7.2 km) west of Hasnot, with an estimated age of between 11.2 and 10.8 Ma (see Appendix 1). The holotype of *S. chinjiensis* is a similar cranium, AMNH 19450, from Brown's Locality B 60, 12 miles (19.3 km) east of the Chinji bungalow. We estimate the age of that locality at between 11.3 and 11.0 Ma (Appendix 1), making AMNH 19450 and the *S. gluten* holotype two of the youngest known specimens of the species.

Diagnosis. A *Strepsiportax* differing from the preceding species in having horn cores with a more definite posterolateral keel, the degree of divergence lessening more strongly distally, a straighter course in side view, a stronger demarcation between the proximal part of the horn core and its more attenuated tip, more torsion, and sinuses more extensive within the pedicels.

Estimated age. 12.4 - (11.2 - 10.8) Ma.

Material.

Locality Y 706 (12.3 Ma)

Y 32816 Right horn core.

Locality Y 756 (11.6 Ma)

Y 28096 Left horn core and part of frontal.

Locality Y 76 (11.4 Ma)

Y 1927 Left horn core.

Y 25055 Left horn core, probably same individual as Y 5333.

Locality B 60 (11.3 – 11.0 Ma)

AMNH 19450 Edentulous cranium with both horn cores, occipital, and damaged basioccipital. Holotype of *S. chinjiensis*.

Locality Y 798 (11.1 Ma)

Y 40952 Left horn core piece.

Locality B 11 (11.2 – 10.8 Ma)

AMNH 19746 Edentulous cranium with both horn cores and an intact occipital and damaged basioccipital. Holotype.

Discussion. The species ranges from 12.4 to perhaps as young as 10.8 Ma. There may be a brief temporal overlap with *Strepsiportax meyeri* and earlier specimens are difficult to separate from that species. Between around 12.3 and 12.1 Ma a number of variable characters not present in *S. meyeri* become more regular and normal although there is still considerable variability. The horn cores become slightly straighter in side view, presumably a reversal from the earlier slight backward curvature in *S. meyeri*. However, some continue to have a slight backward curvature as in Y 28096. The degree of divergence is also generally less, although Y 1927 has quite a curved course in anterior view (Figure 9B). The posterolateral keel is more definite and the demarcation stronger, although not in Y 25075 nor Y 28096. Sinuses in *S. gluten* are generally more extensive, but still variable. They are not present in Y 25465, but horn cores from Locality Y 76 have large sinuses which extend well up in the front half of the pedicel and also far posteriorly at a low level in the pedicel. In Y 10199, which is also from Locality Y 76, the single large sinus in the front of the pedicel lies more centrally and extends further posteriorly at a low

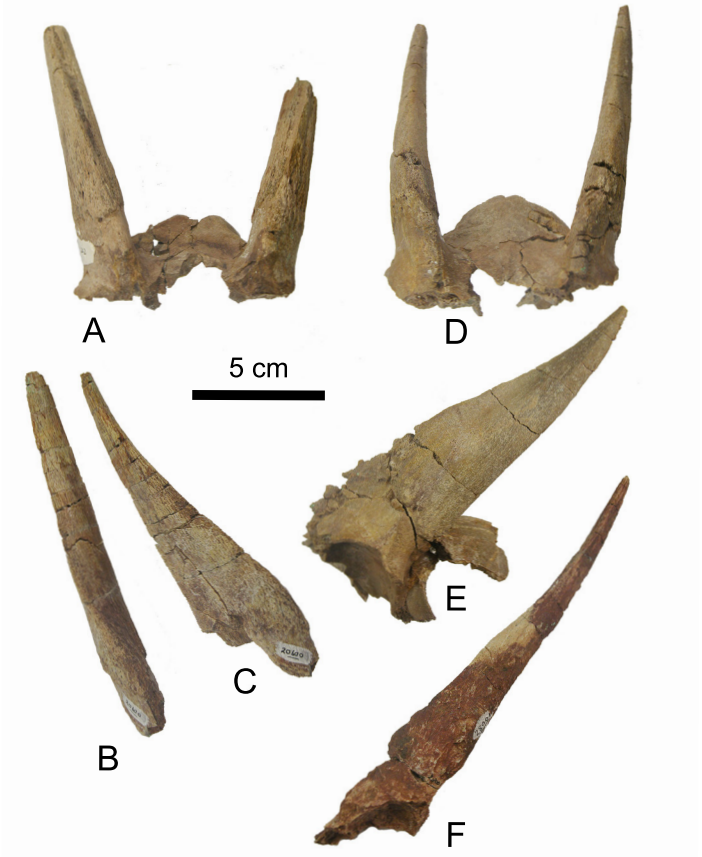

Figure 7. *Strepsiportax meyeri* new species. Y 25422, frontlet in A) anterior view; Y 20600 right horn core in B) anterior and C) lateral views; Y 51500 frontlet with intact horncores. in D) anterior and E) left lateral views. Y 25001, left horn core in F) lateral view. Scale 5 cm.

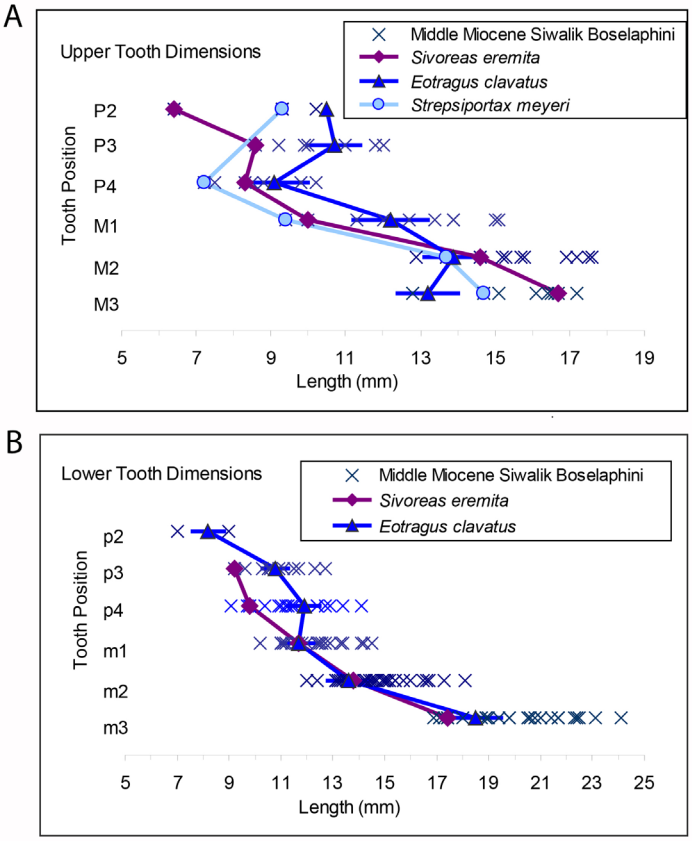

Figure 8. Lengths of premolars and molars of Middle Miocene Siwalik and Eurasian bovids. A) upper dentitions, B) lower dentitions. The cross bars attached to *Eotragus clavatus* are plus/minus one standard deviation.

level in the pedicel. Finally, flattening of the lateral surface of the horn cores is sometimes more obvious and basal divergence may slightly exceed that of *S. meyeri*.

Other characters remain as in *Strepsiportax meyeri.* The level of maximum transverse thickness usually remains central (Y 25066), presumably because of the absence of any appreciable tendency for the proximal part of the horn core to become forwardly extended and in so doing shift the point of maximum transverse thickness posteriorly. However, in Y 28096 the level of maximum transverse diameter lies quite posteriorly. The degree of compression is variable so there is no clearcut change, but the mean index and Figure 10A suggest that compression in *S. gluten* is less than in *S. meyeri* and is close to *Protragocerus chantrei*. (*Kipsigicerus labidotus* is compressed because of the anterior expansion of its horn core bases.) Despite the flatter lateral surface there is still no curving round of its anterior part to meet the anterior keel (Y 27961).

The horn core piece Y 40952 has two keels, with one side flatter than the other and clockwise torsion. If the horn core belongs to a boselaphine, as we believe it does, it must be from the left side, in which case the flat side must be lateral and the horn core therefore could well be a *Strepsiportax*. The anteroposterior dimension reduces markedly over the preserved length of around 45 mm.

Y 32327 is a complete right metatarsal with a length by minimum transverse diameter of shaft 170×15.1 and anteroposterior by mediolateral diameters of the proximal and distal articulations of 24.0×24.3 and 17.5×27.5 respectively. It looks slightly swollen at the distal end and the flanges on the articular surface are not well-marked, characters which would not be remarkable in a Middle Miocene boselaphine.

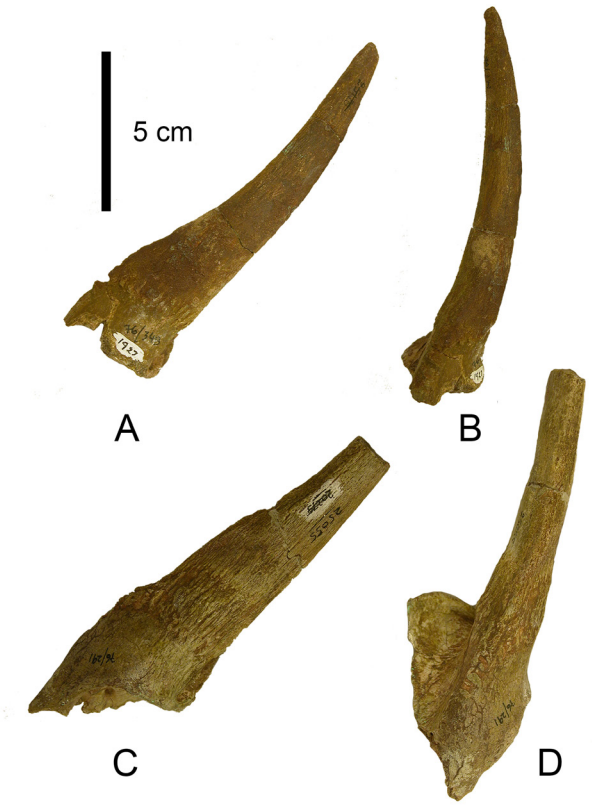

Figure 9. *Strepsiportax gluten*. Y 1927, left horn core in A) lateral and B) anterior views; Y 25055, left horn core in C) lateral and D) dorsal views. Scale 5 cm.

It is a bit longer than six metatarsals at Fort Ternan assigned to *Kipsigicerus labidotus* by Gentry (1970) and having mean length and shaft thickness of 155 × 12.0. The Siwalik locality is 12.0 Ma and has records of a *Strepsiportax gluten* horn core and a boselaphine p3-m3 and on this basis we tentatively attribute the metatarsal to *S. gluten*. But we cannot exclude the possibility of it belonging to the *Sivaceros*, *Sivoreas*, or *Helicoportax* species discussed below.

The holotype (AMNH 19746), the holotype of "*S. chinjiensis"* (AMNH 19450), and Y 40952 are the youngest known specimens of the species.

Comments. *Strepsiportax gluten* possibly evolved from *S. meyeri* in the interval 12.7-12.2 Ma. The demarcation will have evolved independently from that in *Sivaceros.* Several authors, among them Khan, M. A. *et al*. (2013), Abbas *et al*. (2021) and Draz *et al*. (2021), have attributed Pilgrim's species *Strepsiportax gluten* to *Miotragocerus*, following suggestions by Solounias (1981: 115). The two genera, however, are quite different, with *Strepsiportax*, in contrast to *Miotragocerus*, tending to have low wide skulls, with the horn core insertions widely apart and more divergent at the base, and frontals not raised between horn bases.

Strepsiportax gluten shows certain resemblances to *Tragoportax salmontanus*, especially its steady diminution in degree of divergence. Towards the end of its known stratigraphic range, at 11.6 Ma, the pedicel of the horn core Y 28096 extends forward as a ridge in front of the horn core base. Then, at 11.4 Ma the horn cores Y 5333 and Y 25055 (Figure 9) show an enlarged pedicel with its anterolateral surface becoming convex at a fairly low level as the pedicel passes forwards. A relationship to the later *T. salmontanus* is, however, unlikely.

Another interesting comparison is with *Kipsigicerus labidotus* at Fort Ternan. The male skull of the latter shows a rather low and wide cranium, an approach to a condition like *Strepsiportax gluten*. The horn cores show enhanced anteromedial growth of their pedicels and lower parts. The prominent demarcation (Gentry, 1970: plate 2 figure 1) is more obvious than in *S. gluten*. The steady diminution in degree of divergence from base to tip of the horn cores is also marked in anterior view and again reminiscent of *S. gluten*. Fort Ternan is dated to 13.8 Ma and therefore contemporaneous with *S. meyeri* rather than *S. gluten.*

Austroportax latifrons Sickenberg, 1929 was described on a single cranium with horn cores from Hollabrunn (formerly Oberhollabrunn), Austria, of Middle to Late Miocene transitional age (Sickenberg, 1929; Fuss *et al*., 2015: figure 2). It is also known from the Spanish Vallesian (Moyà Solà, 1983). The cranium was low and wide, the horn cores very compressed and inserted widely apart, and the degree of divergence diminishing distally. These and other characters mostly resemble *Strepsiportax* and, interestingly, a strong posteromedial keel is a resemblance to the Siwaliks *Helicoportax* to be discussed below.

Genus *SIVACEROS* Pilgrim, 1937.

Type species. *Sivaceros gradiens* Pilgrim, 1937.

Diagnosis. Small to moderate sized Boselaphini, skulls high and narrow. Horn cores with anterior keel and a posterolateral edge or keel, compressed mediolaterally, some flattening of the lateral and medial surfaces, very little divergent and with some lessening of its degree distally, inclined backwards, little or not

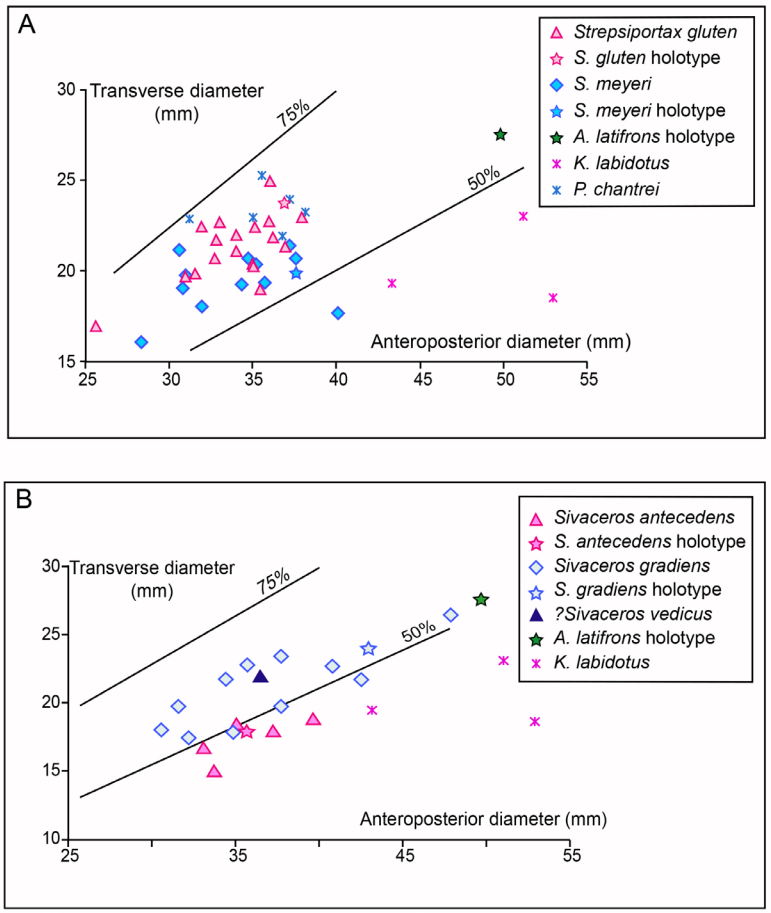

Figure 10. Basal diameters of horn cores. A) of *Strepsiportax* and some of its relatives. B) *Sivaceros* and some of its relatives. Measurements are given in Appendix 4. In both parts the upper diagonal line is that along which transverse diameter is 75% of anteroposterior diameter and the lower line is 50%. Horn cores with more transverse compression lie towards the right and towards the base of the diagram. *Austroportax latifrons* is a European species and *Kipsigicerus labidotus* an African species.

at all curved backwards in side view, a demarcation on the horn cores. Sinuses probably existed within parts of frontals, dorsal orbital rims not horizontal. Back of braincase bent downwards, sometimes sharply at the bregma, a rugose surface on the frontals behind the horn cores, temporal lines approach closely posteriorly, side edges of occipital surface are concave upwards so that the upper part of the occipital is markedly narrowed, paired vertical ridges on the occipital rise from above the lateral edges of the foramen magnum and diverge slightly in their higher parts. Occipital condyles are relatively large and, with the occipital, are strongly backward-projecting. No teeth have been found in association with fossils of *Sivaceros*

Sivaceros coexists with *Strepsiportax* and has hitherto been well differentiated by skull and horn core morphology. But in the older species of each genus the differences diminish. Thenius (1956) made *Sivaceros* a junior synonym of *Miotragocerus*, but while close relationship or generic identity is possible, we retain *Sivaceros* for the present because it is Middle Miocene, restricted to the Siwaliks, and has some morphological differences from *Miotragocerus*. Compared to *Sivaceros*, horn cores of *Miotragocerus* have more definite posterolateral keels with the maximum transverse width more posterior, the sinuses penetrate further into the horn cores, the intercornual ridge of the frontals is more prominent and the cranium is lower and wider with its roof more downturned posteriorly.

Sivaceros antecedens species nov.

Holotype. GSP Y 23415, cranium with base of left horn core (Figure 11). From Locality Y 669 (13.8 Ma) at 32° 74'N, 72° 27.79'E. Correlated to the IR-1 section between 62.6 and 58.5 meters above the base (McRae, 1990).

Diagnosis. A small *Sivaceros* lacking some of the advanced characters of *S. gradiens*. Short horn cores inserted fairly widely apart, a large shallow postcornual fossa, sinuses restricted to within parts of frontals, horn core more compressed (45% - 51%), the front of the cranial roof in profile at a higher level than the top of the face, the back of the cranial roof bent down rather sharply at the bregma.

The trivial name is in reference to coming before *Sivaceros gradiens*.

Estimated age. 14.1 - 13.4 Ma.

Material.

Locality Y 478 (14.1 Ma)

Y 25027 Right horn core base.

Locality Y 758 (14.2 – 13.9 Ma)

Y 28469 Fragment of skull with right horn core.

Locality Y 694 (13.9 Ma)

Y 26410 Distal horn core.

Locality Y 669 (13.8 Ma)

Y 23415 Cranium with left horn core base. Holotype.

Y 23416 Left and right horn cores.

Discussion. *Sivaceros antecedens* ranges from 14.1-13.4 Ma, earlier than previously recorded *Sivaceros*, and shows character differences from contemporaneous *Strepsiportax meyeri*. The horn cores are more compressed, their medial as well as lateral surfaces are flattened, and divergence is probably less. The demarcation along the course of the horn core is a clear boselaphine feature, better developed than in *S. meyeri*. The demarcations on Y 28469 (Figure 12A, B) and Y 26410 are

the earliest localised demarcations in the Siwaliks although the earlier Y 25027 has a front edge with what could be the top of a step. The horn insertions may be closer than in *Strepsiportax*. If true this would be linked with the narrow skull and not with pedicels approaching one another as occurs in one or two *Strepsiportax gluten* specimens. The holotype cranium shows sloping dorsal orbital rims and quite a wide mastoid facing posteriorly. The rugosity of the frontals' surface behind the horn cores, narrow cranium, and occipital morphology are further differences from *Strepsiportax*. The high and narrow cranium of the holotype contrasts to the very low and wide cranium of *Strepsiportax meyeri.* Both states probably developed from the intermediate condition seen in *Eotragus* and other early pecorans.

Sivaceros antecedens appears to be more primitive in its shorter horn cores than *Strepsiportax meyeri*. The sharp bending down of the cranial roof at the bregma as seen in the holotype (Figure 11D) would also be primitive. *Strepsiportax* almost certainly had downwards curvature posteriorly and it was fairly sharp at the bregma in the immature *S. meyeri* skull Y 31882. Temporal lines approach closely posteriorly in *Sivaceros* either because this is primitive or because the cranium was narrow. In addition the braincase sides are locally narrowed on either side of the temporal lines where they are closest.

Comments. A major question for boselaphine phylogeny is whether any species of *Sivaceros* gave rise to *Miotragocerus*, which appears in Europe in the earliest Late Miocene. A possible intermediate is *Paratragocerus caucasicus* Sokolov 1949 from Belometchetskaja, which seems to have preceded boselaphines in western Europe (see Appendix 2 for nomenclatural difficulties with *P. caucasicus*). Horn cores of *Paratragocerus caucasicus* have a long-oval cross section with a convex lateral surface, are almost parallel, show no curvature in anterior view (Orlov, 1968), and have a possible demarcation (Sokolov, 1949: figure 1). These characters bring it closer to *Miotragocerus* or *Sivaceros* than to *Strepsiportax.* Another *P. caucasicus* horn core (Gabunia, 1973: figure 35) is almost straight in side view and appears not to have a demarcation, leading Pickford *et al*. (2000: 264) to suggest that it might be of the non-boselaphine *Tethytragus*. However *Strepsiportax meyeri* shows that an early boselaphine can have almost straight horn cores in side and front views and no demarcation and so Gabunia's horn core may yet be a plausible boselaphine. The narrow cranium of *Sivaceros* was also present in the Early Miocene *Carinameryx lindsayi* of the Vihowa Formation and may indicate a relationship with that much older species. A narrow cranium is also found in the European Early Miocene (MN2) pecoran *Dremotherium feignouxi* (Filhol, 1880: plate 17 figure 4). All sorts of linkages are possible but have still to be explored.

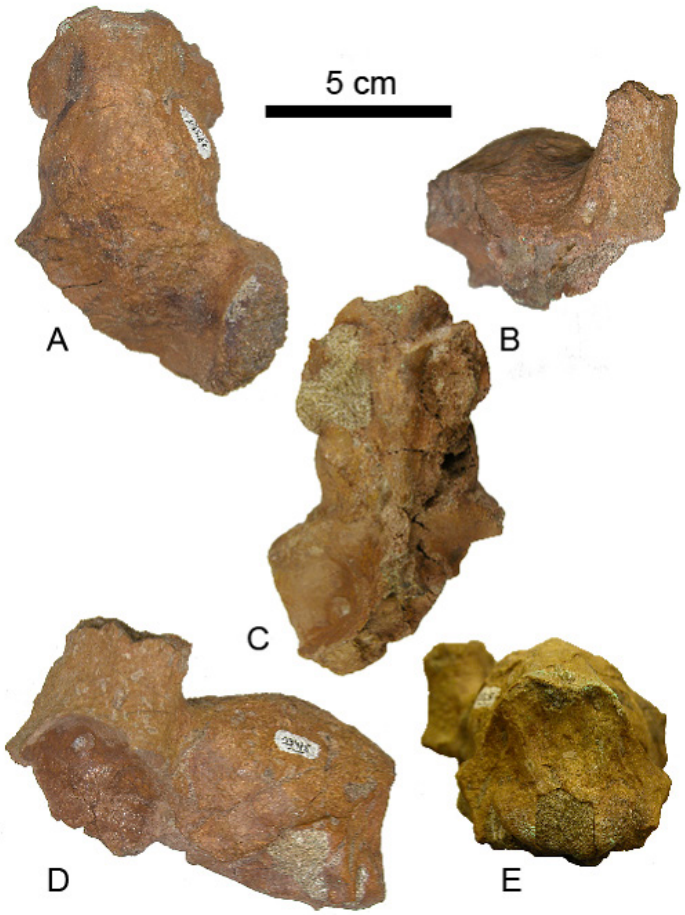

Figure 11. *Sivaceros antecedens* new species. Y 23415, holotype, cranium with left horn core base. A) dorsal, B) anterior, C) ventral, D) left lateral, and E) occipital views. Scale 5 cm. The occipital is distorted.

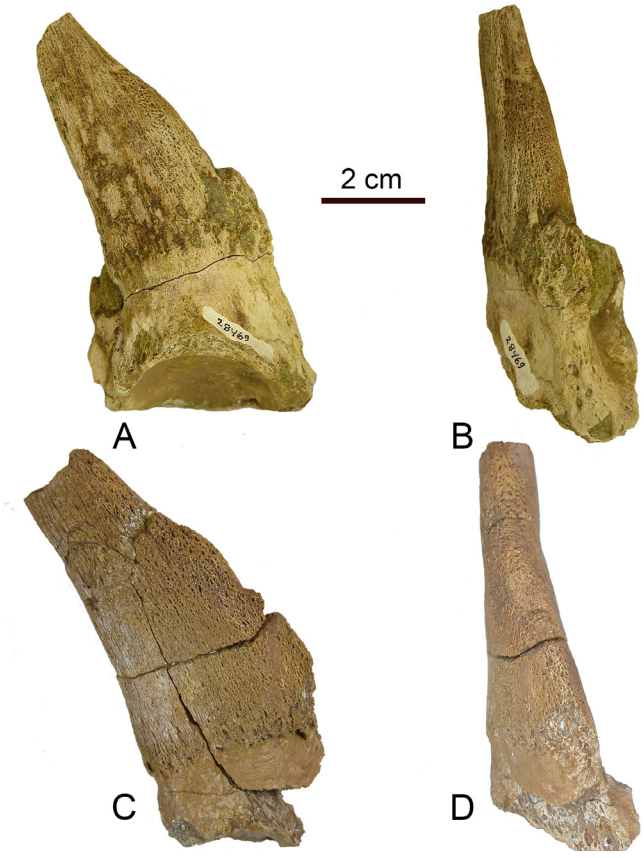

Figure 12. *Sivaceros antecedens* new species. Y 28469, right horn core in A) lateral and B) anterior views; Y 23416, right horn core in C) lateral and D) anterior views. Scale 2 cm.

Species *Sivaceros gradiens* Pilgrim, 1937

Sivaceros gradiens Pilgrim, 1937: 795, figures 30-34.

Holotype. AMNH 19448, cranium with horn cores, from Locality B 59, 12 miles (19.3 km) east of the Chinji bungalow. Brown's Locality B 59 is above the stratigraphic level of Locality Y 76 and just below Collecting Level GB 3. We estimate its age as being between 11.3 and 11.0 Ma (see Appendix 1), making the holotype the youngest *Sivaceros gradiens*.

Diagnosis. A *Sivaceros* slightly larger than and differing from the preceding species in the horn cores being longer, the level of maximum transverse width beginning to be drawn out posteriorly, a stronger expression of the keels, horn cores less compressed (51% - 64%), front of lateral surface curving round to meet the anterior keel, anterior keel descends to an anteromedial insertion and the supraorbital pit lies on the lateral side of this line of descent. Horn cores almost parallel in anterior view, perhaps more uprightly inserted, insertions closer together, and an incipient intercornual ridge. The postcornual fossa may be narrower. The frontals' sinuses extend into the pedicels and their highest point lies posteriorly in the base of the horn core proper, the basioccipital is larger, and paired vertical lines on the occipital are weaker than in the holotype of *Sivaceros.antecedens*.

Estimated age. 13.0 - (11.3 - 11.0) Ma.

Material.

Locality 822 (13.0 Ma)

Y 51286 Left horn core.

Locality Y 750 (12.7 Ma)

Y 47314 Right horn core base.

Locality Y 695 (12.4 Ma)

Y 26631 Cranium with right horn core base and part left pedicel.

Locality Y 705 (12.4 Ma)

Y 30670 Parts of cranium and occipital plus horn cores.

Locality Y 76 (11.4 Ma)

Y 51413 Cranium with right and left horn cores.

Locality B 59 (11.3-11.0 Ma)

AMNH 19448 Skull with left and right horn core and intact cranium. Holotype.

Discussion. *Sivaceros gradiens* ranges from 13.0 to between 11.3 and 11.0 Ma. The character differences from *Sivaceros antecedens* are as variable in the fossil sample as those between the successive species of *Strepsiportax*. A posterolateral keel is not always present but can be seen in Y 30670, Y 51413, and in the holotype AMNH 19448. The lateral surface is essentially flat, but the medial surface is the flatter one, as in Y 26631 (Figure 13), because the anterior part of the lateral surface curves round to meet the anterior keel. The degree of compression is less than in the earlier *Sivaceros antecedens* (Figure 10B), paralleling the situation in *Strepsiportax*. Divergence is usually constant from base to tip but sometimes its degree may lessen very slightly distally as in Y 32773. The insertions seem to be more upright than in *Strepsiportax*, but the state of *Sivaceros antecedens* is not certain. As it happens the horn cores of Y 51413 (Figure 14) are more inclined backwards than in earlier examples of *S. gradiens*, but the significance of this is not clear. A demarcation distally is usually localised but is not well expressed in Y 25001. Sinuses extend well up the pedicel and sometimes into the posterior base of the horn core as in the holotype and Y 30670. The low-rising intercornual ridge is best evident in Y 26631 and Y 30670, but is faint on Y 51413.

Other characters appear to be the same as in *Sivaceros antecedens*. The rearmost part of the horn core is posterolateral. The straightness of the horn cores in side view is made more apparent by their increased length. Bony tissue growth at the base of the anterior keel extends on to the pedicel. The back of the cranial roof is still angled on the front part but only Y 30670 has as sharp a downturning as in *S. antecedens*; it is more gradual in Y 26631 (Figure 13D) and Y 51413 (Figure 14C). Paired vertical lines on the occipital continue to be present but are less strong than in the *S. antecedens* holotype Y 23415.

On the cranium Y 26631 (Figure 13) the horn cores are larger than on the *Sivaceros antecedens* holotype and look more closely inserted. What looks like the right supraorbital pit lies lateral to the extended line of descent of the anterior keel whereas on Y 23415 (Figure 11B) the supraorbital pit lies more directly below the anterior edge of the horn core. The midfrontal suture is slightly raised above the surrounding bone surface behind the horn cores and from there it runs forward into the gently rising intercornual ridge. The basioccipital of Y 26631 is more definitely rectangular than in Y 23415 and the posterior tuberosities do not extent out so far sideways, the anterior tuberosities are small but more obvious than in Y 23415, and there is a shallow central longitudinal groove rather than a longitudinal ridge. The basioccipital of Y 51413 (Figure 14F) is similarly large but without obvious anterior tuberosities or a central longitudinal groove. No cranium of *Sivaceros* shows a transverse constriction across the centre of the basioccipital. The left horn core piece Y 25160 with its index of 63%, is more likely to be this species than a *Strepsiportax*.

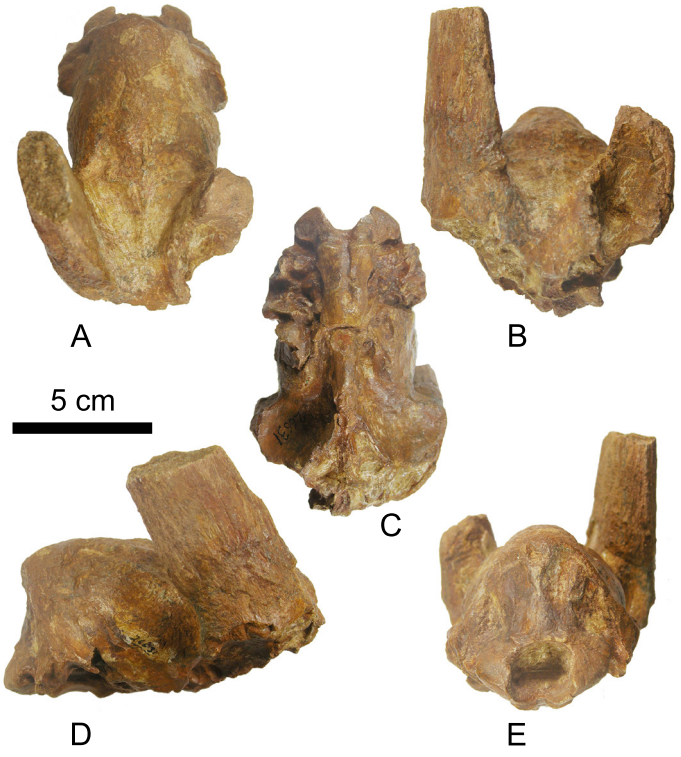

Figure 13. *Sivaceros gradiens*, Y 26631. Cranium with right horn core base and part left pedicel. A) dorsal; B) anterior; C) ventral, D) right lateral and E) occipital views. Scale 5 cm. The intercornual ridge is visible in the dorsal and anterior views. The occipital is slightly distorted.

The identification of the 12.7 Ma horn core Y 47314, which is one of the older specimens of this species, is problematic in that it is much larger than the other specimens (48.0×26.5 mm, Figure 10B) and the slightly curved medial surface of the pedicel suggests a greater divergence of the horn core as in *Strepsiportax* and unlike *Sivaceros gradiens*. However, it has a large sinus at the base of the pedicel with a smaller upwards extension reaching to the irregular top of the pedicel and, although damaged, there are some signs of the front of the lateral surface curving round to meet the anterior keel and of flattening of the medial surface, which are characters of *S. gradiens.*

Thomas (1984a) and Khan, M. A. *et al*. (2011, 2014) reported additional specimens of this species, but we have not seen the fossils. The skull described by Khan, M. A. *et al*. (2013) and identified as "*Miotragocerus gluten*" (*Strepsiportax gluten* in our usage) is probably a specimen of *Sivaceros gradiens*, as evidenced by the close insertions of the horn cores and the tall, narrow skull, which does not curve downwards posteriorly.

Comments. Among Siwalik bovids, *Sivaceros gradiens* is a clear-cut species other than in its apparent gradual evolution from the earlier *Sivaceros antecedens*. Most of the differences from *Sivaceros antecedens* are advances but they cannot all be seen as unidirectional departures away from an all-primitive ancestor. Horn core compression, for example, is less pronounced in *S. gradiens* than in the earlier *Sivaceros antecedens* (Figure 15C, D, and E). Horn cores of *Sivaceros* are less common than those of *Strepsiportax*, but four of six retrieved crania of these two genera are *Sivaceros*. *Sivaceros gradiens* is an unlikely ancestor for *Miotragocerus pilgrimi* which supersedes it in the Late Miocene of the Siwaliks.

Species ?(*Sivaceros*) *vedicus* Pilgrim, 1939

Sivaceros vedicus Pilgrim, 1939: 244, figures 29a-d.

Holotype. GSI B796 (cast NHML M42955), cranium with horn cores from Nila (33º10´N, 72º 37´E). Nila is on the south side of the Soan River and is surrounded by outcrops of the Dhok Pathan Formation that are around 7.8 Ma. However, on the north side of the river there are progressively older and highly fossiliferous outcrops that are older than 9 Ma. Pilgrim (1939: plate 4 figure 6,6a) also referred to this species an immature left horn core from near Hasnot, GSI B632.

Diagnosis. A small bovid with horn cores of moderate length, level of maximum transverse thickness close to the anteroposterior centre, somewhat irregular keels including on the holotype anterior and posterolateral ones and another on the medial surface, mediolateral compression, little divergence and no alteration of degree of divergence along its course, markedly inclined backwards, no backward curvature, no demarcation, horn core insertions fairly close, no torsion but the anterior keel or edge turns somewhat anteromedially as it descends, little or no raising of frontals between horn core insertions, a high

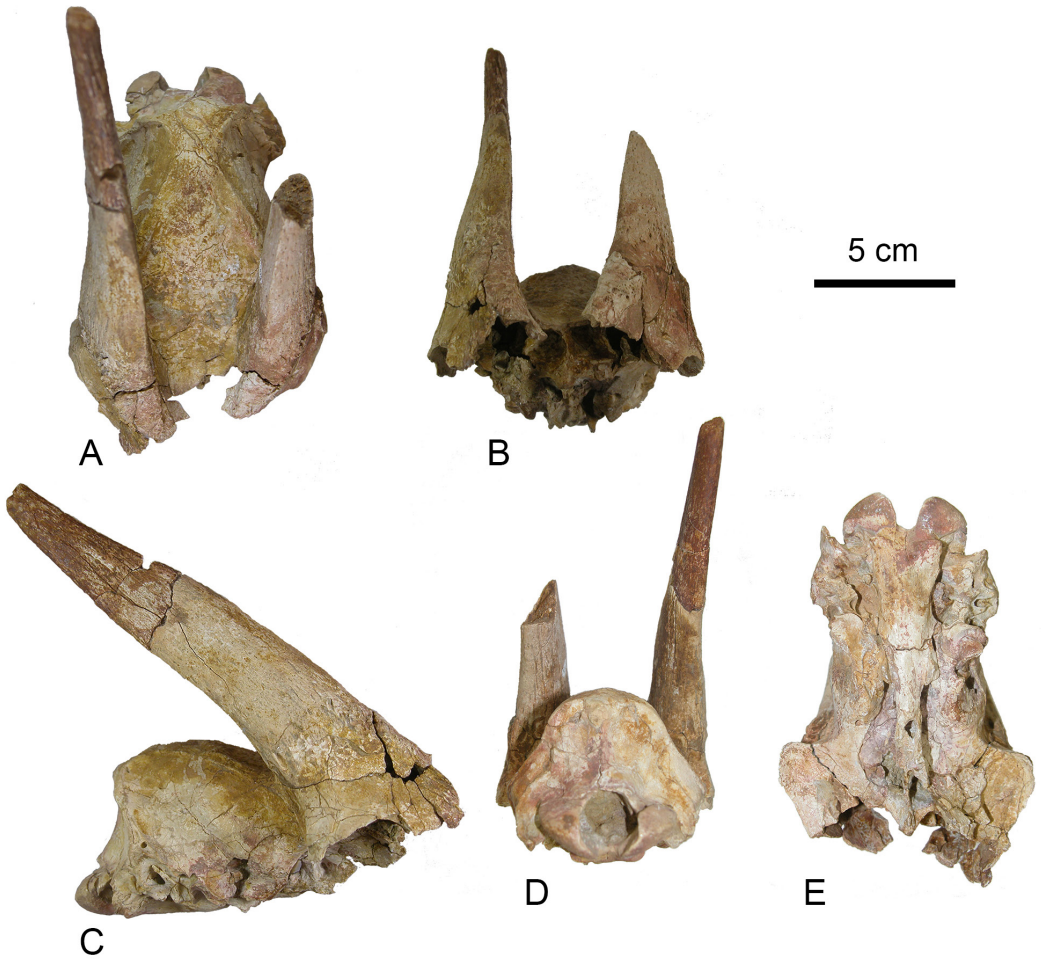

Figure 14. *Sivaceros gradiens*, Y 51413. Cranium with nearly complete right and partial left horn cores. A) dorsal; B) anterior; C) right lateral; D) posterior; and E) occipital views. Scale 5 cm.

cranium, convex transverse curvature of cranial roof behind horn insertions giving a somewhat arched appearance, back of cranial roof with a slight downwards curvature in side view.

Estimated age. 9.8 Ma. (Based on the single GSP specimen.)

Material.

Locality Y 874 (9.8 Ma)

Y 46349 Frontlet with most of left and base of right horn core.

Discussion. The addition of a new fossil from the Harvard-GSP collection to this species may be more presumptive than convincing. Y 46349 (Figure 16) largely agrees with the diagnosis based on the holotype, which together with GSI B632 are otherwise the only known specimens of Pilgrim's taxon. But the horn cores of Y 46349 differ in a more uniformly flattened medial surface, more compression, slight backward curvature, and in the maximum backwards extension lying posteromedially. No demarcations exist in the *S. vedicus* holotype, and probably would have been absent in Y 46349 as well. Sinuses in the frontals extend well up the horn pedicels in Y 46349 and there is a shallow postcornual fossa, but the cast of the holotype does not allow either character to be known. Y 46349 also shows a rugose surface behind the frontals, a character not clear on the holotype cast but believed by Pilgrim (1939: 246) to be present.

Comments. Neither the holotype GSI B796 nor Y 46349 is unmistakably a member of *Sivaceros*. Both are from the Late Miocene and an alternative approach might link them with the Georgian Late Miocene (MN13) short horned *Miotragocerus*-like *Phronetragus* Gabunia, 1955 (Appendix 2). It might also be noted that the short, straight and much inclined horn cores with their irregular keels, and the slight inflation of the cranium are reminiscent of African Cephalophini, but the horn cores are not inserted so far behind the orbits as in modern duikers. Additional material of *Sivaceros vedicus*, or *?(Sivaceros) vedicus* as we prefer to call it, will be of great interest.

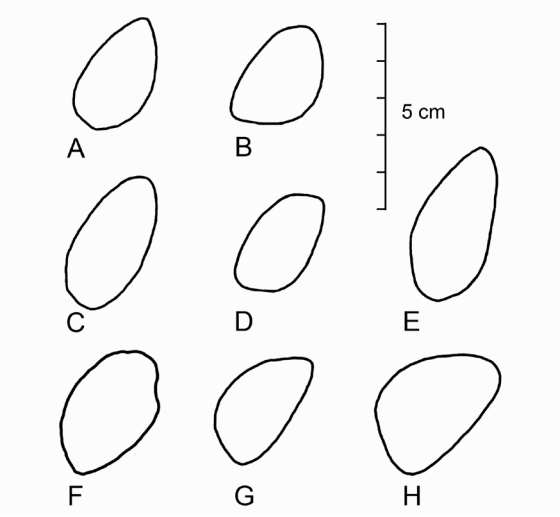

Figure 15. Horn core cross sections near the bases for *Strepsiportax*, *Sivaceros*, *Sivoreas*, and *Helicoportax*. All are shown as of the left side with the anterior direction towards the top of the illustration and lateral side towards the left. A) *Strepsiportax meyeri* (new species), Y 15828b, reversed. B) *Strepsiportax gluten*, Y 28096. C) *Sivaceros antecedens*, Y 23416. D) *Sivaceros gradiens*, Y 30670. E) *Sivaceros gradiens*, Y 26631, one of the larger horn cores of the species. F) *Sivoreas eremita*, holotype, MNHL cast M43977, reversed. G) *Helicoportax praecox*, Y 25153. H) *Helicoportax tragelaphoides*, holotype, MNHL cast M43976, reversed. Scale 5 cm.

Genus *SIVOREAS* Pilgrim, 1939

Type species. *Sivoreas eremita* Pilgrim, 1939

Diagnosis. A small to moderate sized boselaphine in which the skull has low and wide rather than high and narrow proportions. Horn cores moderately long, the level of maximum mediolateral width of cross section at their base lying more or less centrally, having an anterior keel, which can extend down onto the pedicel, and a posterolateral keel. Horn cores compressed but slightly less so than in *Strepsiportax*, neither lateral nor medial surfaces flattened, anterior keel descending to an anteromedial insertion, moderately divergent, overall degree of divergence remaining constant from base to tip, insertions fairly inclined in side view, no backward curvature, no demarcations, keels rather tightly twisted around a straight axis, long axis of basal cross-sections of horn cores at a large angle to the skull midline, insertions wide apart and above back of orbits, probably a large shallow postcornual fossa, no sinuses in pedicels but some present in the frontals below and lateral to supraorbital pits, pedicels low, frontals very slightly raised between horn bases. Small supraorbital foramina in a shallow but quite extensive supraorbital pit. The face shows long nasals slightly narrowing posteriorly, with single central points anteriorly and posteriorly, ethmoidal fissures fairly long and not very wide, a large deep preorbital fossa, and a maxillary tuberosity situated well back and high above the front edge of M2. The back edge of M3 lies below the front edge of the orbit, and the median indentation at the back of the palate passes behind the level of the two lateral ones. The surface of the frontals behind the horn insertions is somewhat uneven rather than definitely rugose. Braincase roof downcurved posteriorly in profile. Moderately prominent temporal ridges on the cranial roof pass quite sharply inwards as they progress posteriorly. Occipital surface low and wide, facing mainly backwards, no central vertical ridge, nuchal crests shallowly curved with an upwardly convex outline. The basioccipital is small, the anterior tuberosities are not wide apart but neither are the posterior ones so the overall shape of the bone is rectangular rather than triangular. It has no central longitudinal groove nor is any longitudinal ridge visible between the anterior tuberosities. The premolar row is short relative to the molar row, in other respects the teeth are like those of other boselaphines of the period.

New material in the GSP collection, especially the skull Y 24304, has enabled us to give an expanded diagnosis. The key feature of *Sivoreas* is the tight torsion of the horn cores.

Made and Hussain (1994) founded a second species, *Sivoreas sondaari*, with a holotype (KA 65) from Kanatti, a village near extensive outcrops of the lower and middle Chinji Formation. They observed weaker torsion in *S. sondaari* horn cores and believed they were geologically older than those of *S. eremita*. However, their listed material is hard to place stratigraphically and our measurements on the cast of the *S. eremita* type suggested a torsion index between 115 and 165, far below the 202 value for the same specimen in their appendix 1. The illustration of the *S. sondaari* holotype (their plate 4 figure 1A-D) is captioned as *Sivoreas eremita*, despite the number visible on the horn core being that given in the text for the *sondaari* holotype. We shall continue to use only the one original species name within *Sivoreas*.

Species *Sivoreas eremita* Pilgrim, 1939

Sivoreas eremita Pilgrim, 1939: 131: plate 4 figures 1, 1A.

Sivoreas sondaari Made and Hussain, 1994: 111: plate 4 figure 1A-D.

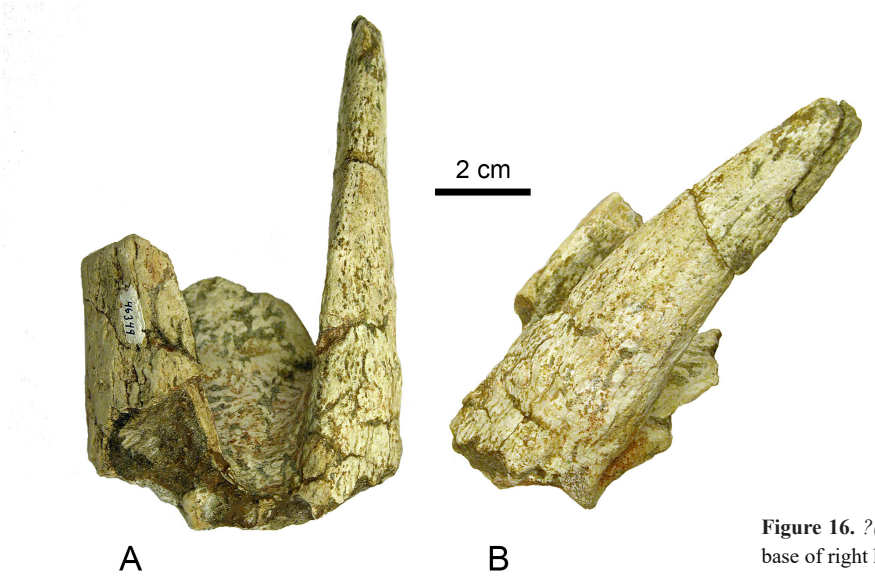

Figure 16. *?(Sivaceros) vedicus,* Y 46349. Frontlet with most of left and base of right horn core. A) anterior and B) lateral views. Scale 2 cm.

Holotype. GSI B758, frontlet with basal 15-20 mm of the horn core bases. Cast NHML M43977, horn core index 38.0×23.6 (62%). From the neighbourhood of Chinji (Pilgrim, 1939: 131) or near the Chinji Bungalow, Chinji Formation (Pilgrim, 1939: caption to plate 4 figure 1). The Chinji Bungalow is a government rest house sitting more or less on the top of the Kamlial Formation. Chinji is a village about 5 km to the north, which although surrounded by fields is near the base of the Nagri Formation. Although the formation boundaries are time transgressive, the base of the Chinji Formation is about 2.5 million years older than the top.

Diagnosis. As given above for the genus, much it is based on the skull Y 24304 (Figure 17).

Estimated age. 14.1 - 12.1 Ma.

Material.

Locality Y 478 (14.1 Ma)

Y 24304 Slightly deformed skull with both horn cores and P2-M3.

Locality Y 878 (14.1 Ma)

Y 47046 Crushed cranium with part of left horn core.

Locality Y 758 (14.2 – 13.9 Ma)

Y 28477 Frontlet with left and right horn cores.

Locality Y 69 (13.8 Ma)

Y 1431 Right mandible with roots of p2 and crowns of p3-m3.

Locality Y 71 (13.3 Ma)

Y 41322 Frontlet with left and right horn cores.

Discussion. *Sivoreas eremita* is notable in so early a period as the Middle Miocene for the strong torsion of its horn cores and the short premolar row. Its horn cores often look small in comparison with skull size. Although some examples are larger than *Strepsiportax* or *Sivaceros*, the holotype as well as the cranium Y 47046 could be from quite small animals. The species has many characters which may be advanced on an ancestor at an *Eotragus*-like level of development, for example the horn cores are quite long, keels and strong torsion have developed, and there is a slight elevation of the frontals between the horn bases. Other characters are still primitive: insertions fairly upright in side view and wide apart, and a shallow, albeit moderately large, postcornual fossa. Sinuses are present in the frontals but do not extend into the pedicels. Apart from the short premolar row, teeth have changed little.

On the horn core the posterior keel is apparently posterolateral rather than posteromedial and is better expressed distally than proximally. The visual effect of the anteromedial insertion of the anterior keel is enhanced by its descent onto the pedicel. This is a minimum expression of a boselaphine advanced character, but the pedicels remain low. There may be some flattening of the medial surface and perhaps more than

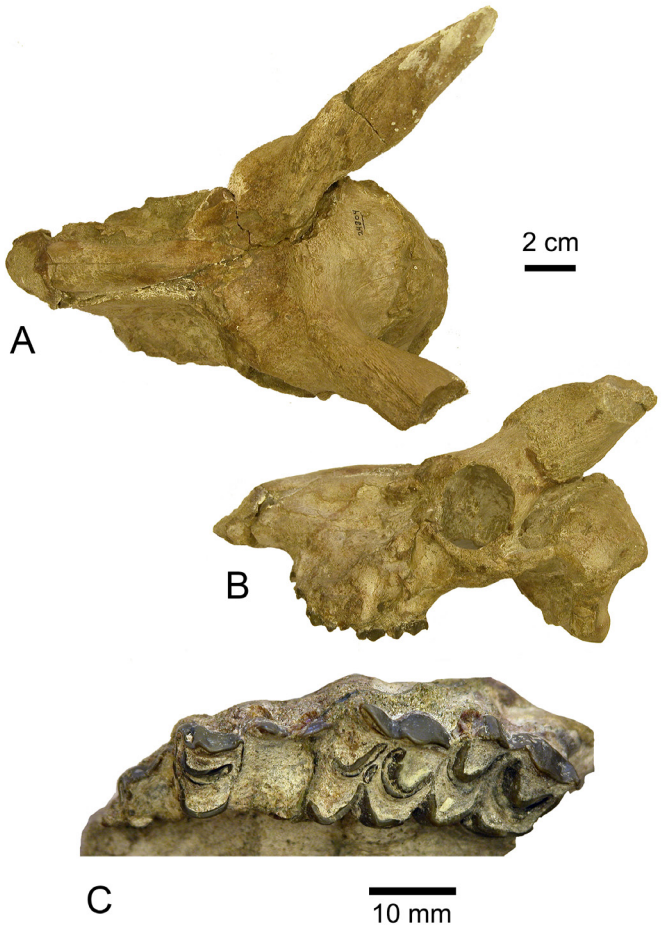

Figure 17. *Sivoreas eremita*, Y 24304. Skull in A) left lateral view; B) dorsal view, C) close up view of dentition. Scales 2 cm and 10 mm.

on the lateral surface (neither surface is flattened in Y 41322). The divergence is stronger than in *Strepsiportax* or *Sivaceros*. The very limited raising of the frontals between the horn bases means that in anterior view they are slightly above the level of the dorsal orbital rims (Figure 18A). It looks as if there would have been fairly deep depressions lying mediposteriorly to the horn bases as in other boselaphines. The anterior part of cranial roof of the skull Y 47046 looks nearly horizontal in contrast with the posterior downturning, but the back of the cranium has certainly been crushed forwards post-mortem and no posterior downturning can be seen. P3 might have had a vertical groove on its lingual face.

The frontlet Y 41322 (13.3 Ma) (Figure 18A, B) differs from the older frontlet Y 28477 (14.2-13.9 Ma) (Figure 18C, D) by its larger size and apparently by increased divergence of the horn cores and possibly more inclined horn cores. The frontals between the horn bases of Y 28477 are not much higher than the dorsal orbital rims and show no intercornual ridge, which could be primitive in Y 28477, but more probably the difference simply indicates variation. The temporal ridges of Y 41322 are oriented to pass mainly inwards, as also on the skull Y 24304. On Y 41322, as also on the holotype, the supraorbital foramina are in line with the anterior central point of the pedicels – the primitive condition – but on Y 24304 the supraorbital foramina lie lateral to the extended descent of the anterior keel onto the pedicel.

The dentition on the skull Y 24304 is in late wear and no central fossettes are left on M1 or P3. Its most striking feature is the shortness of the premolar row (57% of the length of the molar row). The late wear state need not have affected this ratio; in ten old adults of the extant East African *Gazella thomsoni* the upper premolar row length was 56% of the molar row length and in eight younger adults it was 58%. The range for the younger ones was 56 – 60% and for the older 48 -59% suggesting for these small samples an almost complete overlap, but with greater variability in the older ones. The dentition of *Sivoreas eremita* was about the size of *Strepsiportax meyeri*. The M3 length looks somewhat long relative to M2 length (Figure 8) as happens in late wear (Appendix 3, character 31), but the effect is not excessive. The mandible Y 1431 agrees with the dentition on the skull in its fairly small size and in the shortness of its premolar row (38% of the molar row), but the p2 crown has not been preserved and the estimated p2–p4 length may be inaccurate.

Comments. The temporal ridges of *Sivoreas eremita*, its Middle Miocene age, and some likenesses to *Helicoportax* (see below) suggest that *Sivoreas eremita* is a boselaphine and not a tragelaphine (cf. Pilgrim, 1939, who at that time still believed *Prostrepsiceros* and *Palaeoreas* to be Tragelaphini) nor a spiral horned antilopine (cf. Gentry, 1970, 1971). The short premolar row (57% molars) is a problem in either a tragelaphine or boselaphine species. However, the premolar rows in the Fort Ternan boselaphine *Kipsigicerus labidotus* were also shorter than in Siwaliks boselaphines, but less markedly so.

A few horn core pieces in the Ngorora Formation, Kenya, have been claimed to be *Sivoreas* (Thomas, 1981), but their identity is uncertain. Material in the Namurungule Formation formerly attributed to the southeast European *Palaeoreas* or *Ouzocerus* (Nakaya *et al*., 1984; Nakaya, 1994) may be the species later thought by Tsujikawa (2005) to be more similar to *Sivoreas*. If *Sivoreas* were present in Africa, its time span would be something like 12.0-10.5 Ma, near and after the end of its likely Siwaliks span.

Genus *HELICOPORTAX* Pilgrim, 1937

Type species. *Helicoportax praecox* Pilgrim 1937

In this paper we accept only one species of *Helicoportax*, so a diagnosis of the genus is given under that species.

Species *Helicoportax praecox* Pilgrim, 1937

Helicoportax praecox Pilgrim, 1937: 748, figures 6, 7, 62.

Helicoportax tragelaphoides Pilgrim, 1937: 751.

Holotype. AMNH 19476, face with much of left horn core, fragment of right horn core and palate with right P3-M3 and left M1-M3, all in late middle wear. The specimen came from four miles (6.4 km) west of Hasnot (Locality B 10) with an estimated age of between 11.2 and 10.8 Ma (Appendix 1). The type locality is near the type locality of *Selenoportax vexillarius* (Pilgrim, 1937: 741; also see Pilgrim, 1939: 173, 178), but the beds are steeply dipping in the area and the levels for the two holotypes could be very different.

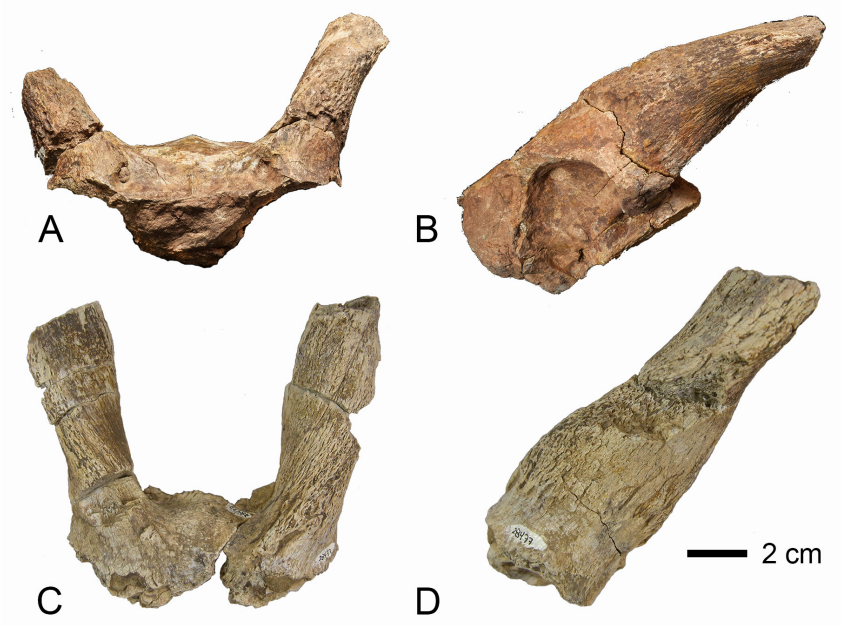

Figure 18. *Sivoreas eremita*, Y 41322. Frontlet in A) anterior and B) left lateral views. Y 28477, Frontlet in C) anterior and D) left lateral views. Scale 2 cm.

The holotype of *H. tragelaphoides* is a right horn core, GSI B797 (not illustrated until Pilgrim, 1939: plate 4 figures 3, 3a), supposedly from one mile south of Bhilomar. This location would put the horn core in the middle of the Chinji Formation and make it considerably older than the holotype of *Helicoportax praecox*, but it is our experience that the placements of old GSI sites are unreliable.

Diagnosis. Small to moderate sized Boselaphini, horn cores moderately long with a strong anterior keel and a posteromedial edge or keel, compressed but less so than in *Strepsiportax* or *Sivaceros*, flattening of the medial surface, fairly strong divergence, little or no distal diminution in degree of divergence, inclined in side view, little or no backward curvature, usually without much or any sign of a demarcation, the long axis of cross section of the horn core is at quite a strong angle to the midline of the skull, inserted widely apart, usually slight torsion of the keels around an otherwise straight axis. Frontal sinuses present, but not extending into the pedicels. Pedicels growing anteromedially and sometimes forming an incipient intercornual ridge, and with supraorbital pits lateral to the line of descent of the pedicels, but frontals not raised between horn bases. The back edge of M3 lies below the front edge of the orbit, and the median indentation at the back of the palate passes behind the level of the two lateral ones. In side view braincase roof is somewhat curved downwards posteriorly.

Estimated age. 13.4 - (11.2 - 10.8) Ma.

Material.

Locality Y 66 (13.4 Ma)

Y 1202 Midsection of a left horn core.

Locality Y 496 (12.4 Ma)

Y 25003 Right horn core.

Locality Y 647 (12.4 Ma)

Y 23966 Left horn core base.

Y 23967 Left horn core with parts of top of pedicel.

Y 40714 Right horn core in two parts.

Locality Y 507 (11.7 Ma)

Y 25153 Left and right horn cores.

Locality Y 76 (11.4 Ma)

Y 23010 Left horn core on frontal.

Y 46298 Left frontal with base of horn core pedicel.

Locality B 10 (ca. 11.2 -10.8 Ma)

AMNH 19476 Holotype skull with much of left horn core, fragment of right horn core and palate with right P3-M3 and left M1-M3. Our measurements in Appendix 5 differ from those given by Pilgrim (1937: 858).

Discussion. The stratigraphic record of *Helicoportax praecox* is most securely established in the Middle Miocene as from 12.4 until 11.4 Ma. However, a single much older find, the horn core Y 1202, gives a much older possible first appearance at 13.4 Ma. This piece is difficult to identify, but has anterior and posterior keels, the medial face flatter than the lateral, backward curvature, and more torsion than would be expected in a *Strepsiportax*. It was identified as *Helicoportax tragelaphoides* by Thomas (1984a). Similarly, the most probable age of the last occurrence is between 11.2-10.8 Ma, our estimated age of the holotype (Appendix 1).

The species shows a number of well-marked differences from *Strepsiportax* and *Sivaceros*, contrary to Gentry (1970). Many of them look as if they are closely linked: the rearmost part of the horn core being posteromedial and not posterolateral, the main posterior keel (or main angle between lateral and medial surfaces) being posteromedial, the medial surface being flatter than the lateral one (Figure 15G, H), the fairly strong divergence, the long axis of the horn core being angled on the skull mid-line, and the supraorbital pits lying laterally to the line of descent of the pedicels. The divergence is as much as in the most divergent *Strepsiportax*, and strongly different from *Sivaceros.* The torsion of keels around a more or less straight axis is usually obvious (but very weak in Y 25153), and there is no trend to a more open lyration.

Other advances are shared with other boselaphines: a demarcation is present but only as a drawn-out feature or as one or two steps along the course of the horn core (Y 25153, Y 40714) (Figure 20C), and the pedicels grow forward and medially and so participate in an incipient intercornual ridge or swelling. A possible posterior edge of such an intercornual ridge on the holotype lies posterior to the line of descent of the anterior keel, but in Y 25003 and Y 40714 the pedicel seems to be the main contributor to the ridge. Other characters continue to show a primitive condition. The size is small to moderate although the holotype of *Helicoportax tragelaphoides* is relatively large. Compression is less than in *Strepsiportax* or *Sivaceros*. Divergence usually does not vary along the course of the horn cores, although Y 23967 shows a diminution in its degree distally. Horn cores are perhaps less inclined than in *Strepsiportax gluten*. They usually show little or no backward curvature in side view, but Y 40714 and Y 23010 (Figure 20A) do show some. Horn core insertions are wide apart on frontals. Sinuses are present only in the frontals anteromedial or anterolateral to the supraorbital pits. The absence of sinuses in the pedicels is visible in several specimens such as Y 25003 and Y 23966. Unfortunately, the fossil sample of *Helicoportax* does not allow the presence or absence of a rugose cranial surface behind the horn insertions to be determined.

The upper molars on the *H. praecox* holotype show crescentic rather than V-shaped central fossettes, but the dentition is in late middle wear and this may account for the difference. The molar teeth happen to be larger than those on the holotype of *Strepsiportax meyeri*, but are normally sized for Middle Miocene boselaphines in general, while the P3 and P4 are quite large (Figure 19A). Without larger samples we cannot deduce anything more from this than individual variation.

Four other Middle Miocene boselaphine dentitions can be mentioned here as they are large and possible examples of *Helicoportax praecox*: Y 15806 a right maxilla with P3-M3, Y 40898 a right mandible with p3, m2 and most of m3, Y 40967 a left mandible with p3-m3, and Y 40968 a mandible with roots of p2-p3 and crowns of p4-m3 (Figure 19, dimensions are given in Appendix 5 under the heading *Helicoportax praecox*?). The maxilla is 14.1 Ma (Locality Y 478) while the three mandibles are 12.8 Ma (Locality Y 825).

The maxilla Y 15806 is quite large among the plotted Middle Miocene boselaphine dentitions. Apart from size, the P3 is nearly as wide as the tooth is long, with a distinctive lingual inflation of the hypocone, and the molars were probably also high crowned. Locality Y 478 has specimens of *Hypsodontus sokolovi*, but Y 15806 differs from dentitions of *Hypsodontus* by P3 exceeding P4 in length and by not showing individual molar lengthening in relation to the premolars (Table 5). P3 length is more than 100% of P4 length in Y 15806 and the Siwalik boselaphines (Table 5) and below 100% in the two hypsodontines. An average boselaphine upper molar in the table has a length 56% more than that of P4 whereas an average

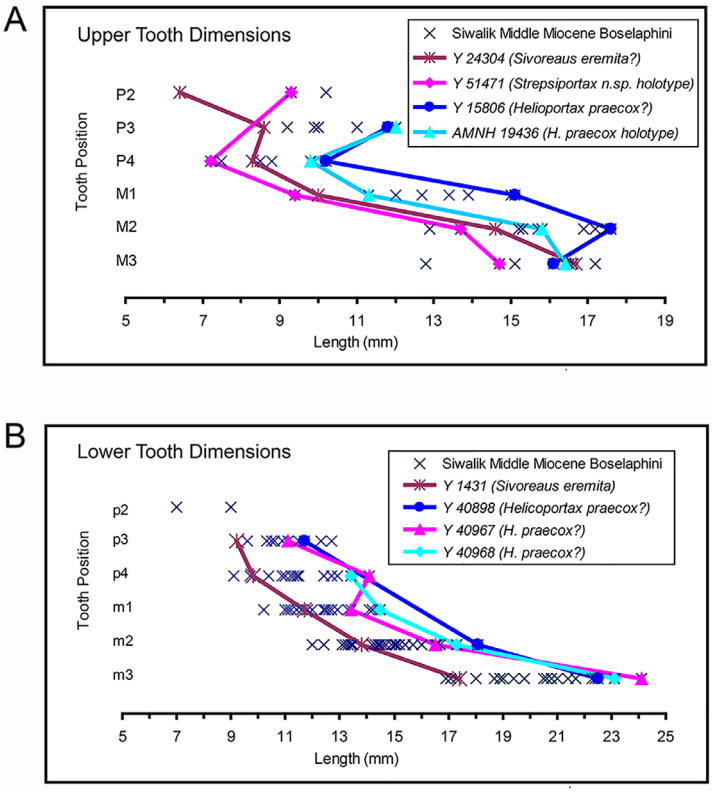

Figure 19. Lengths of premolars and molars of Middle Miocene Siwalik Boselaphines. A) upper dentitions, B) lower dentitions.

hypsodontine upper molar is 73% longer. The ratio for Y 15806 is 62% which makes it more likely to be boselaphine. Y 15806 is unlikely to be *Sivoreas* given that the *Sivoreas* skull Y 24304, also from Locality Y 478, is no larger than in *Strepsiportax* or *Sivaceros* and has a very short premolar row (Appendix 5). Y 15806 is less different from *Helicoportax*, but at 14.1 Ma it is well outside the chronostratigraphic range of *Helicoportax* as established by horncores.

The mandibles Y 40898,Y 40967 and Y 40968 are rather large among the boselaphine dentitions of Middle Miocene age (Figure 19). The mandibles' p3s are short, which could be a resemblance to *Sivoreas eremita*, but the p4 and molars are considerably longer. The specimens have rugose enamel; a small but high basal pillar on m2 (and probably there had been one on m1), molars wide anteriorly but without a goat fold, ribs on lingual walls smoothly and widely outbowed, anterior and posterior walls of p3 turned transversely. At 12.8 Ma these specimens are also outside the securely established range of *Helicoportax* except for the single horncore at 13.4 Ma.

Among the specimens from Locality Y 76, Y 23010 (Figure 20A, B) is a puzzling smaller frontlet with a left horn core of short to medium length. It is not readily identifiable as *Helicoportax praecox*, but less easily identifiable as anything else. Like *Helicoportax praecox* it has little compression, the long axis of the cross-section is at quite a strong angle to the midline of the skull, and the rearmost limit of the cross section lies posteromedially. However, it has neither posterolateral nor posteromedial keels as such, no flattened medial (or lateral) surface, the divergence is not very strong, there is a slight backward curvature and no intercornual ridge. Torsion is strong around the straight axis and especially affects the base of the anterior keel as it curves medially. There is a moderately sized and moderately deep postcornual fossa. These differences from other *Helicoportax praecox* are seen in comparison to Y 25153 (Figure 20C, D). Y 23010 could eventually prove to be an additional species of *Helicoportax*.

The holotype of *H. tragelaphoides* is a large and long horn core and regarded here as conspecific with *H. praecox*.

Pilgrim identified several partial skull remains as *Helicoportax*. The first was a hornless cranium, presumably of a female, AMNH 19654 (cast NHML M42959), (Pilgrim, 1937: 751, figures 8-11), from near Kariti, 6 miles (9.6 km) west of Chinji bungalow. Pilgrim assigned it to *Helicoportax tragelaphoides*, but it is small in relation to the holotype horn core, the cranial proportions are low and wide, and it is not clear why the fossil could not be of *Strepsiportax*. The temporal ridges approach closely posteriorly. A second cranium with a right horn core pedicel, GSI B804 (cast NHML M42958), (Pilgrim, 1939: 182, figures 17a-c, e) came from near Mundi (33º 1.4′ north, 73º 8.4′ east). There seems to have been a medial insertion of the anterior keel and a slight rising of the frontals between the horn core bases, so this specimen could well be of *Helicoportax*. Pilgrim assigned it to *H. tragelaphoides*. The widths across the lateral edges of the supraorbital pits and across the skull between the orbital rims might have been around 57 and 114 mm. Such measurements would agree in size with *Strepsiportax.* A third somewhat crushed, female skull, GSI B576 (cast NHML M42953), has cheek tooth rows in early middle wear (Pilgrim, 1939: 178, figures 16 a-f) and comes from Bhilomar about 5 miles (8 km) north east of Chinji bungalow. Measurements, from the NHML cast, are P2-P4 35.0, M1-M3 43.0, P2 12.8×8.4, P3 11.2×9.0, P4 9.8×8.9, M1 13.8×13.6, M2 15.5×14.2, M3 15.4×10.6. This was supposed to be *H. praecox*, but again the cranium is low and wide and it is not clear why the fossil could not be a *Strepsiportax*. The premolar row was longer relative to the molar row (81%) than an estimated value of 73% for the holotype of *H. praecox*.

Comments. Hitherto the main interest of *Helicoportax* has been in its possible relationship to the later boselaphine *Selenoportax*, the evidence for which is summarised below under *S.* aff. *vexillarius.* As to the origin of *Helicoportax*, the wide insertions of its horn cores (presumably a primitive character) and the probable low and wide skull proportions suggest this would lie with *Strepsiportax* or *Sivoreas*, and not with *Sivaceros*. The basal diameters of the horn cores of

	?Helicoportax praecox (Y 15806) Loc. Y 478 N = 1	*Hypsodontus tanyceras* Fort Ternan N = 10 to19	*Hypsodontus grangeri* Tung Gur (holotype) N = 1	*Helicoportax praecox* (AMNH 19476) (holotype) N = 1	*?Helicoportax praecox* GSI B576 (cast) N = 1	*Miotragocerus punjabicus* Loc. Y 17 N = 4 to 6	*Tragoportax salmontanus* GSP Y 270 N = 1
P3	11.8	9.1	10.6	12	12.2	12.7	12.6
P4	10.2	9.3	11.8	9.8	10	11.1	11.1
M1	15.1	13.3	18.4	11.3	13.5	17	17.4
M2	17.6	17.8	21.6	15.8	16.1	18.8	19.4
M3	16.1	18.2	20.2	16.4	15.6	17.9	17.6

Table 5. Occlusal lengths (mm) of preserved upper teeth in maxilla Y 15806 compared with two *Hypsodontus* species and three Siwalik boselaphines. N = number of individuals measured. P3s are longer than P4s in the two boselaphines but not in the two hypsodontines; molars are relatively longer in the hypsodontines than in the boselaphines.

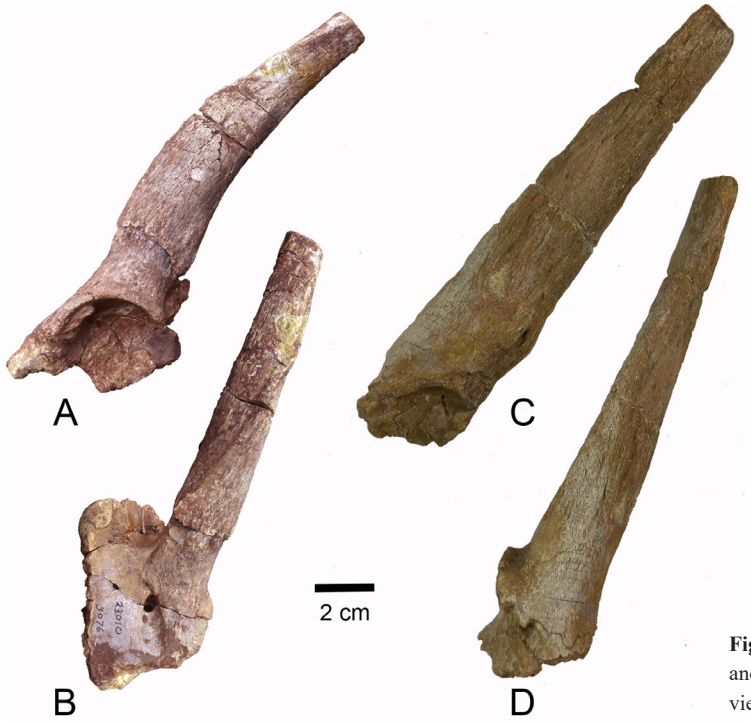

Figure 20. *Helicoportax praecox*, Y 23010. Left horn core in A) right lateral and B) dorsal views. Y 25153. Left horn core in C) left lateral and D) dorsal views. Scale 2 cm.

Sivoreas eremita and *H. praecox* are similar (Figure 21). Both the latter species contrast with species of *Strepsiportax* and *Sivaceros* by their occasionally longer horn cores, the anterior keel inserted medially so that supraorbital pits lie laterally to the line of descent of the keel, the long axis of the horn core cross-section at a considerable angle to the mid-line of the skull, divergence fairly strong, with torsion of their keels around an otherwise straight axis, and with a tendency to raise the frontals almost as a ridge between the horn core bases. Both *Sivoreas eremita* and *H. praecox* also share some probable primitive characters, such as failing to show as much compression of the horn cores as in *Strepsiportax* or *Sivaceros* and in not developing backward curvature or sinuses in the pedicels. On the other hand, the posterior keel of *Sivoreas eremita* cannot be identified as posteromedial; by its insertion position it would be more likely to be the posterolateral keel. There is no flattening of the medial surface of the horn core in *S. eremita*, and torsion is generally stronger. The premolar row on the holotype of *H. praecox* is likely to have been relatively longer when complete than in *S. eremita*.

Records of *Sivoreas* at 14.1 Ma pre-date known *Helicoportax* horncores by nearly 0.8 myr. If *Sivoreas eremita* should be an early *Helicoportax* species, then the hypothesized connection of the latter with *Strepsiportax* would be of very early date.

Siwalik Middle Miocene boselaphine teeth

Associations of teeth with horn cores and crania are rare among the Middle Miocene boselaphine species and identifying unassociated teeth below tribal level is problematical. Many such teeth will belong to *Strepsiportax* or *Sivaceros*, but *Sivoreas* is also present for much of the Middle Miocene and *Helicoportax* towards its end.

Material.

Locality Y 478 (14.1 Ma)

Y 41756 Right maxilla with P4-M3.

Locality Y 496 (12.4 Ma)

Y 25100 Right mandible with roots of p2, and crowns of p3-m3.

Locality Y 502 (12.0 Ma)

Y 40857 Right mandible, p3-m3.

Locality Y 65 (11.7-11.5 Ma)

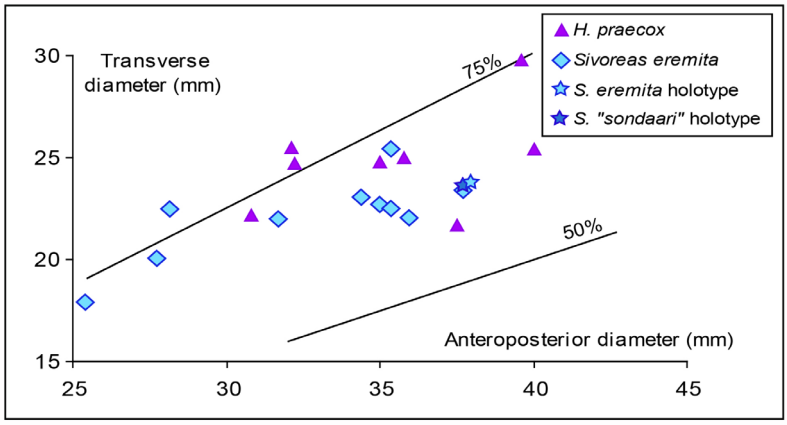

Figure 21. Basal diameters of horn cores of *Helicoportax* and *Sivoreas*. Measurements are given in Appendix 4. The upper diagonal line is that along which transverse diameter is 75% of anteroposterior diameter and the lower line is 50%. Horn cores with more transverse compression lie towards the right and towards the base of the diagram.

Y 1147 Left mandible with roots of p2-p4 and crowns of m1-m3.

Locality Y 76 (11.4 Ma)

Y 1156 Left mandible, p2-m3.

Y 1821 Left mandible, dp3-m2.

Y 3966 Right mandible, p3-m3.

Y 25120 Right maxilla, P2-M3.

Discussion. These teeth differ from those of the *Eotragus* at Sansan in probable higher crowns and in the upper and lower M2s and M3s being longer so that complete tooth rows look larger. In addition, while it is difficult to find unworn or even minimally worn teeth and consequently the available samples are small, a selection of eleven Siwalik Middle Miocene lower third molars has a mean hypsodonty index of 68%, with a range from 59% to 80% (Appendix 5). These values compare with 51% and 52% on two nearly unworn *Eotragus* m3s from Sansan in Paris and Lyon and 62% for an unworn m3 from La Grive St Alban (MN7/8) which may be *Protragocerus chantrei* (Lyon, Musée Guimet, L.Gr. 557). Estimates of lower premolar row lengths as a percentage of lower molar row lengths are also available for eight Middle Miocene mandibles although several have only the alveoli of the anterior premolars preserved. This sample has a mean of 66% and a range of 61% to 74%. These are then slightly longer than in the Fort Ternan *Kipsigicerus labidotus* in which 12 left mandibles had a range of 56-64% and mean of 60% (measurements by AWG). Finally, upper third premolars are longer than P4s and the P2 is also longer in the holotype of *Strepsiportax meyeri* and in Y 25120, but not in the skull of *Sivoreas eremita*.

Concerning the third or hypoconulid lobe of the m3, like other Middle Miocene bovids these Siwalik boselaphines tend to have the lingual wall offset labialwards with a lingually-directed hook at the back. The appearance of an additional lingual element leading sometimes to the creation of a closed central fossette seems only to have happened in Late Miocene boselaphines.

The usual individual variation can be seen (Figure 22). For instance, compared with Y 1156 (11.4 Ma), Y 40857 (12.0 Ma) looks larger, the lower molars higher crowned, perhaps with less narrowly pointed labial lobes, and stronger anterior cingular folds, and on p3-p4 the paraconid is better differentiated from the parastylid. Y 40857 also has basal pillars moderate and evenly sized from m1 to m3 whereas Y 3966 had them small on m1 and declining to tiny on m3. The p4s also have considerable variation, as often occurs in bovids, in degree of separation of parastylid from paraconid, how well slanted backwards is the metaconid crest, and whether there are forward or backward projections at its lingual end.

Genus *SELENOPORTAX* Pilgrim, 1937

Type species. *Selenoportax vexillarius* Pilgrim, 1937

Comments. With *Selenoportax* we pass from the Middle to the Late Miocene. We accept previous opinions (Pilgrim, 1937: 748, 1939: 159; Thomas, 1984a: figure 18) that it is related to the earlier *Helicoportax*. We recognise only the type species (contra Gentry *et al*., 2014 where we included species we now place in *Pachyportax* as *P. falconeri* and *P. giganteus*), so a diagnosis and further discussion follow under that heading. Later in this paper we differentiate *Pachyportax* from *Selenoportax*.

Species *Selenoportax vexillarius* Pilgrim, 1937

Selenoportax vexillarius Pilgrim, 1937: 740, figures 2-5.

Holotype. AMNH 19748, cranium top with horn cores (Pilgrim, 1937: figures 2-5), from four miles (6.4 km) west of Hasnot (Locality B 9), with an estimated age of between 11.2 and 10.8 Ma, which is very close to the start of the Late Miocene. As noted above (see also Appendix 1) this is near where the holotype of *Helicoportax praecox* was found, but the actual locations and stratigraphic levels of the specimens are uncertain and the published statements unreliable. In this case the concept of "locality" as interpreted by Colbert (1935a,b) is different from ours and there is no reason to assume that the two holotype fossils came from the same place and are the same age.

Diagnosis. Moderate-sized to large Boselaphini (80 – 150 kg?), skulls low and wide. Horn cores long, an anterior keel and a posteromedial edge or keel are both strong, a posterolateral keel is less pronounced especially basally, little mediolateral compression, anterior keel descends to a medial insertion at its base, medial surface flattened, strong divergence, divergence diminishing distally so that the tips approach and the horn cores have a crescentic appearance in anterior view, slight torsion

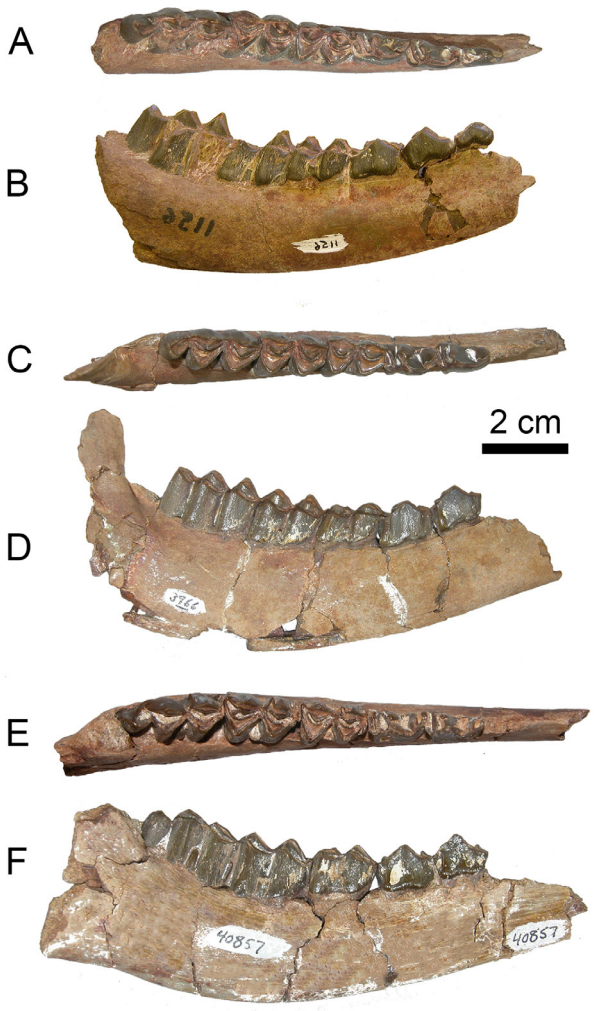

Figure 22. Boselaphini sp. Y 1156 (inverted), left lower dentition with p2-m3 in A) occlusal and B) labial views. Y 3966, right lower dentition with p3-m3 in C) occlusal and D) labial views. Y 40857, right lower dentition with p3-m3 in E) occlusal and F) labial views. Scale 2 cm.

of the keels around the axis, horn cores somewhat inclined in side view, little or no backward curvature, no apparent demarcations, the long axis of cross section of the horn core is at quite a strong angle to the midline of the skull, inserted widely apart. Sinuses of restricted extent in the frontals and not reaching into pedicels. Supraorbital pits large (exceptionally so for Boselaphini), wide apart, and tending to lie laterally to the line of descent of the pedicels, frontals little raised between horn bases. Braincase rather short relative to its width, it may widen posteriorly, its roof slopes slightly and is not appreciably turned downwards posteriorly, strong temporal ridges, no rugosity on the surface behind the horn insertions, occipital surface facing posteriorly. The few referred teeth are larger and more hypsodont than in *Miotragocerus pilgrimi*, the other common Siwalik boselaphine of the time.

Estimated age of holotype. (11.2 - 10.8) Ma (Appendix 1).

Material.

Only the holotype AMNH 19748 from Locality B 9.

Species *Selenoportax* aff. *vexillarius*

Our material looks as if it might be from a less gracile and possibly larger animal than the holotype cranial roof and frontlet and we refer to it as *Selenoportax* aff. *vexillarius*. All the GSP material is younger than the holotype. To resolve the uncertainity about whether this is distinct from the holotype of *Selenoportax vexillarius* more material from between 11.2 and 10.2 Ma will need to be collected in order to better define the limits of *Selenoportax vexillarius*.

Nishioka *et al*. (2019; 2020) referred fossils from Myanmar and Thailand to *Selenoportax vexillarius*. The material, however, is on average the same size in horn core and cranial dimensions as the Siwalik material we place in *Selenoportax* aff. *vexillarius* (Nishioka *et al*., 2020, Tables 1 and 2; Appendix 4 this paper). The ages of the Thai and Myanmar fossils are not known with any certainty and some seem to be from the latest Late Miocene or even the Pliocene (Nishioka *et al*., 2019). For that reason they do not help define the relationship between *S. vexillarius* and *S.* aff. *vexillarius* a transformation that took place much earlier.

In contrast to those of the Early Miocene, most species of Siwalik Late Miocene boselaphines are of markedly different sizes, making it possible in many cases to assign skeletal elements and isolated teeth to a species. However, in the following because of the very large number of specimens we list only a limited selection of the available fossil material. The list for Locality Y 311 in particular is very selective, as there are nearly 400 specimens of this species from that locality.

Estimated age. 10.2 - 9.8 Ma.

Material.

Locality Y 450 (10.2 Ma)

Y 14289 Right base horn core.

Locality Y 311 (10.1 Ma)

Y 12150 Female skull without horns, much broken with partial palate and P2-M3 on both sides.

Y 41412 Left mandible, p3-m3.

Y 46750 Male cranium with horn cores.

Y 47519 Left maxilla with P2-P4.

Discussion. This species appears to have a very restricted temporal range. If based only on Siwalik horn cores and teeth the range is 10.2 to 10.1 Ma, but the range extends to 9.8 Ma if isolated Siwalik skeletal elements are correctly identified and could be even as young as 6-4 Ma if the material from Myanmar and Thailand is included (Nishioka *et al*., 2019; 2020). As noted we estimate the age of Pilgrim's holotype of *Selenoportax vexillarius* to be considerably older (between 11.2 and 10.8 Ma), while fragments of teeth of a large bovid that could be this species come from sites between 10.6 and 10.5 Ma. Outcrops of the Siwaliks between 11.4 and 10.5 are poorly fossiliferous (Barry and Behrensmeyer, 2025: figure 3.3b).

The oldest horn core in the GSP collection, Y 14289 from Locality Y 450 (10.2 Ma), can be distinguished from *Miotragocerus* by its flat medial surface, the fairly localised cross-sectional swelling at the base of the lateral surface and by the continuing medialwards course of the descending lateral wall of the pedicel. The latter character indicates considerable basal divergence. The other less complete piece of horn core from Locality Y 450 (Y 18019) also matches Y 14289 better than it does *Miotragocerus*.

The male cranium Y 46750 (Figure 23) is about 15% larger than the holotype of *Selenoportax vexillarius* in linear dimensions. Between the horn insertions the frontals are only slightly above the level of the dorsal orbital rims and sinuses do not extend into the horn pedicels. There is no rugosity on the frontals behind the horn insertions. The braincase is wide and widens posteriorly. The rear of the cranial roof is not turned downwards in profile, the temporal ridges are strong, the occipital is wide but not particularly low, and there is a longitudinal ridge along the centre of the basioccipital.

The female skull (Y 12150) is nearly as large as the male. The specimen was found as three large, separate fragments that include the roof of the skull, some of the basicranium, and the maxilla. The skull roof, which preserves the left orbital rim and supraorbital pits, clearly shows there were no horn cores in this individual (Figure 24).

The few teeth in our collection from the established time span of *Selenoportax* aff. *vexillarius* are too large to fit *Miotragocerus pilgrimi*, but are slightly smaller than those assigned to *S. vexillarius* by Pilgrim (1937: 851-2). An erupting m2 (Y 12171) and unworn m3 (Y 20393) are strongly hypsodont (97% and 94% respectively), while the unworn m3 of Y 52428 (Figure 25D, E) has a lower value of 82%, largely due to a lengthened hypoconulid lobe. These are suggestive of a bovine. The teeth of Y 12150 (Figure 26), Y 36968, and Y 47519 look like those of a large boselaphine, but with some differences from early *Miotragocerus*. P3 has a lingually inflated hypocone, the basal pillars are well marked, and the labial rib on the M1 paracone is more subdued.

There are a very large number of additional unlisted large skeletal elements from Locality Y 311 that are presumably this species as well as many large specimens from other localities both within and outside its established range. Fragmentary and isolated teeth of a large bovid that could be this species are known from older sites between 10.6 and 10.5 Ma, although it is possible and perhaps likely they belong to *Protoryx* aff. *solignaci* (Robinson, 1972), which is discussed in Part 2 of this work. Ikram *et al*. (2016), Abbas *et al*. (2018), Waseem *et al*. (2020), Draz *et al*. (2020, 2021), and Naz *et al*. (2024) have also attributed dental material to *Selenoportax*, but we have not seen their material.

Comments. Although it is unlikely that *Selenoportax* descends from the latest *Helicoportax*, it must be significant that several characteristic features of the Middle Miocene *H. praecox* are

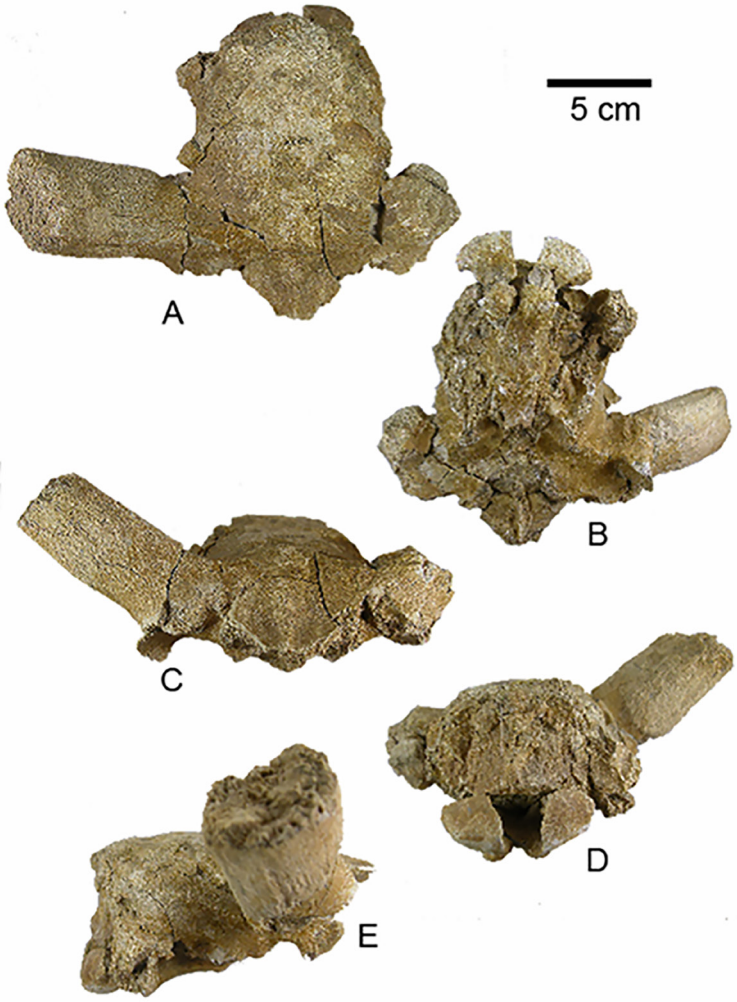

Figure 23. *Selenoportax* aff. *vexillarius*. Male cranium Y 46750 in A) dorsal, B) ventral, C) anterior, D) posterior, and E) right lateral views. Scale 5 cm.

found in *S. vexillarius* and our *S.* aff. *vexillarius*. The rearmost part of the horn core is posteromedial not posterolateral and exhibits a strong keel, a posterolateral keel is only visible near the tip, compression is poor, the horn core long axis of the cross-section is angled on the skull mid-line, the anterior keel descends to a medial insertion at its base, and the medial surface continues to be flatter than the lateral one. *Selenoportax* aff. *vexillarius* is larger than the contemporaneous boselaphine *Miotragocerus pilgrimi*, a condition which may also have distinguished *Helicoportax* from *Strepsiportax* or *Sivaceros* in the Middle Miocene. Other advanced resemblances not unique to *Helicoportax* and *Selenoportax* are: horn cores with little or no backward curvature in side view, demarcation absent, and a limited torsion of the keels but no trend to a more open lyration.

Advances of *Selenoportax* on *Helicoportax* are longer horn cores and very strong basal divergence rapidly diminishing so that the horn core tips approach one another. These give the holotype its crescent-like horn cores in anterodorsal view and hence Pilgrim's apt name *Selenoportax vexillarius*, referring both to the moon and to the ensign who carries the colours and has to be visible to all. Other characters remain primitive, such as the horn core insertions wide apart on the frontals, sinuses present only in the frontals anteromedial or anterolateral to the supraorbital pits, frontals not raised between horn bases, and no rugose surface behind frontals.

The likelihood of linkage between various characters of *Selenoportax vexillarius* is worth noting. Given that the horn cores are long and have pronounced concave curvature on the medial side, then their strong basal divergence will avoid the tips overlapping or becoming tangled. The flattening of the medial surface and prominence of the posteromedial keel could be linked with the partial rotation of the long axis of the base of the horn cores towards a more transverse alignment so that the anterior keel descends to an almost medial insertion. In being thus "dragged round" the basal part of the posterolateral keel disappears. Even accepting that the flat medial surface and strong posteromedial keel were inherited from *Helicoportax* or a related form, they make it structurally easier for the horn core's medial surface in *Selenoportax* to become strongly concave in anterior view. Which of these characters "caused" the rest does not matter; the point is their likely mechanical and functional linkage.

Genus *MIOTRAGOCERUS* Stromer, 1928

Type species. *Miotragocerus monacensis* Stromer, 1928

Diagnosis. Moderate sized Boselaphini, skulls moderately wide and high. Horn cores with heteronymous torsion, somewhat compressed mediolaterally, strong anterior keel and a posterolateral edge or keel, sometimes a posteromedial keel distally, anterior keel descending to an anteromedial insertion so that supraorbital foramina may lie anterolaterally to the base of the keel, some flattening of the lateral surface and less on the medial surface, divergence little to moderate at the base and sometimes slightly less near the tips, inclined backwards, often or usually a demarcation, inserted close together. Shallow

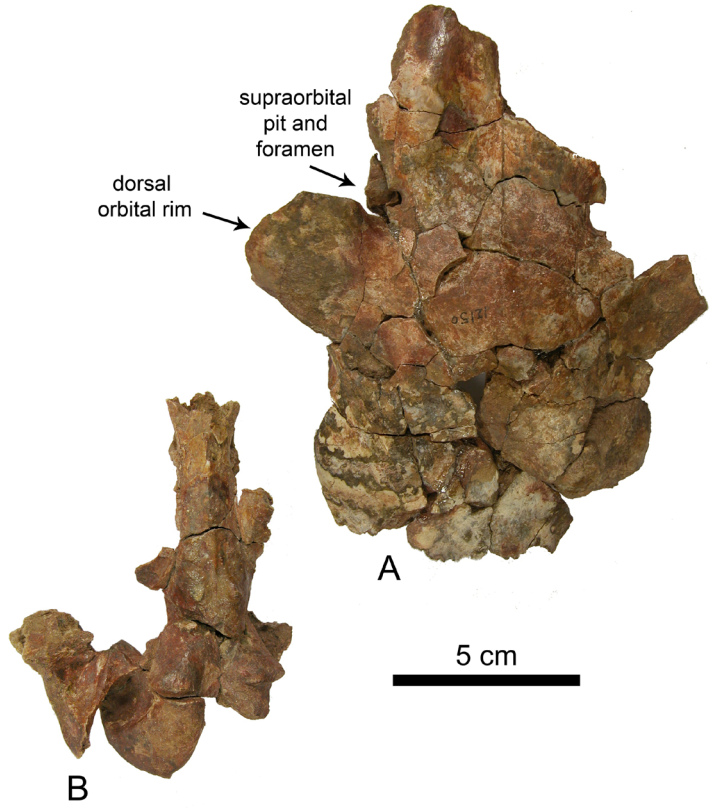

Figure 24. *Selenoportax* aff. *vexillarius*. Female cranium Y 12150. A) fragment of roof of the skull, in dorsal view, B) fragment of basicranium, in ventral view. Scale 5 cm.

Figure 25. *Selenoportax* aff. *vexillarius*. Y 41412 left mandible in A) labial, B) occlusal, and C) lingual views; Y 52428 very slightly worn m3 in D) labial, E) occlusal, and F) lingual views. The hypsodont index for Y 52428 is 82%. Scale 5 cm.

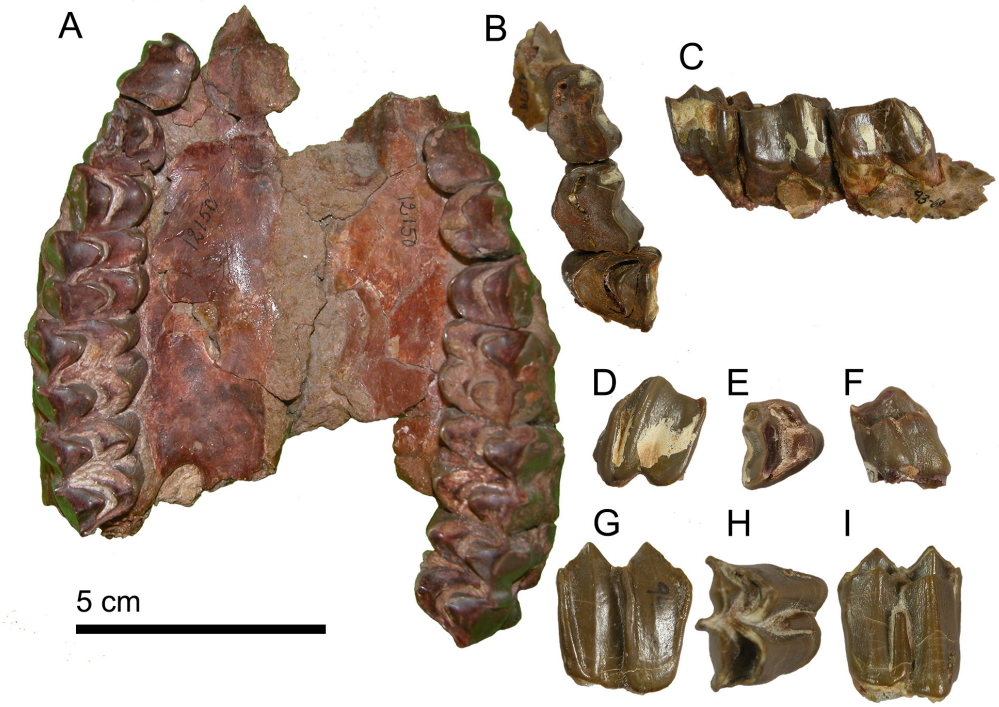

Figure 26. *Selenoportax* aff. *vexillarius*. Y 12150 palate of female skull with P2-M3 in A) occlusal view; Y 47519 left maxilla with P2-P4 in B) occlusal and C) labial views; Y 50497 right P3 with early wear in D) labial, E) occlusal, and F) lingual views; Y 53563 right upper molar, probably M3 with early wear in G) labial, H) occlusal, and I) lingual views. Scale 5 cm.

and narrow postcornual fossa. Sinuses within frontals rising high through the pedicels and into the lowest parts of the horn cores. Braincase roof almost horizontal immediately behind the horn cores and then with only a slight slope not culminating in enhanced downward bending or curvature near the top of the occipital, strong temporal ridges on cranial roof. Rugose surface on cranial roof behind horn bases. Basioccipital with a narrow central longitudinal ridge best seen between the anterior tuberosities and little development of longitudinal ridges behind the anterior tuberosities.

Comments. *Miotragocerus* is the common and characteristic boselaphine of the Old World Late Miocene. It has many characters shared with or only slightly different from the Middle Miocene *Sivaceros*. The main difference is its larger size. Others are that the horn cores have more definite posterolateral keels and slight torsion, their maximum transverse width of cross-section lies more posteriorly, the sinuses penetrate further into the horn pedicels and horn cores, the intercornual ridge of the frontals becomes stronger, the cranium is not as narrow and high, its roof is not so strongly downturned posteriorly, and the top of the occipital shows no accentuated narrowing. The teeth differ from those of Middle Miocene boselaphines by the changes shown in Table 6.

In our usage the genus includes nearly all species formerly in *Tragocerus* and *Tragoportax* (Appendix 2). They have a long history of discussion and rearrangement (among others Bohlin, 1935a; Solounias, 1981; Bouvrain, 2001; Spassov and Geraads, 2004; Spassov *et al*., 2004; Kostopoulos, 2005, 2022). Until Fuss *et al*. (2015) provided an extended account, the type species (Figure 27) was for many years known mainly by the illustrated and presumably juvenile frontlet from earliest Late Miocene deposits at Oberföhring near Munich. The horn cores of *Miotragocerus monacensis* are short and some of their characters appear to be less advanced than in other *Miotragocerus*, as for example the anterior keel descending to an anterior rather than an anteromedial insertion and the

insertions being fairly wide apart. *M. monacensis* is likely to pre-date the earliest Siwaliks *Miotragocerus* by about a million years.

Abbas *et al*. (2021) have suggested that *Graecoryx* should be used instead of *Miotragocerus* as it was proposed as a replacement name for *Tragocerus valenciennesi* Gaudry 1861. However, as noted in Appendix 2, the generic name *Miotragocerus* predates *Graecoryx*.

The main extra-Siwaliks *Miotragocerus* species relevant to this paper include *M. amalthea* (Roth and Wagner, 1854), *M. valenciennesi* (Gaudry, 1861), *M. rugosifrons* (Schlosser, 1904), *M. leskewitschi* (Borissiak, 1914), *M. monacensis* Stromer, 1928, and *M. pannoniae* (Kretzoi, 1941). The first, *M. amalthea*, is a late, large, and advanced species long known from its type locality of Pikermi (ca. 7.5 – 7.2 Ma). Pilgrim and Hopwood (1928) called the illustrated horn core a holotype, but it was one of three syntypes. We designate the illustrated specimen the lectotype. However, a cast of the lectotype in London (NHML M4069) is a right horn core so the picture in Roth and Wagner (1854) is a reversed image and depicts the horn core at around three quarters natural size. The tip is not inwardly swung as alleged by Roth and Wagner and in fact may have an extremely slight outward swing. This is a character of *M. valenciennesi*, also present at Pikermi, but is not sufficiently strong to endanger the identification of the specimen as *amalthea*. The lateral surface, and not as stated the inner (medial) surface, has extensive flattening just as in *amalthea*. There is no step, but the condition is close to several other London Pikermi *amalthea* horn cores. Unless a demarcation is strong, much depends on the angle of view of a horn core.

Table 6. Differences in tooth characters between Middle and Late Miocene Boselaphini and with the probable bovine *Pachyportax*. [1] Characters cross-referenced to the numbers used in the list in the Introduction. B = boödont characters.

CHARACTERS (Number[1])	MIDDLE MIOCENE Boselaphini	LATE MIOCENE *Miotragocerus*	LATE MIOCENE *Pachyportax*
UPPER AND LOWER TEETH			
Overall size	smaller	larger	larger again and with large occlusal
Rugose enamel (28)	present	often still present	sometimes detectable
Tooth height (29)	lower crowned	higher crowned	higher crowned again
Basal pillars (32)	present; stronger on lower molars	becoming larger on lower and some upper molars **B**	more integrated with rest of the tooth **B**
P2 is shortest premolar (34)	**yes**	P2-3 may lengthen so that P4 is shortest premolar	P2 not reduced, P3 may become shorter relative to P4
Styles and stylids (35, 41)	present	present	perhaps larger
UPPER MOLARS			
Anterior and posterior lingual cingula (33)	usually present	sometimes seen	probably occasional
Labial rib on paracone (36)	present	stronger and more localised **B**	stronger on metacone as well **B**
Outline of central fossettes (37)	simple	occasionally less simple **B**	becoming more complicated **B**
Lingual lobes (38)	narrowing to a point	a few also show pinching at the sides	as in *Miotragocerus* **B**
Posterior half of M3 (39)	small in early wear	not as small	as in *Miotragocerus*
LOWER MOLARS			
Anterolabial cingulum (33)	present	often a goat fold **B**	goat folds may occur **B**
Lingual walls (40)	with two outbowings	more nearly flat	sometimes becoming more localised
Position of metastylids (41)	rarely slightly anterior to back of metaconid crest	in centre of lingual wall	in centre of lingual wall
Central fossettes (42)	simple outline	simple outline	sometimes a central constriction **B**
Labial lobes (43)	pointed and narrow	pointed and perhaps wider	as in *Miotragocerus*
m3 hypoconulid lobe (44)	offset labially from lingual wall of the rest of the tooth	lingual side slanted	occasionally slanted
m3 hypoconulid lobe (44)	no central fossette	occasionally a central fossette at least in early wear	rarely a central fossette
UPPER PREMOLARS			
Labial ribs and central fossettes forwardly placed (45)	slightly less forward on P4	more centrally placed on P4 than on P2-3	as in *Miotragocerus*
P2-3s with a vertical groove in their lingual walls (46)	present	less frequent	rare
LOWER PREMOLARS			
Anterolabial wall of p3-4 (47)	not turned transversely	often turned transversely	less often turned transversely
Separate paraconid & parastylid crests (48)	occasionally still not separated	usually differentiated	both normally present
Metaconid ridge (49)	still directed partly backwards on many p3s	more often transverse on p3s and thus more like p4s	less often transverse on p3s
Lingual end of metaconid ridge (50, 51)	may bend slightly forwards or backwards	stronger lobes to the front and back; front one may contact paraconid but not fuse with it	front lobe present but projecting far towards paraconid

Miotragocerus amalthea is closely related to and perhaps derived from *M. rugosifrons*, type locality Samos (Mecquenem, 1924-5: 35 footnote). Horn cores of *M. rugosifrons* are longer, more backwardly curved, with a weak or absent demarcation and divergence sometimes increasing distally, whereas those of *M. amalthea* are shorter, a demarcation is often present and often strong, the course of the anterior keel has a degree of curvature and the horn core itself often comes to show some lyration. Divergence does not increase distally. *Miotragocerus amalthea* and *M. rugosifrons* and their many synonyms constitute the main larger *Miotragocerus* of western Eurasia.

Miotragocerus valenciennesi, type locality also Pikermi, is a smaller species with a complicated nomenclatural history (Appendix 2). It differs from *M. amalthea* by its shorter horn cores, often a narrow front surface on the distal horn cores above the demarcation, either no distal diminution in degree of divergence of its horn cores or a slight increase in it, horned females (different from most *amalthea* populations), only poorly raised frontals between the horn bases, weaker temporal ridges behind the horn insertions and hence a more curved transverse curvature of the cranial roof in that area, and by its larger anterior premolars. It differs from *M. monacensis* in horn cores more curved backwards, the anterior keel descending to a more anteromedial base and thereby giving the impression of closer insertions, a firmer hint of raised frontals between the horn insertions, and the more transversely curved cranial roof, perhaps linked with the less prominent temporal ridges.

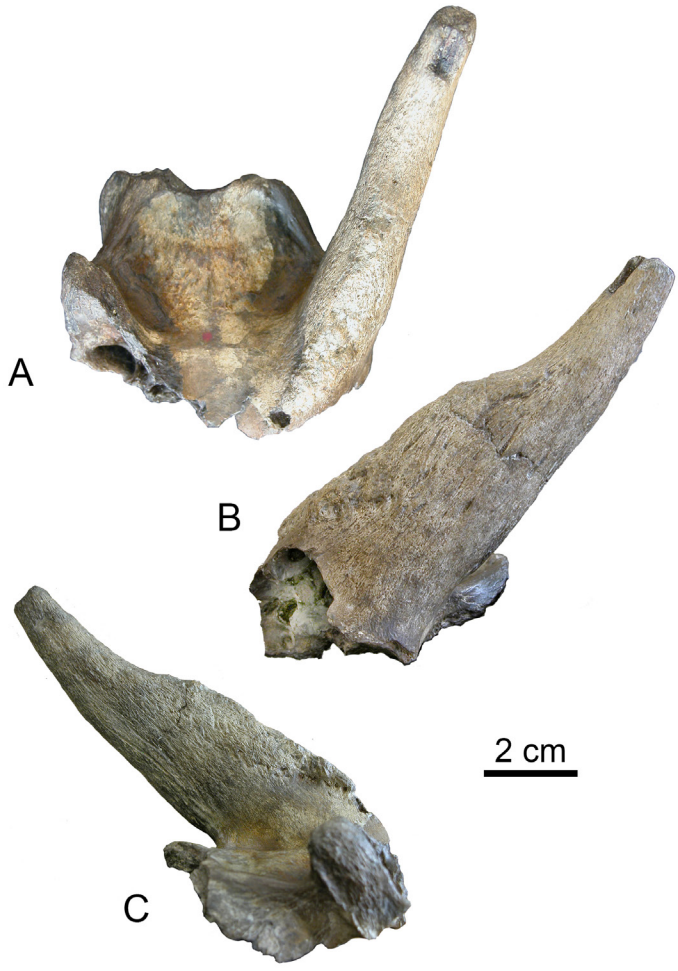

Figure 27. *Miotragocerus monacensis*, type species of *Miotragocerus*. Syntype frontlet from Oberföhring, Germany, illustrated in Stromer 1928 as Textfig. 1a-b and Fuss et al. (2015) as Fig. 6 with dorsal and left lateral views. This is the most informative syntype of the species, but was not designated a lectotype by Fuss et al. (2015). We add a medial view. A) dorsal; B) left lateral; and C) medial views. Scale 2 cm.

Miotragocerus leskewitschi, type locality Sevastopol (Sébastopol), Ukraine (MN9), thought to date from between 11 and 9.9 Ma, is a small Vallesian species of more primitive aspect than *valenciennesi*.

Miotragocerus pannoniae occurs in the early Late Miocene in immediate succession to *M. monacensis* in Austria and southern Germany as set out in Fuss *et al*. (2015), although the holotype (not mentioned in their paper) comes from Sopron in westernmost Hungary and has usually been taken as late Middle Miocene. *Miotragocerus pannoniae* evolved large size, distally-massive horn cores, a relatively low position for the demarcation, little or no backward curvature of the horn cores, and metatarsals with a unique concavity in the proximal part of the lateral surface. Thenius (1948: 218) related it to *M. monacensis* in which the proximal shaft of the metatarsal is not known.

Miotragocerus in the Siwaliks consists of an earlier species *M. pilgrimi* and the later *M. punjabicus*, neither of them as large as *M. amalthea*. It is difficult to know where and when to draw the taxonomic boundary between them, a problem compounded by the appearance of the related *Tragoportax salmontanus* and a new supposedly boselaphine species around the most likely period for the change. The teeth of our earlier *Miotragocerus* differ from Middle Miocene boselaphine teeth in larger size and the gradually evolving characters shown in Table 6. From about the time of the new appearances onwards such teeth increasingly acquire a degree of occlusal complexity, a boödont trend unlike Late Miocene boselaphines elsewhere in the world but similar to that which appears in the larger *Pachyportax* of the Siwaliks, a genus seemingly linked with Bovini. Solounias *et al*. (1995b) determined western Eurasian *Miotragocerus* to be browsers or mixed feeders.

Species *Miotragocerus pilgrimi* (Kretzoi, 1941)

Sivaceros sp. Pilgrim, 1939: 247: plate 4 figure 5.

Indotragus pilgrimi Kretzoi, 1941: 342, figure 2 13-13A.

Tragoceridus pilgrimi Thomas, 1984a: 46: plate 2 figures 1-2 and 7, plate 3 figures 1 and 3-6, plate 4 figure 1.

Holotype. GSI B631, a small piece of a right horn core with a demarcation, from "near Chinji village" (Pilgrim, 1939: 247 and caption to plate IV). Pilgrim's illustration suggests that the holotype is about 80 mm long and is very like Y 6558 (illustrated in Thomas, 1984a: plate 2 figure 1). Pilgrim was uncertain about the stratigraphic horizon, noting that it "might or might not belong to the lower part of the Nagri Stage" (Pilgrim, 1939: 247).

Diagnosis. A small to moderate sized *Miotragocerus*. Horn cores with greatest transverse diameter lying posteriorly, slight divergence, degree of divergence lessening distally, curving backwards, one or more demarcations along the horn core, slight torsion of the anterior keel; sometimes a shallow longitudinal concavity on the medial side of the horn core immediately behind the lower part of the anterior keel. The sinuses frequently rise higher within the posterior parts of the pedicel than they do more anteriorly. Females hornless (Thomas, 1984a: plate 3 figure 6). Differs from *Miotragocerus monacensis* and some members of the *Miotragocerus* complex

in the closely inserted and longer horn cores that are more divergent; anterior keel descending to an anteromedial insertion medial to the supraorbital pit and forming a medial longitudinal concavity; slight backward curvature of horn cores; no or low intercornual ridge.

Estimated age. ?10.5 - 8.8 Ma.

Material.

Locality Y 450 (10.2 Ma)

Y 18024 Right horn core base.

Locality Y 258 (10.2 Ma)

Y 9413 Left horn core.

Locality Y 311 (10.1 Ma)

Y 10441 Right horn core without pedicel and tip.

Y 12022 Cranium, hornless.

Y 21086 Cranium with horn cores.

Y 49596 Right horn core, complete.

Y 51383 Left horn core, complete.

Locality Y 224 (9.4 Ma)

Y 22157 Cranium with horn cores.

Locality Y 211 (9.3 Ma)

Y 21946 Frontlet and parts of skull.

Locality Y 325 (8.8 Ma)

Y 12390 Left horn core base.

Discussion. The species ranges from at least 10.2 to 8.8 Ma and more likely from 10.5 to 8.8 Ma. It is very abundant in the Harvard-GSP collection. The specimen Y 18024 (Figure 28A-C), together with other horn core fragments and teeth, is the earliest known Siwalik *Miotragocerus* horn core (10.2 Ma) and comes from the same locality as the earliest *Selenoportax* in the Harvard-GSP collections. There are a few additional astragali and unlisted skeletal elements from sites between 10.5 and 10.3 Ma that may be this species, including three astragali that are the same size as those from 10.1 Ma (Appendix 6).

There is considerable variation among individuals of this species, especially over time. The cranium Y 21086 from Locality Y 311 (Figure 29) is the most complete specimen of this species and is representative of the early *Miotragocerus* of the Siwaliks. It has a fairly high cranium, horn cores not very long, little divergent, inserted close together, and with no intercornual ridge. In it, but not other specimens, the occipital condyles are relatively large and, with the occipital, are strongly backward-projecting as in *Sivaceros*. Relatively high crania are also shown by Y 17568 and Y 20392 from the same locality. Another cranium Y 22157 (Figure 30) occurs about 700,000 years later and differs from Y 21086 by horn cores more inclined backwards, a shorter, lower and wider cranium and occipital, the temporal lines not approaching so closely posteriorly, and a wider basioccipital. More minor differences are closer horn core insertions; stronger lessening of divergence distally; frontals higher between the horn core bases; pedicels with more expanded bases and the anterior tuberosities being smaller on the basioccipital. The supraorbital pits on Y 22157 can be seen to be tiny and situated at the foot of the pedicels and lateral to the lower ends of the anterior keels. The auditory bullae are moderately large and also moderately inflated medial and posterior to the tympanohyal pit.

Variation in the horn cores can be seen among the specimens, but other than for an increase in size (Figure 31) there is no temporal pattern to this variation. Y 20392 and Y 15695 (both 10.1 Ma), and Y 6925 and Y 6839 (both 9.4 Ma) are among those showing the anterior keel in a curving downward spiral to its anteromedial insertion accompanied by a longitudinal shallow hollowing immediately medial to the keel. Y 9413 (10.2 Ma) (Figure 28D, E) and Y 46353 (9.8 Ma) are examples with an anterior keel showing torsion to the extent of swinging outwards as it rises to end in the demarcation. Y 52510 shows that by 9.8 Ma the horn cores could be very large or anteroposteriorly extended across the base. The frontlet Y 21946 (9.3 Ma) has long horn cores which are little curved backwards and also less compressed than others listed above (Figure 32). The lateral surface of the pedicel descends directly to the top of the orbit and leaves no flat and projecting orbital rim. In contrast Y 51383 (10.1 Ma) is a complete, rather short and narrow, but massive horn core with some backward curvature. That specimen together with Y 49596 and Y 10441, which are all from the same site, show that there is considerable variation even among individuals living at same time (Figure 33). Y 12390 (8.8 Ma) is the latest horn core assigned by us to *M. pilgrimi*. Despite some curvature of the anterior keel there is no sign of a gradually decreasing degree of divergence such as one might expect to see in *Tragoportax salmontanus*.

Thomas (1984a: 25: plate III figure 6) reported a hornless skull from Locality Y 311 (Y 12022) that presumably is a female of this species. We have, however, not seen this specimen. Among the presumed male horn cores from Locality Y 311, many such as Y 49596 are slender and long, while others such as Y 51383 are more massive (Figure 33).

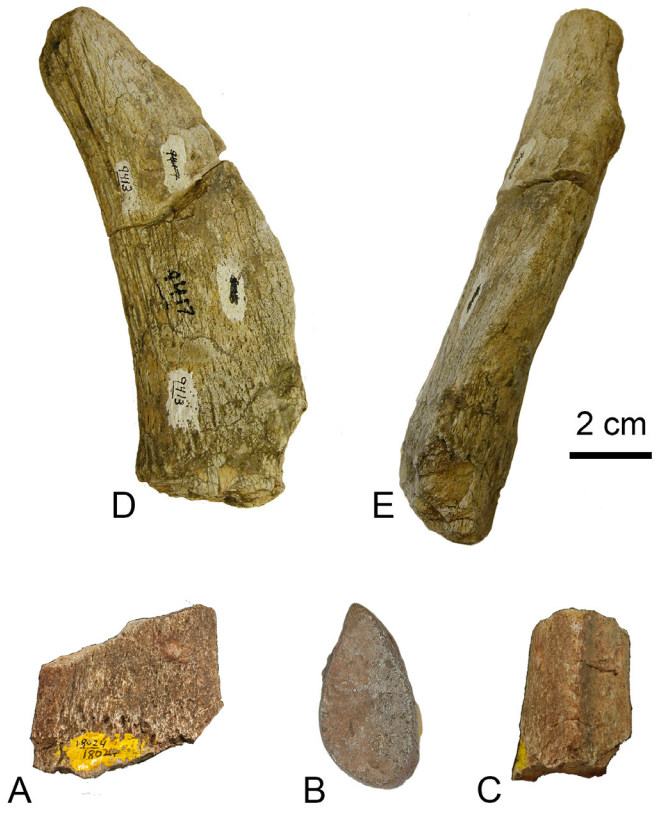

Figure 28. *Miotragocerus pilgrimi*. The oldest horn cores of the species in the GSP collection.Y 18024, base of right horn core in A) right lateral, B) dorsal, and C) anterior views. Y 9413, left horn core in D) medial and E) anterior views. Scale 2 cm.

There is much additional skeletal and dental material of this species which is not included for the 57 localities in Appendices 4 through 7. In particular, abundant material is known from the three oldest localities, as well as from Localities Y 310, Y 227, and Y 211. In addition, there is dental and cranial material of the species from another 46 localities and apart from the astragali in Appendix 6 only a very small fraction of the known skeletal material of this species is listed anywhere. Although we do not include it, this unreferenced material adds to our understanding of the species.

Associations of teeth with horn cores and crania are rare, but both horn cores and dentitions identified as *M. pilgrimi* increase slightly in size over time (Appendices 4 and 5). In the case of the horn cores the increase is predominantly in the transverse dimension (Figure 31). Further discussion of teeth and horn cores will be found in the account of *M. punjabicus.*

Some of the character differences of *M. pilgrimi* from *Sivaceros* could be advanced: larger size, longer horn cores, level of maximum transverse thickness lying more posteriorly (more clearly different from the earlier *Strepsiportax meyeri*), the proximal part of the anterior keel perhaps lying more medially and thereby creating a shallow longitudinal concavity on the medial surface, degree of divergence usually lessening distally, backward curvature of horn cores often detectable, slight torsion possible along the anterior keel, more extensive

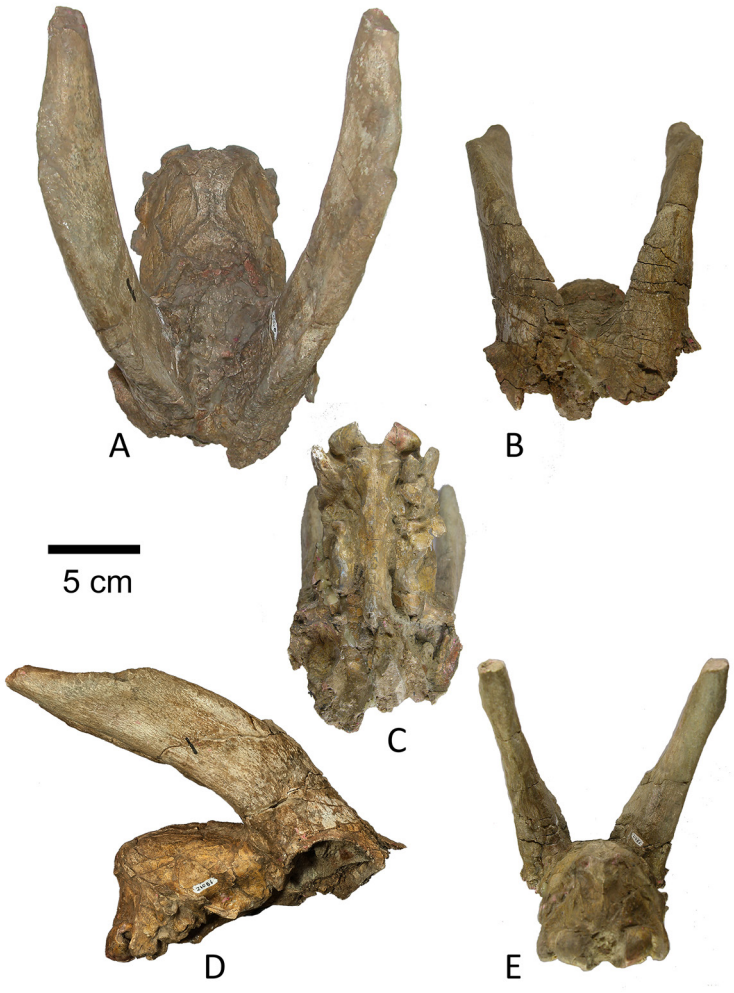

Figure 29. *Miotragocerus pilgrimi*, Y 21086. Cranium in A) dorsal, B) anterior, C) ventral, D) right lateral, and E) posterior views. Scale 5 cm.

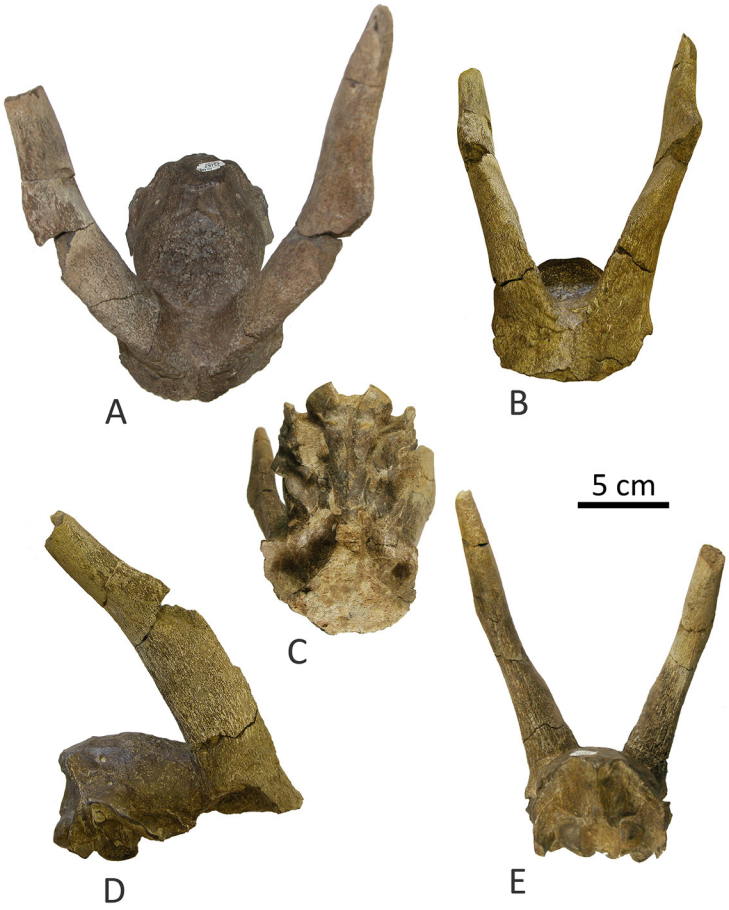

Figure 30. *Miotragocerus pilgrimi*, Y 22157. Cranium in A) dorsal, B) anterior, C) ventral, D) right lateral, and E) posterior views. Scale 5 cm.

sinuses in the pedicel, cranial roof less strongly turned downwards posteriorly and not sharply localised at the bregma, temporal ridges strong. Other differences look less advanced than in *Sivaceros*: the curvature of the lateral surface of a horn core as it approaches the anterior keel is usually less sharply turned (but Y 26888 is very like *S. gradiens*), the medial surface is more rounded, divergence is greater than the parallel or sub-parallel state in *Sivaceros*, the level of the frontals between the horn bases is sometimes less raised even than in *S. gradiens*, and nuchal crests are usually not concave upwards as in species of *Sivaceros*.

The complete horn core Y 49596 (Figure 33A) is noteworthy as being straight in side and front view, having no torsion of the anterior keel and no longitudinal concavity at the front of the medial surface, all of which fail to differentiate it from *Sivaceros*. It also has a drawn-out demarcation, apparently individual variation in this horn core. Other characters of *M. pilgrimi* are like *Strepsiportax meyeri* and *Sivaceros gradiens*, particularly the demarcation, close horn insertions, narrow postcornual fossa, rugose frontals behind horn bases, fairly narrow cranium, and close approach of temporal lines. Paired vertical lines or ridges on the occipital above the outer edges of the foramen magnum can be seen in the cranium Y 21086.

The old name *Miotragocerus perimensis* (Lydekker, 1878: plate 28 figures 4 and 5) appears not to fit comfortably to *M. pilgrimi.* The species was described on a frontlet from Piram (formerly Perim) Island in the Gulf of Khambhat (formerly Cambay) and there is a right horn core in London, NHML

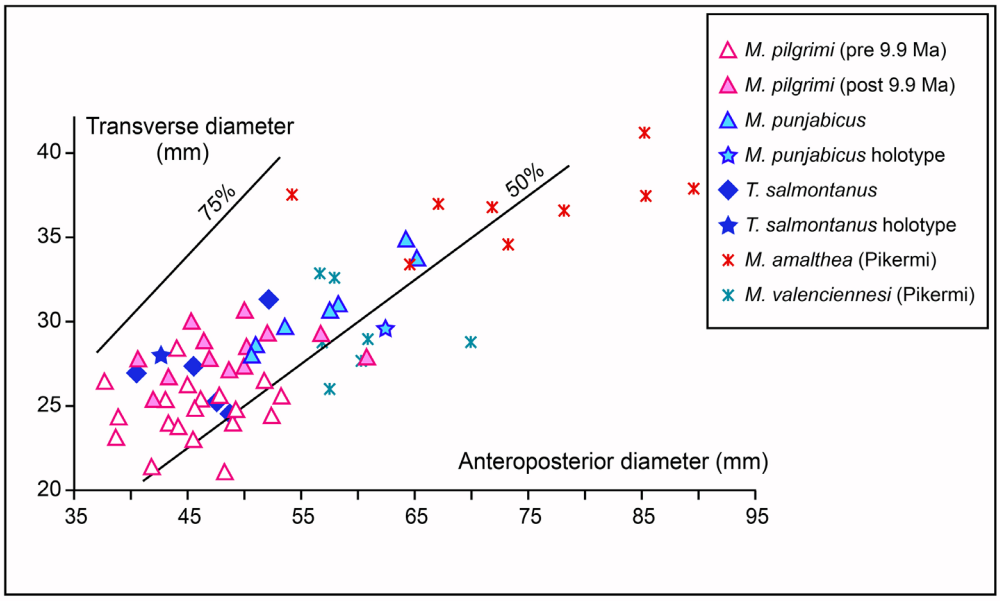

Figure 31. Basal diameters of *Miotragocerus* and *Tragoportax* horn cores. The upper diagonal line is that along which transverse diameter is 75% of anteroposterior diameter and the lower line is 50%. Horn cores with more transverse compression lie towards the right and towards the base of the diagram. *M. pilgrimi* specimens younger than 9.9 Ma overlap with smaller *M. punjabicus*, while *M. punjabicus* overlaps with the smaller of the Pikermi species.

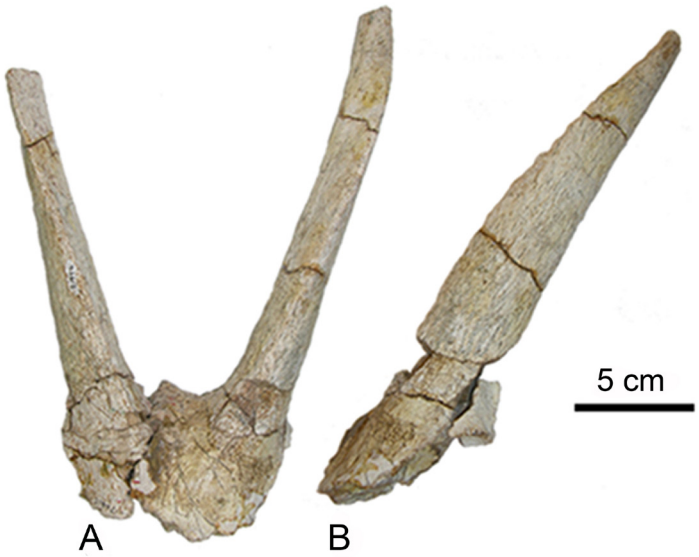

Figure 32. *Miotragocerus pilgrimi*, Y 21946. Frontlet in A) anterior and B) left lateral views. Scale 5 cm.

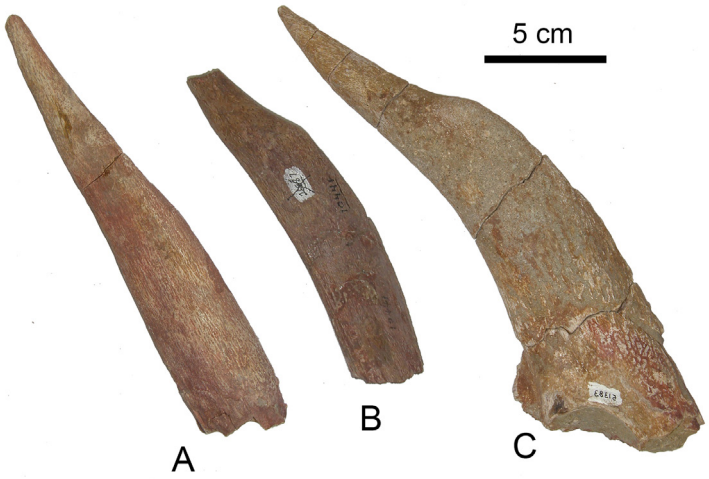

Figure 33. Varation in *Miotragocerus pilgrimi* horn cores in lateral view. A) Y 49596 right horn core without pedicel; B) Y 10441, Right horn core without pedicel and tip; C) Y 51383, complete left horn core with superior margin of the orbit (reversed). Scale 5 cm.

18786. The horn cores diverge quite strongly, have quite a wide basal separation and the basal diameters of 58×37 mm given by Pilgrim (1939: 223) are too big for *M. pilgrimi.*

Comments. In general *Miotragocerus pilgrimi* looks like a satisfactory intermediate between *Sivaceros* and later *Miotragocerus*, although not necessarily a direct descendant of *Sivaceros*. Its horn cores are larger than those of *Sivaceros* and *Strepsiportax,* but not as large as the younger *Miotragocerus punjabicus* (Figure 31). The species must be part of an early Late Miocene radiation of *Miotragocerus* species from an ancestry shared with *M. monacensis* in Europe which had characters appropriate for an ancestral species: shorter horn cores, greatest transverse width positioned centrally or anteriorly rather than posteriorly, stronger compression and flatter lateral and medial surfaces, anterior keel descending to an anterior rather than an anteromedial insertion, the insertions fairly wide apart, a constant degree of divergence, greater inclination of horn cores in side view, no backward curvature, and absence of any lyration or torsion**.** Other *Miotragocerus* species such as *M. pannoniae* and *M. leskewitschi* have evolved on different paths from *M. pilgrimi*. Compared to *M. pilgrimi, M. pannoniae* has distally-massive horn cores, a low demarcation, and little or no horn core curvature, while *M. leskewitschi* has shorter horn cores, a more downturned back of the braincase roof in profile (Borissiak, 1914: plate 4 figure 5a), a smaller basioccipital, lower crowned teeth, and probably longer premolar rows relative to the molar rows. *M. leskewitschi* might have been a woodland or more closed-cover species linked with later small-

horned species north of the Black Sea placed in *Mirabilocerus, Mesotragocerus* and *Phronetragus* (Appendix 2).

Species *Miotragocerus punjabicus* (Pilgrim, 1910)

Tragocerus punjabicus Pilgrim, 1910: 70.

Tragocerus browni Pilgrim, 1937: 781, figures 23-28.

Tragoportax islami Pilgrim, 1939: 230, figure 25d-f.

Holotype. GSI B486, a skull with the basal part of the left horn core, from a quarry in the Dhok Pathan Formation on the Soan River about 3 miles west of Dhok Pathan (Pilgrim, 1939). Cast NHML M11081.

The holotype of *Miotragocerus browni*, AMNH 19662 (cast NHML M15758), is an informative skull from a different quarry near the Dhok Pathan Rest House. It had long complete horn cores similar to *M. rugosifrons* in the west and differed from *M. punjabicus* according to Pilgrim (1937, 1939) by its face being less angled on the cranium, skull width across the orbits relatively greater in comparison with that across the mastoids or horn bases, the horn cores more tilted back, and a smaller anteroposterior diameter at the base of the horn core. We prefer to accommodate a range of horn core size and morphology within one species, a synonymy already suggested by Moyà Solà (1983: 122). The estimated age of the AMNH holotype of *Miotragocerus browni* lies between 8.6-8.4 Ma (Appendix 1). The GSI *M. punjabicus* holotype is probably between 8.6 and 8.1 Ma.

Diagnosis. Slightly larger than *Miotragocerus pilgrimi*, horn cores larger, longer, and backwardly curved, demarcations sometimes weak, the sinuses more extensive within the frontals, and a prominent intercornual ridge or raising of the horn pedicels between the very closely inserted horn cores. Very large and deep preorbital fossae. Cranial proportions are higher and narrower and the roof nearly horizontal in profile throughout its length. Teeth higher crowned. Females hornless.

Estimated age. 8.7 - 6.4 Ma.

Material.

Locality Y 199 (8.7 Ma)

Y 4763 Left mandible, p3-m3.

Locality Y 389 (8.6 Ma)

Y 14882 Parts of both upper and lower tooth rows, plus associated skeletal elements.

Locality B 138 (8.6-8.4 Ma) (Appendix 1)

AMNH 19662 Holotype of *Miotragocerus browni,* Pilgrim, 1937: 781, figures 23-28.

Locality B 25 (8.3 Ma) (Appendix 1)

AMNH 19463 Paratype of *Miotragocerus browni*, Pilgrim, 1937: 781.

Locality Y 176 (8.2 Ma)

Y 52070 Female skeleton with dentition and cranial fragments lacking horn cores. Maxilla with P2-M3 and mandible with p2-m3.

Locality YPM VP.04804 (8.1–7.8 Ma)

YPM 19825 Partial face with complete tooth rows. Hornless in life.

Locality Y 97 (7.9 Ma)

Y 2523 Cranial roof with pedicel bases.

Locality Y 953 (7.9 Ma)

Y 50931 Frontlet with left and right horn cores.

Y 52082 Partial face with orbits and complete tooth rows. Hornless in life.

Locality Y 913 (6.4 Ma)

Y 49795 Right horn core part.

Discussion. The species ranges from 8.7 to 6.4 Ma and like *M. pilgrimi* is also very abundant in the Harvard-GSP collections. It can be accepted that the type specimens of *Miotragocerus punjabicus* and its junior synonym *M. browni* are a morphologically different species from *M. pilgrimi* crania such as Y 21086 and Y 22157. Of the *M. punjabicus* material in the GSP collections the most secure identifications are Y 2523, Y 49502, and Y 49694 (Figures 34-35) and these too are different from *M. pilgrimi*. For example, both Y 49502 and Y 49694 are large with a straight anterior keel and sinuses extending well above the pedicel top – by about 34 mm in Y 49502. This latter specimen has a large ridge on the frontals medial to the base of the anterior keel on the pedicel, and this ridge shows an extensive sinus system. On Y 2523 (Figure 34) the occipital has no elevated central top region as in the crania of *M. pilgrimi*, while the frontals rise gradually from behind the horn cores to a higher intercornual summit than has appeared in earlier fossils. This cranium is incomplete ventrally and it is impossible to be sure of its height/width proportions. It was certainly bigger than the earlier *Miotragocerus* crania.

The posteromedial keel on the *M. browni* holotype is more apparent than in most other specimens. Tooth lengths taken on the London cast of *M. browni* (P2 15.9, P3 15.3, P4 12.9, M1

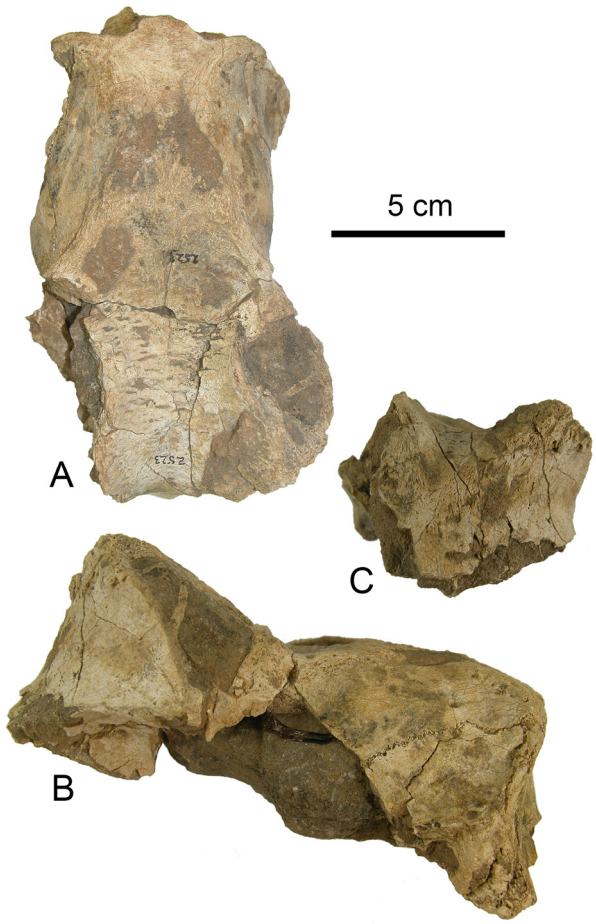

Figure 34. *Miotragocerus punjabicus*. Y 2523, cranium in A) anterior, B) dorsal, and C) left lateral views. Scale 5 cm.

16.2, M2 20.0, M3 19.9 mm) agree fairly well with those of *M. punjabicus*. The holotype of *Tragoportax islami*, a partial cranium GSI B565 (NHML cast M43978), from the Dhok Pathan Formation "of Padhri, near Hasnot" (Pilgrim, 1939: 232, caption to figure 25d-f), can also be satisfactorily included in *M. punjabicus* by the narrow and high cranium.

For the more abundant incomplete or fragmentary individual horn cores in the GSP collection hard and fast distinctions are difficult to make and our identifications are more tentative, making the stratigraphic range of the species uncertain. The oldest securely identified horn cores of *M. punjabicus* in the GSP collection (Y 49502 at 8.0 Ma and Y 49694 at between 8.1-7.8 Ma) (Figure 35) are 800,000 years younger than the youngest *M. pilgrimi*, but we have tentatively identified horn cores at 8.1 Ma and dental and skeletal material between 8.7 and 8.5 as *M. punjabicus*, with the interval between 8.8 and 8.0 Ma as when *M. punjabicus* replaces *M. pilgrimi* or, more probably, the transition from *M. pilgrimi* to *M. punjabicus* is completed. The *M. browni* holotype and paratype skulls with likely ages of 8.6-8.4 Ma and 8.3 Ma (Appendix 1) fit this chronologic scheme.

Y 49795 (6.4 Ma) is the youngest horn core identified as a possible *Miotragocerus punjabicus*, but it is only about 65 mm long, does not include the base, and the appearance of a demarcation is caused by damage to the upper part of the anterior edge. Y 18168 (6.5 Ma) is no more satisfactory as definitely being this species.

The oldest securely identified horn core of *Tragoportax salmontanus* (described below) appears at 8.4 Ma and it is hard to differentiate the more fragmentary horn cores of *Tragoportax salmontanus* from those of *M. punjabicus*. Of the horn cores listed above as *M. punjabicus* the most certain identifications (Y 49694, Y 49502, and Y 2523) all postdate the appearance of *T. salmontanus*. The others are smaller pieces or fail to show any indication of belonging to *T. salmontanus*. As to teeth, our oldest specimen of *M. punjabicus* is the mandible Y 4763 at 8.7 Ma (the premolars are illustrated on Figure 36), following much sooner on the last *M. pilgrimi* than did the earliest horn core. The mandible is larger than those of *M. pilgrimi* (and might just have fitted a small *Selenoportax* of a million years previously). For teeth younger than 8.4 Ma we have assigned only a limited number to *T. salmontanus* as detailed under that species.

The teeth of the Late Miocene Boselaphini *Miotragocerus pilgrimi*, *M. punjabicus* and perhaps *Tragoportax salmontanus* are larger and higher crowned than the Middle Miocene teeth likely to be *Strepsiportax*, *Sivaceros*, or *Sivoreas*. We noted previously Middle Miocene values for m3 hypsodonty that range between 59% and 80% (mean: 68%) and these may be compared with the Late Miocene aggragate values for *M. pilgrimi* and *M. punjabicus* that range from 69% to 87% (combined mean: 76%) (Table 7 and Appendix 5). The latter group are as high crowned as in *M. amalthea* at Pikermi and more so than the *Miotragocerus* of central Europe. *M. punjabicus* appears to be more hypsodont than *M. pilgrimi* (Table 7), the

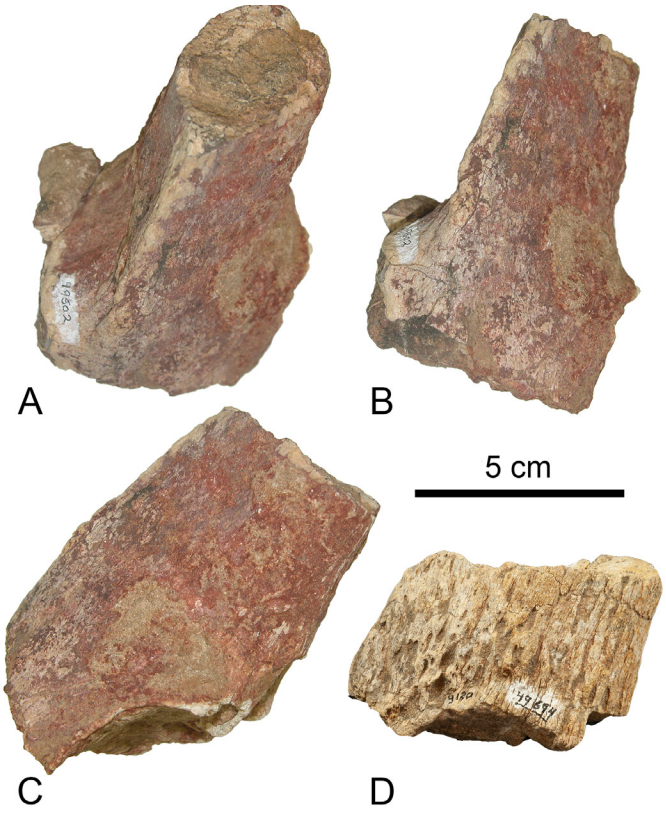

Figure 35. *Miotragocerus punjabicus*. Y 49502, left horn core base in A) dorsal, B) anterior, and C) left lateral views; Y 49694, left horn core base in D) left lateral view. Scale 5 cm.

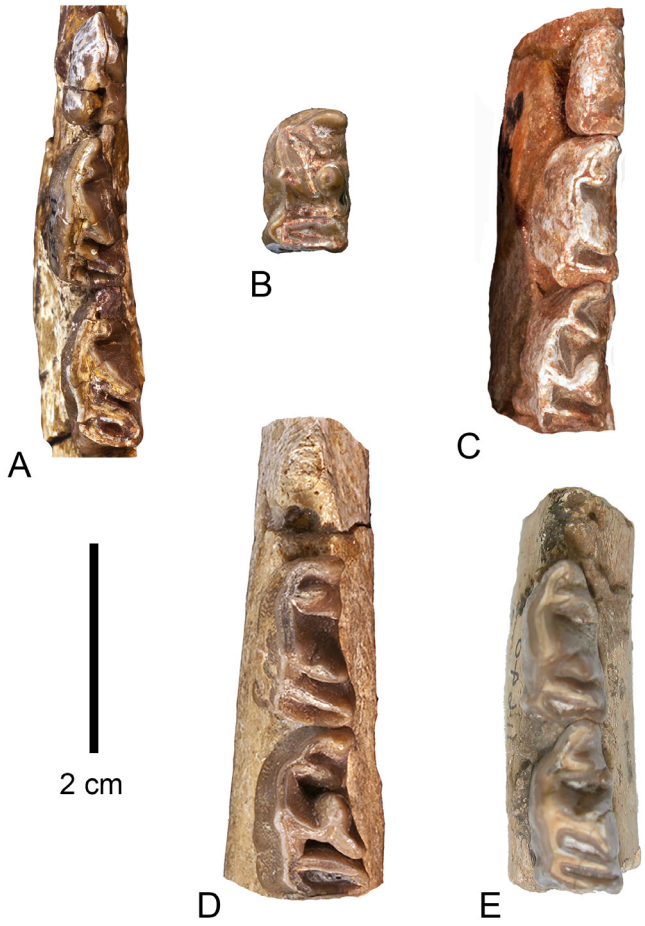

Figure 36. Lower premolars in occlusal view. A) Y 15611 in part, reversed, *M. punjabicus*, Loc. Y 467, 8.6 Ma; B) Y 5692, *M. punjabicus*, Loc. Y 17, 8.0 Ma; C) Y 178 in part, reversed, *M. punjabicus*, Loc. Y 17, 8.0 Ma; D) Y 4763 in part, *M. punjabicus*, Loc. Y 199, 8.7 Ma; E) Y 11640b, reversed, *M. pilgrimi*, Loc. Y 317, 9.3 Ma. Scale 2 cm.

two differing in means and ranges, but the samples are very small and a Mann-Whitney U test fails to show significance.

The ratios of premolar row to molar row length can best be judged from lower dentitions. Middle Miocene Siwalik boselaphines have values of 64, 61, 74, 64, 64, 69, and 65% while Late Miocene *Miotragocerus* have values of 68, 71, 78, 74, and 67% with means of 66% and 72% for the Middle and Late Miocene respectively. Within the premolars, length increases from p2 to p4, a situation unchanged from *Eotragus*, while in the upper premolars P2 tends to be longer than P3 and both are certainly longer than P4. The Siwalik species are both smaller than the western *M. amalthea* and do not develop the enlarged P2 seen in *M. amalthea* (Figure 37A). The Siwalik sample of *M. pilgrimi* is very similar to the Dorn-Dürkheim 1 boselaphine, both in size and tooth proportions, but in the contemporaneous *M. punjabicus* the molars are longer relative to the premolars (Figure 37A). The caprine *Pachytragus* differs from the boselaphines in shortening its premolars anteriorly and lengthening its molars posteriorly (Figure 37B).

Table 7. Hypsodonty[1] of lower molar teeth of Miocene boselophines and bovines in the Siwaliks compared with boselophines from Europe[2].

[1]The ratio used is crown height/occlusal length, expressed as a percentage. The m3s being longer will have lower values than m2s. All teeth are unworn or in earliest wear.

[2]A right m2 and a right m3 from La Grive St Alban, France (Middle Miocene), (Musée Guimet, Lyon, L.Gr.472 and 557, thought to be *Protragocerus chantrei*) had indices of 75% and 62% respectively, values well below those for the Siwaliks Late Miocene.

	m2	m3
Dorn Dürkheim 1, Germany, MN11 *Miotragocerus* indet.	Range: 76-79% Mean: 77.5% N = 2	Range: 55-72% Mean: 64% N = 6
Rudabanya, Hungary, MN9 *Miotragocerus* indet.	Range: 72-75% Mean: 73.5% N = 2	Range: 57% Mean: 57% N = 2
Baltavar, Hungary, MN12 *M. monacensis*	75% N = 1	Range: 63-64% Mean: 63.5% N = 2
Pikermi, Greece, MN12 *M. amalthea*		84% N = 1
Pikermi, Greece, MN12, *M.valenciennesi*	82% N = 1	
Siwaliks, Early and Middle Miocene	Range: 73-100% Mean: 90% N = 9	Range: 59-80% Mean: 68% N = 11
Siwaliks, *S. aff. vexillarius*	Range: 97-106% Mean: 102% N = 2	Range: 82-94% Mean: 88% N = 2
Siwaliks, *M. pilgrimi*	Range: 84-90% Mean: 87% N = 3	Range 69-80% Mean: 73% N = 6
Siwaliks, *M. punjabicus*	Range: 87-99% Mean: 94% N = 4	Range: 71-87% Mean: 79% N = 6
Siwaliks, *T. salmontanus*		68% N = 1
Siwaliks, *P. falconeri*	91% N = 1	
Siwaliks, *P. dhokpathanensis*	Range: 105-127% Mean: 118% N = 3	Range: 83-109% Mean: 96% N = 9

In their morphology the teeth of *Miotragocerus pilgrimi* and *M. punjabicus* mostly retain a generalised aspect, but showing some changes from Middle Miocene boselaphines (Table 6), masked as always by much individual variation. Y 15611 at 8.6 Ma (Figure 36A), for instance, is a rather large lower jaw of *M. punjabicus* with an unusually primitive appearance of its p3 and p4 in that neither tooth has a transversely turned anterolabial wall nor a paraconid markedly differentiated from a parastylid. The younger *M. punjabicus* palate Y 556 at 8.0 Ma shows a vertical indent on the lingual wall of the left P3 but not on the right one (Figure 38A). The rugose enamel and the rather deep indent on its only surviving P2 show the persistence of some older characters in some individuals well into the Late Miocene, yet other character changes are exemplified on this same palate. These include quite large basal pillars on all its molars, styles that are narrow and prominent and persist quite low down, and labial paracone ribs that are quite localised, while the metacone ribs are clear albeit much less prominent than on the paracone. A larger and slightly younger (7.9 Ma) hornless individual Y 52082 (Figure 39) does not have the vertical indents on P3 and P2.

Some dental characters can be puzzling. The p4 Y 5692 (8.0 Ma) for instance looks unusual in several respects – the near closure of the lingual wall anteriorly by the forward projection of an anterior metaconid cristid and backward extension of the paraconid, its transversely aligned front and back walls, the salient posterometaconid cristid originating labially behind the protoconid, and the labially projecting hypoconid (Figure 36B). Such characters could carry it outside the Boselaphini altogether except that other *M. punjabicus* specimens such as Y 178 and Y 224 from the same locality together with the earlier Y 4763 (8.7 Ma) approach the same morphology with an irregular course of the walls of p3-p4 (Figure 36C, D). While this configuration is more common in *M. punjabicus* than in *M. pilgrimi*, which typically has a more open p4 structure (Figure 36E), it occurs in both species and appears to be no more than individual variation.

The most interesting aspect of the Late Miocene boselaphine teeth concerns the divergence of the molars in a boödont direction which is unlike *Miotragocerus* in western Eurasia (Table 6). The process is similar to the evolution of boödonty seen at various periods in Bovini, Reduncini and Hippotragini (Gentry, 2010). It involves such characters (Appendix 3) as large basal pillars (32), strong and localised labial ribs (36), and central fossettes with a more complicated outline (37). Lower teeth show basal pillars on all lower molars (32), and goat folds on m1-m2 (also seen in some aegodonts) (33). Table 8 shows the state of two specimens from Locality Y 311 (10.1 Ma) and a much larger and younger sample, where characters marked "present" differ from *M. amalthea* at Pikermi. It looks as if boödont features appear in later wear and then increase in earlier wear as well.

The complete metatarsal found with Y 14882 has a narrow longitudinal groove down the anterior surface, a wide shallow groove proximally on the posterior surface, and no deep excavation on the lateral surface such as characterises *Miotragocerus pannoniae*. It is a little bigger than complete metatarsals of *M. pilgrimi* (Y 46732, Y 48746, and Y 48815 from Locality Y 311 and Y 14581 from Locality Y 269) and substantially bigger than the Middle Miocene metatarsal Y 32327.

As with *M. pilgrimi*, adult crania of *M. punjabicus* without horn cores in life have been found at GSP Locality Y 176

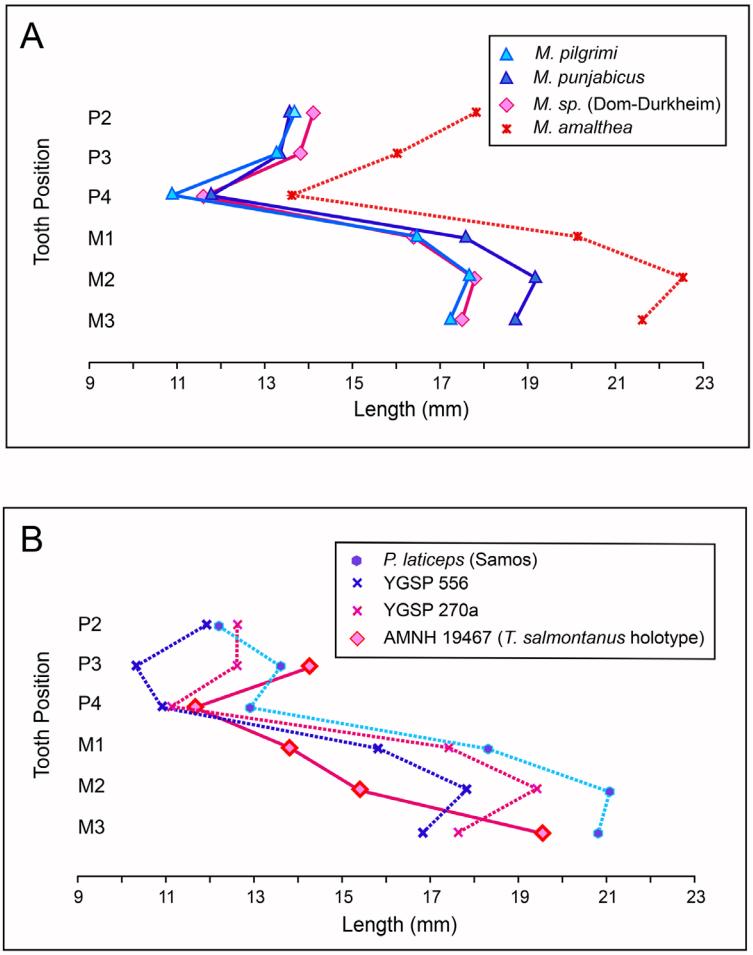

Figure 37. Plots of means of occlusal lengths of upper premolars (P2, P3, and P4) and molars (M1, M2, and M3) in some Late Miocene boselaphines and a caprine. A) comparison of Siwalik *Miotragocerus* samples (*M. pilgrimi* and *M. punjabicus*) to two samples from Europe (*M. amalthea* from Pikermi and *Miotragocerus* indet. sp. from Dorn-Dürkheim 1). Pikermi is ca. 7.5-7.2 Ma, Dorn-Dürkheim 1is between 8.9 and 7.6 Ma. B) comparisons of a caprine (*Pachytragus laticeps*) from Quarry 1 at Samos, the holotype of *Tragoportax salmontanus* (AMNH 19467), and two Siwalik individuals (YGSP 556, *M. punjabicus*, and YGSP 270a, *T. salmontanus*). Quarry 1 is between 7.1 and 5.3 Ma, the *T. salmontanus* holotype is about 8.3 Ma, and both YGSP specimens are 8.0 Ma.

(specimen Y 52070) and Locality Y 953 (specimens Y 52082 and Y 52083) (Figure 39), as well as at G.E Lewis's locality 12 (renumbered YPM VP.04804 by Jukar and Brinkman, 2021). These follow the appearance of *Tragoportax*. Those at Locality Y 953 are accompanied by males of *Miotragocerus punjabicus* (Y 50931 and Y 52084). The preorbital fossa on Y 52083 is less deep than in the two holotypes of *M. punjabicus* and *browni*, as often happens in females of bovid species with these fossae.

Khan, M. A. *et al*. (2014, 2024), as well as Ikram *et al*. (2016) and Abbas *et al*. (2018) identified a large number of teeth of *Miotragocerus punjabicus*, which they attributed to the genus *Tragoportax*. As noted above we restrict *Tragoportax* to the single species *Tragoportax salmontanus*.

Comments. *Miotragocerus punjabicus* is slightly larger than *M. pilgrimi* as seen in both horncores (Figure 31) and dentitions. In samples of teeth, means of the lengths of p4 and m3 of *M. pilgrimi* are about 4 % smaller than the means of *M. punjabicus*, although the individual measurements show considerable overlap between the species (Figure 40) and the

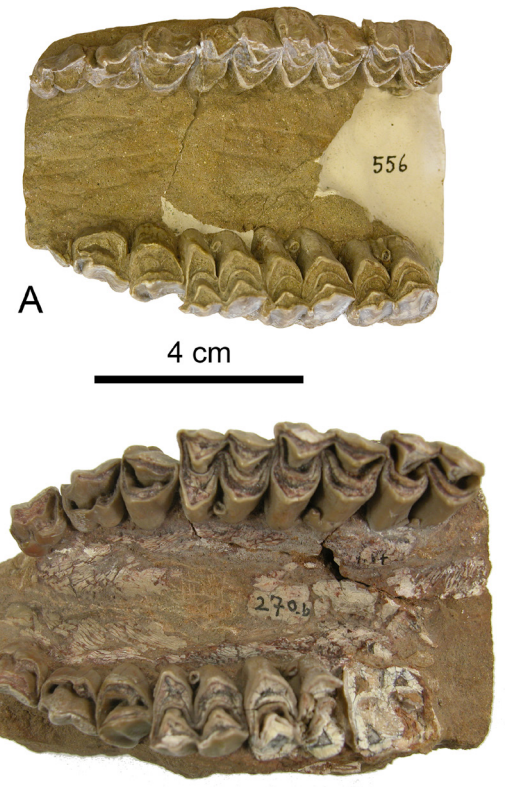

Figure 38. Two palates in occlusal view. A) *Miotragocerus punjabicus*, Y 556; and B) *Tragoportax salmontanus*, Y 270b. Scale 4 cm.

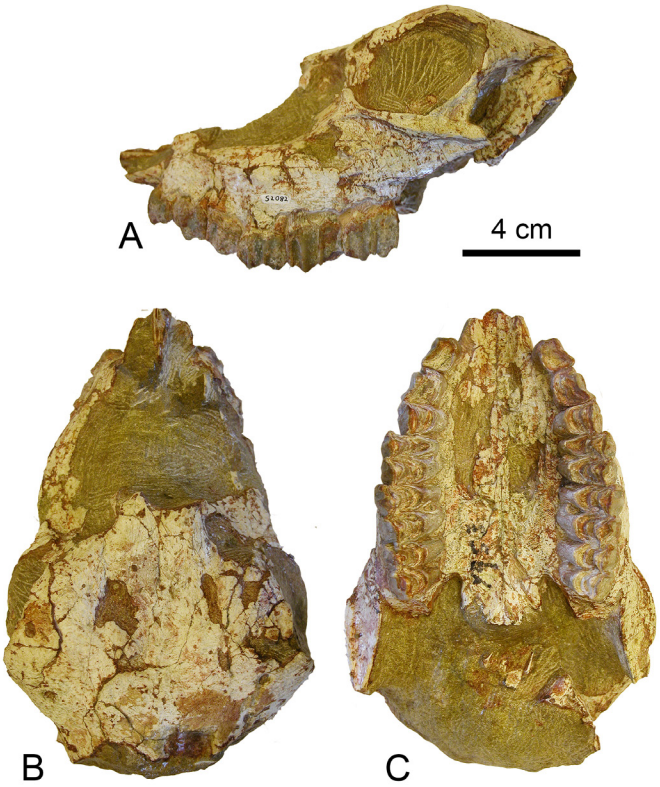

Figure 39. *Miotragocerus punjabicus*, Y 52082 Partial female skull in A) left lateral; B) dorsal; and C) occlusal views. Scale 4 cm.

Table 8. Comparison of two specimens of *M. pilgrimi* to a much larger and younger sample of *M. punjabicus*. Characters marked "present" differ from *M. amalthea* at Pikermi.

Species	Loc	Age (Ma)	Specimen Number	Wear	GENERAL		UPPER MOLARS				LOWER MOLARS					LOWER PREMOLARS		P2/p2
					Enlarged basal pillars	Central fossettes more complicated	Stronger styles	Stronger labial ribs	Central fossette becomes U-shaped	Lingual lobes with localised pinching	Lingual walls outbowed	Metastylid more prominent	Labial lobes narrowly pointed	Labial lobes with localised pinching	Goat folds present	Central fossettes more curved	Front and back walls notably transverse	Enamel walls with irregular outline	Reduced
pilgrimi	Y311	10.1	Y 19950	earlier	Absent						Absent	Absent	Present	Absent	Absent	Absent			
pilgrimi	Y311	10.1	Y 26871	earlier	Absent	Absent	Absent	Absent	Absent	Absent							Absent	Absent	
punjabicus	Y176	8.2	Y 52070	later		Present	Absent	Absent	Present	Absent	Absent	Absent	Present	Present	Absent		Absent	Absent	Present
punjabicus	Y 17	8	Y 178	earlier	Absent						Absent	Present	Present	Present	Present	Absent	Absent	Absent	Present
punjabicus	Y 17	8	Y 236	earlier	Present	Absent	Present	Absent	Absent	Present									
punjabicus	Y 17	8	Y 254	earlier	Absent						Present	Absent	Absent	Present	Absent	Absent	Absent	Absent	Absent
punjabicus	Y 17	8	Y 263	earlier	Absent						Absent	Absent	Absent	Absent	Absent	Present			
punjabicus	Y 17	8	Y 332	earlier	Absent						Absent	Absent	Present	Absent	Absent	Absent	Absent	Absent	
punjabicus	Y 17	8	Y 421	earlier	Present						Absent	Absent	Absent	Absent	Present	Absent			
punjabicus	Y 17	8	Y 422	earlier	Absent						Present	Absent	Present	Absent	Absent	Absent			
punjabicus	Y 17	8	Y 556	earlier	Present	Absent	Present	Present	Absent	Present									Present
punjabicus	Y 17	8	Y 2818	earlier	Absent						Absent	Absent	Absent	Absent	Absent	Present			
punjabicus	Y 17	8	Y 9203	earlier	Absent						Present	Present	Present	Present	Present	Present	Absent	Absent	
punjabicus	Y 17	8	Y 15261	earlier	Present						Present	Absent	Absent	Absent	Present	Present			
punjabicus	Y 17	8	Y 21985	earlier	Absent	Absent	Absent	Absent	Absent	Absent									
punjabicus	Y 17	8	Y 208	later	Absent	Absent	Absent	Absent	Absent	Present									Absent
punjabicus	Y 17	8	Y 224	later							Absent	Absent	Present	Absent	Absent	Absent	Present	Absent	Absent
punjabicus	Y 17	8	Y 228	later	Absent						Present	Absent	Present	Present	Present	Present		Present	
punjabicus	Y 17	8	Y 238	later	Absent						Absent	Absent	Present	Present	Absent	Absent		Absent	
punjabicus	Y 17	8	Y 381	later							Absent	Absent	Present	Absent	Present	Present	Present	Present	
punjabicus	Y 17	8	Y 2812	later	Absent						Absent	Absent	Present	Absent	Absent	Absent			
punjabicus	Y953	7.9	Y 52082	later	Present	Absent	Absent	Absent	Absent	Absent									Absent
punjabicus	D 13	6.35	Y 50737	later	Present	Absent		Present		Present									Present

distribution of the values is quite different between the p4s and m3s. MannWhitney U tests indicate the two samples of m3's are unlikely to have been drawn from a single population (ZScore = -2.47191, with a *p* of .01352 and n= 41 for *M. pilgrimi* and n=25 for *M. punjabicus*), while the smaller samples of p4 (n=14 and n=19) are not significantly different at p < .05.

Miotragocerus punjabicus resembles the larger species *M. rugosifrons* in western Eurasia in the backward curvature of its horn cores, the poor or absent demarcation, and in the raised intercornual area of the frontals to which growth of the horn pedicels has contributed much. The auditory bulla on the holotype of *M. punjabicus* is large and inflated as in *M. rugosifrons* (Bouvrain, 1994: plate 3 figure 2), and there is a similar flat top edge of the occipital. *Miotragocerus punjabicus* differs from *M. rugosifrons*, however, in that it is smaller, its horn cores are not as steeply inclined backwards, the preorbital fossae is larger and deeper, and the tooth row is perhaps slightly less anterior relative to the front of the orbit. The same differences exist between *M. punjabicus* and *M. amalthea* and the latter also has a more rounded top edge of its occipital. The horn cores and teeth of *M. punjabicus* are smaller than in *M. amalthea* (Figure 31) and *M. punjabicus* fails to enlarge its anterior premolars (Figure 37a).

Miotragocerus punjabicus differs from the Chinese *M. spectabilis* cranium (Bohlin, 1935b: figures 49-53) in not having a wide angle of the anteroposterior axis of the horn cores to the longitudinal midline of the skull, nor a transversely convex surface of the frontals anterior to the horn bases, nor a short and wide braincase, nor a sharply-downturned cranial roof posteriorly. *M. spectabilis* is a specialised and probably late species.

Miotragocerus punjabicus and *Tragoportax salmontanus* in their later levels of occurrence are likely to be contemporaneous with large *Miotragocerus* elsewhere in the world, e.g. *M. cyrenaicus* or aff. *M. cyrenaicus* at Sahabi, the Late Miocene (ca. 7.9-6.9 Ma) Baynunah Formation in the United Arab Emirates, and Lothagam, and *M. acrae* of Langebaanweg. *Miotragocerus cyrenaicus* has divergent and sometimes lyrated horn cores while *M. acrae* has short, non-curved horn cores supported on much raised frontals.

Boselaphine females are usually hornless (Thomas, 1979: 275; 1984a: 18). The hornless females of *M. punjabicus* agree with *M. amalthea* at Pikermi (Dames, 1883; Weithofer, 1888: 289: plate 19 figure 1) and *M. frolovi* at Novoukrainka (MN10), Ukraine (Korotkevich, 1981: figures 36-37, plate 9). A hornless female of *Miotragocerus* is also known from Samos (AMNH 86626) and one from Vathylakkos, Ravin C (Siq-718). This satisfying and widespread consistency is contradicted by two horned females of *M. rugosifrons* at Hadjidimovo, Bulgaria (MN12) (Spassov and Geraads, 2004: 344, figure 6A). The smaller *Miotragocerus* species, *M. valenciennesi*, also seems to have had horned females as at Piera, Spain (MN11), at Pikermi, and at Dytiko 1 and 3, Greece (MN13) (Moyà Solà, 1983: 150; Bouvrain, 1988: 49), and a possible horned female of *M. pannoniae* is known from the earlier (MN9) locality of Kettlasbrunn, Austria (Naturhistorisches Museum, Vienna, AWG personal observation, 1986).

Genus *TRAGOPORTAX* Pilgrim, 1937

Type species. *Tragoportax salmontanus* Pilgrim, 1937

Comments. Because proposed diagnoses of *Miotragocerus* and *Tragoportax* are "difficult to consistently apply in a wide context" (Bibi *et al*, 2009, p. 4) we retain only the type species in this genus. But even then it might be insufficiently distinct to be separated from *Miotragocerus*.

Species *Tragoportax salmontanus* Pilgrim, 1937

Tragoportax salmontanus Pilgrim, 1937: 774, figures 21, 22, 60.

Tragoportax cf. *salmontanus* Pilgrim, 1939: 231, figures 25a-c.

Tragoportax aiyengari Pilgrim, 1939: 228, figures 24a-c.

Tragoportax cf. *islami* Pilgrim, 1939: 231, figures 26a-c.

Holotype. AMNH 19467, a partial skull (Pilgrim, 1937: figures 21, 22, and 60), from a quarry one mile south of Dhok Pathan in the Dhok Pathan Formation at about 8.3 Ma (see Appendix 1). Cast in NHML, M15757. It has some dorsoventral compression of the face. Unfortunately, the dentition is in late wear (Pilgrim, 1937: figure 60).

Diagnosis. Perhaps smaller than *Miotragocerus punjabicus*, but overlapping or being of equal size cannot be ruled out. Like *M. punjabicus* except in the following characters. Skull lower and wider. Horn cores only short-moderately long, level of maximum transverse thickness lying just behind the anteroposterior centre, more divergent basally and then with a smoothly diminishing degree of divergence which gives a medially concave course to the horn cores in anterior view, little or no backward curvature, demarcation generally present (but poor or absent in the holotype), close horn core insertions but less extremely so than in *M. punjabicus*, slight torsion of the anterior keel. Back of cranial roof more obviously curved or bent downwards, preorbital fossae large but less so than in *punjabicus*.

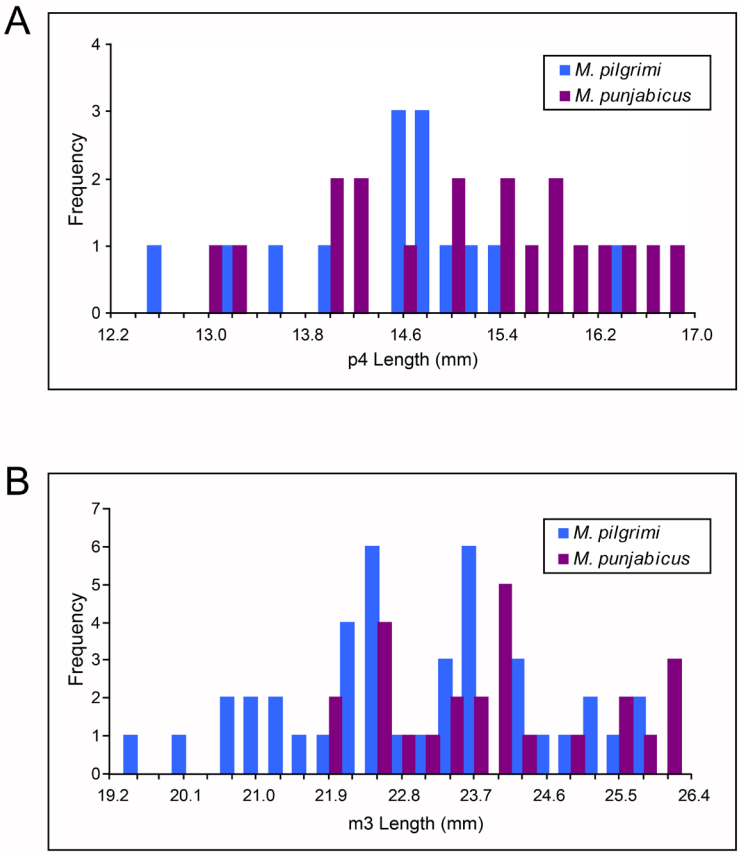

Figure 40. Histograms of A) p4 and B) m3 lengths of *Miotragocerus pilgrimi* and *M. punjabicus*.

Estimated age. 8.4 - 7.2 Ma.

Remarks. The *Tragoportax salmontanus* holotype is the firmest evidence we have of a second species-lineage of the *Miotragocerus* group in the Siwaliks. Some of its differences from *M. punjabicus* might be retentions of primitive states: shorter horn cores, level of maximum transverse width lying more anteriorly, little or no backward curvature, back of cranial roof more definitely curved downwards. Two characters might be seen as autapomorphic: the steady decrease in degree of divergence of horn cores from base to tip and the low and wide cranium. Three further specimens described by Pilgrim (1939) and briefly considered below appear to belong to this species. Thomas (1984a: plate II figure 3 and plate III figure 2) identified two additional specimens in the GSP collection as *T. salmontanus* (Y 6147 and Y 4700), which are respectively 9.4 and 9.0 Ma. We have not seen this material, which is in France, and are not sure about the attributions. Both fall within the time range of *M. pilgrimi* and are older than the *T. salmontanus* material listed here.

Material.

Locality Y 535 (8.4 Ma)

Y 16183 Right horn core, nearly complete, and base of left horn core.

Y 16232 Left and right mandibles, both with p4-m3. Also a partial skeleton.

Locality Y 545 (8.1 Ma)

Y 16998 Left horn core.

Collecting Level KL 11 (8.1 – 7.8 Ma)

Y 16394 Right horn core.

Locality Y 17 (8.0 Ma)

Y 270a,b Frontlet with both horncores and palate with P2-M3.

Locality Y 581 (7.2 Ma)

Y 52736 Right horn core base.

Discussion. The diagnosis is based mainly on the holotype. The GSP specimens listed occur within the time range 8.4 to 7.2 Ma with the holotype being 8.3 Ma (Appendix 1). The more fragmentary horn cores are hard to differentiate from *M. punjabicus*. Since we have placed the last *M. pilgrimi* at 8.8 Ma there is no confusion with this species unless definite *T. salmontanus* is found before that date. The only teeth we place in *T. salmontanus* are (1) those on the holotype, (2) the mandible of Y 16232 at Locality Y 535 where a horn core of *T. salmontanus* but no *M. punjabicus* occurs, (3) two teeth at Locality Y 545 where a horn core of *T. salmontanus* occurs, and (4) a palate associated with the frontlet Y 270 (Figure 41).

Some of the *Miotragocerus* or *Tragoportax* horn cores younger than 8.5 Ma have acquired stronger basal divergence and stronger compensating diminutions of degree of divergence along their course, taken by us to indicate a greater probability of the animal being *T. salmontanus*. The horn core Y 16183a (Figure 42A, B) is not very long, nearly straight in side view and with a regularly diminishing degree of divergence from base to tip. Its anterior edge tapers rapidly to a localised demarcation at ca.130 mm above the base. The associated left horn core fragment (Y 16183b) has a maximum cross-sectional transverse thickness situated not very far behind its central point. Y 15661 also shows a steadily reducing divergence from the base upwards, and it is of interest here too that the only two boselaphine dental specimens at Locality Y 24 have been identified as *M. punjabicus*. The right horn core Y 16394 from Collecting Level KL11 (Figure 42C, D) is not large, its degree of divergence diminishes distally, it has a demarcation, and a sinus just reaches into the posterior part of the base of the horn core. Such horn cores resemble the holotype *T. salmontanus*.

The horn core Y 16998 (Figure 42E, F) has a demarcation and its degree of divergence appears to diminish gradually along its course. A sinus penetrates at least 32 mm into the horn core above the line marking the erstwhile base of the sheath. At this level the approximate anteroposterior diameter is 37 mm. The other horn core fragment from the same locality (Y 18645) shows no sign of a sinus, but its anteroposterior diameter at this presumed equivalent level is very much larger at ~ 47 mm. A similar combination of slender and larger horn cores was also found at Locality Y 311 in *M. pilgrimi* (i.e. Y 49596 and Y 51383) at 10.1 Ma (Figure 33). Locality Y 545 also has two slightly smaller and probably boselaphine lower molars and they are here assigned to *T. salmontanus.* The same locality also has one of the rare specimens of *Punjabameryx inflata* sp. nov.

The horn cores of the frontlet Y 270 show definite wider basal divergence than in the *M. browni* holotype thereby agreeing well with *Tragoportax salmontanus.* This frontlet is associated with a palate (Figure 41) having premolars that are rather short (Appendix 4), but the M1 and M2 are not as short as the well-worn molars in the holotype of *T. salmontanus*. The palate of Y 270 has vertical indents on the lingual walls of both the P3 and P2.

On first sight the upper dentition on the holotype looks small, but its advanced wear (Pilgrim, 1937: figure 60) could be affecting comparisons with other dentitions which are mostly in various stages of middle wear. Figure 37B shows that the M1 and M2 are short but the M3 is not. The relatively excessive length of the M3 probably results from the late wear stage (Appendix 3, character 31). None the less the overall length of the complete molar row of the holotype is 45.6, a small figure in comparison with our other boselaphine teeth listed by default

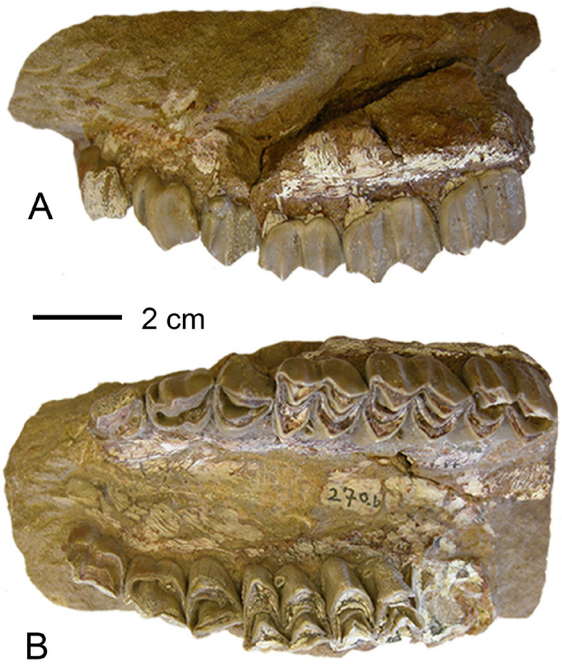

Figure 41. *Tragoportax salmontanus*, Y 270 palate 1) left buccal; 2) occlusal view. Scale 2 cm.

as *M. punjabicus* (mean = 52.5, N = 9, range 48.3-56.7). If the two surviving premolars had their present lengths in middle wear, one could conjecture that *T. salmontanus* was a smaller species with a longer premolar row relative to the molar row. However, the premolar row of Y 270 is shorter, not longer, so the real situation remains undecided.

The only m3s of *T. salmontanus* are Y 17007 and that on the mandible of Y 16232. Both are fairly long but not notably long among boselaphine m3s of the period. For the present we cannot establish any dental characters for *T. salmontanus*.

Other previously described Siwaliks material may also belong to *T. salmontanus*. The *T. aiyengari* holotype (GSI B828, NHML cast M42954, Pilgrim, 1939: 228, figure 24a-c) is similar in some features to the *T. salmontanus* holotype, but could be slightly larger and with less backwardly inclined horn cores. The low inclination of the horn cores on the *T. salmontanus* holotype may, however, have been affected by postmortem distortion. A partial cranium, GSI B310, was described by Pilgrim (1939: 226, figure 25a-c) as *T.* cf. *salmontanus.* The ages of both fossils are uncertain, but they are quite likely to be late in the Late Miocene. GSI B828 came from one mile south west of Athem, Jammu, 32^0 46$^{'}$ 30$^{"}$ N, 75^0 0$^{'}$ 30$^{"}$ E, and was said to belong to the "Dhok Pathan stage." GSI B310 came from Hasnot and was of later "Dhok Pathan age." Finally, a right horn core and part of the frontal, GSI B566, of *Tragoportax* cf. *islami*, found in the Punjab long ago and thought by Pilgrim (1939: 231, figure 26) to have come from the "Dhok Pathan stage" near the Soan River, looks as if it could be *T. salmontanus*. None of the three fossils are definitely or appreciably smaller-sized than *M. punjabicus*. The identifications of the dental remains allocated by Pilgrim to these names are very uncertain.

Figure 42. *Tragoportax salmontanus*. Y 16183a; Right horn core, A) anterior and B) lateral views. Y 16394; Right horn core, C) anterior and D) lateral views. Y 16998; Left horn core (reversed), E) anterior and F) lateral views. Y 52736; Right horn core, G) anterior and H) lateral views. Scale 5 cm.

Asim *et al*. (2020) identified a small sample of isolated teeth, one mandilbe fragment, and three small horn core fragments from the Chinji Formation as *Tragoportax* cf *salmontanus*. We have not seen this material and are not sure about the attributions. We regard the teeth as being problematic because as noted there are no established dental characters for *T. salmontanus*. The basal horn core fragment (PUPC 18/36) is too small for *Tragoportax salmontanus*, being more the size of our smaller *Sivaceros gradiens* horn cores (Appendix 4).

Comments. A few clues favour the hypothesis that *T. salmontanus* descended from *M. pilgrimi*. For example, while the *M. pilgrimi* cranium Y 22157 (Figure 30) fits a little awkwardly on a hypothetical line leading from the earlier cranium Y 21086 to *M. punjabicus*, its wide braincase and ventrally expanding pedicels are similar to *T. salmontanus* and suggest a possible relationship. However, the distortion and partial reconstruction of the *T. salmontanus* holotype, the known infraspecific variation in Siwalik boselaphines, and the consequent difficulties of identifying individual fossils all mean that much remains uncertain. A good example of a difficult fossil to identify is the horn core Y 52736 (Figure 42G, H) at 7.2 Ma. It is large for *T. salmontanus* but the divergence changes too much along its course for *M. punjabicus* and the sinus in its pedicel extends at least 27 mm into the base of the horn core proper. It is the youngest *T. salmontanus* in the GSP collection.

Tragoportax salmontanus is unlike the west Eurasian *Miotragocerus valenciennesi* in the diminishing degree of distal divergence of the horn cores, a slight hint of torsion, and a relatively lower and wider cranium. Its preorbital fossa is certainly not smaller than in the London skull of *M. valenciennesi*, and may be as big as in the holotypes of *M. browni* and *M. punjabicus.* The teeth of Y 270 are near to *M. valenciennesi* in size but the P2 is short by comparison with P3, and the P4 is rather small. It may also be mentioned that the two skulls of the Chinese *M. gregarius* described by Zhang (2005) look closer to *M. valenciennesi* than to *Tragoportax salmontanus*. They came from Late Miocene levels in Shaanxi Province perhaps coeval with the early Turolian (MN11) of western Eurasia.

PUNJABAMERYX genus nov.

Type species and only included species. *Punjabameryx inflata* species nov.

Diagnosis. A moderate to large-sized species with pedicels very inflated in front and containing enlarged sinuses penetrating a short distance into the horn core, short and rather small horn cores with irregular longitudinal grooves and ridges, little compression at base with distally a nearly circular cross section, strong backward inclination, upwardly curved along posterior edge, insertions close, moderate basal divergence with slightly diminishing divergence distally. The inflated pedicels and massive sinuses together with the short and little compressed horncores set this species apart from other bovids.

The generic name refers to the Punjab region of Pakistan, where the fossils were found.

Punjabameryx inflata species nov.

Holotype. GSP Y 49501, frontlet with orbit and base and lower part of left horn core (Figure 43). From Locality Y 20 (8.0 Ma) at 33° 6.791'N, 72° 20.464'E. Correlated to the Dhok Pathan section of Barndt (1977) between 432.8 and 414.5 meters above the base.

Diagnosis. As for the genus.

The trivial name refers to the swollen or inflated pedicel and frontal.

Estimated age. ?9.4 - 7.3 Ma.

Material.

Locality Y 227 (9.4 Ma)

Y 6842 Complete left horn core, broken at the base of the horn core proper. Tentatively included in this species.

Locality Y 166 (8.8 Ma)

Y 3928 Frontlet with complete left horn core and orbit.

Locality Y 545 (8.1 Ma)

Y 16966 Left horn core.

Locality Y 20 (8.0 Ma)

Y 49501 Left frontlet with most of the horn core. Holotype.

Locality Y 452 (7.3 Ma)

Y 50790 Frontlet with the bases of both horn pedicels.

Discussion. This is a very rare taxon. The four more securely identified specimens range from 8.8 to 7.3 Ma, with a fifth tentatively identified individual extending the temporal range to 9.4 Ma, a long period of sympatry with *Miotragocerus* spp. and *Tragoportax salmontanus*. The species is probably boselaphine as one of them has a keel and one or two have demarcations. Three have enlarged and swollen pedicels while a fourth has a smaller, but still very swollen pedicel.

The holotype, Y 49501 (Figure 43), is most of a short horn core having a very short posterolateral keel in its basal part, moderate basal divergence with slightly diminishing degree of divergence distally, a low inclination and posterior edge slightly upwardly curved in side view, and with a demarcation near its base. The enlarged pedicel is expanded anteromedially but ends without joining its partner of the right side, as also happens in *M. punjabicus*. There are extensive sinuses within the pedicel that penetrate about 2 cm into the base of the horn core.

The first of the three other securely identified specimens, Y 3928 (Figure 44A, B), is an almost complete short horn core. It has no keels, neither the lateral nor medial surface is flattened, the back edge is slightly convex backwards in profile and what looks like a demarcation in side view right at its base might be a misleading appearance arising from postmortem destruction of the top of the front of the pedicel. The postcornual fossa is very shallow. Although the pedicel was extended anteriorly its lateral surface is not very filled-out. Extensive sinuses inside it are visible from the medial side. Like the holotype the horncore of Y 3928 looks small in relation to the pedicel. It is slightly smaller than the holotype and the frontlet Y 50790. Y 16966 (Figure 44C, D) diverges slightly from the other two preserved horn cores in having a straighter course, but does have the distinctive swelling of the front of the pedicel. It has no keels and very little compression (Figure 44D). The last specimen (Y 50790) (Figure 44E) has very prominent pedicel mounds closely approaching across the former intercornual gap but failing to contact centrally, an appearance reminiscent of the *M. browni* and *M. punjabicus* holotypes and the Samos *M. rugosifrons* lectotype in Schlosser (1904: plate 12 figure 6a). The pedicel mounds contain massive sinuses. The minimum width across the lateral edges of the horn pedicels and the width across the supraorbital pits would have been about 109 and 62 mm respectively. The convex transverse profile across the frontals in front of the horn cores looks like the Chinese *M. spectabilis* (Bohlin 1935b: figures 49-53).

Y 6842 (Figure 44F) is a smaller and earlier horn core (9.4 Ma), which possibly goes with this group. It compares favourably with Y 3928, although considerably shorter (ca. 70 mm). It is a short, rounded horn core (basal index 28.4×24.3: 86%) without keels. It has a slightly convex back edge and as shown in the figure an extensive sinus penetrating high into the horn. We believe Y 6842 probably is a juvenile.

Comments. These remains seem to belong to a boselaphine. Its horn core and pedicel characters could have developed from a *Miotragocerus* by suspension of horn core lengthening in immature individuals, so that growth in length proximally to the demarcation never takes place. Such large and bulky pedicels mounted on transversely convex frontals recall some modern goats and might reflect a similar behavioural pattern of display or fighting. Y 50790, the frontlet from Locality Y 452, has numerous preserved fossil worm casts both on the outer surface and inside the braincase and frontal sinuses.

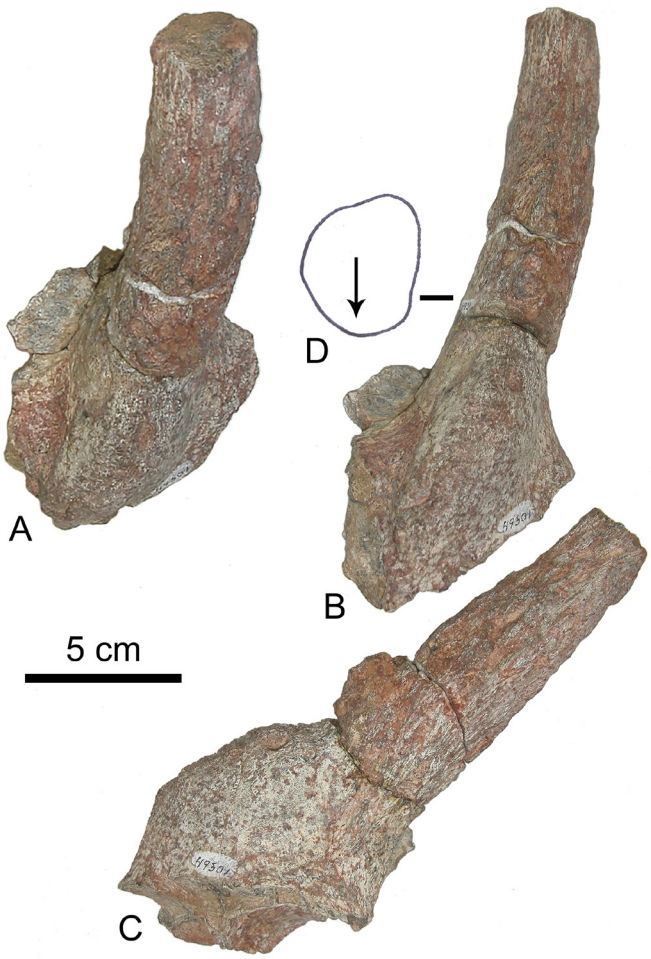

Figure 43. *Punjabameryx inflata* sp. nov. Y 49501, holotype. Left horn core in A) dorsal, B) frontal, and C) lateral views, D) cross section at the base, with arrow indicating anterior. Scale 4 cm.

A note on Ruticeros pugio Pilgrim, 1939

Ruticeros pugio was founded for a left horn core about the size of a Miocene gazelle. It came from an unknown locality (Pilgrim, 1939: 240, plate 4 figure 2). The two assigned horn cores in London from Hasnot agree with the holotype in Calcutta in the accentuated longitudinal grooves and ridges among which an anterior and posterior keel are barely discernible. The backward curvature of the horn core sets this species apart from our new species *Punjabameryx inflata*, which is about the same size. *Ruticeros pugio* could be a small boselaphine as Pilgrim believed.

Tribe ?BOVINI Gray, 1821

Genus *PACHYPORTAX* Pilgrim, 1937

Perimia Pilgrim, 1939: 165.

Type species.. *Cervus latidens* Lydekker, 1876: 65, plate 8 figures 7, 10.

Included species. *P. latidens*, *P. falconeri*, *P. dhokpathanensis*, and *P. giganteus*.

Diagnosis. *Pachyportax* is larger than *Miotragocerus* and also slightly larger than *Selenoportax*. Horn cores moderately long, with a strong anterior keel, a posterolateral edge or keel, and a more rounded edge in the posteromedial position. Anterior keel descending to an anterior insertion, slightly compressed mediolaterally, some flattening of the lateral surface, while the medial surface is more rounded, basal divergence moderate to strong, crescentic curvature in anterior view not pronounced, inclined backwards, inserted fairly wide apart. State of postcornual fossa is not known in the Siwalik material, but Nishioka *et al*. (2019) describe a very shallow one in material from Myanmar. Sinuses within frontals, frontals not raised between horn bases, shallow and poorly delimited preorbital fossa. Cranial roof almost horizontal or slightly sloping and with strong temporal ridges. Occipital surface faces posteriorly. Compared with the Siwaliks *Miotragocerus,* molar teeth with larger basal pillars that become more integrated with the body of the teeth (Appendix 3 character 32), more prominent styles and stylids (character 35), strong labial ribs of upper molars, even on the metacone (character 36), a more complicated outline of the central fossettes on upper molars (character 37), and outbowings of lingual walls of lower molars present and sometimes becoming more localised ribs (character 40). These characters become more frequent and more obvious in later fossils. Upper molars acquire large occlusal areas, a feature presumably linked with larger body size.

Remarks. Material of *Selenoportax* aff. *vexillarius* already described above from between 10.2 and 9.8 Ma seemed to be larger and with a somewhat less distinctive morphology than the holotype of Pilgrim's *S. vexillarius*. Fossil bovids of this size continue to be found between 9.8 and 7.3 Ma, but are more like *Pachyportax* in younger deposits. Some of the tooth characters of *Pachyportax* are suggestive of a stem-Bovini status (Bibi, 2007a) and the morphological limits of its various species are uncertain.

The best known specimen, the holotype cranium of *P. dhokpathanensis* (Pilgrim, 1939: figures 19a-d), has clear differences from *Selenoportax vexillarius*: larger size (Table 9, columns A and E), the keel on the back of the horn cores is posterolateral instead of posteromedial, the medial surface is not flattened, the anterior keel descends to an anterior insertion, horn cores usually less divergent and more inclined in side view, long axis of cross section not at a notably strong angle to skull midline, sinuses more extensive, perhaps a rugose surface behind the horn insertions, and braincase with a stronger short slope in lateral profile as it approaches the top of the occipital.

The type species of *Pachyportax* was founded by Lydekker (1876) on two teeth, a right lower and a right upper molar. The latter is in early middle wear and was chosen by Pilgrim (1937: 766) as lectotype. It came from near Hasnot and was thought by Pilgrim (1937: 767-768) to be from the Tatrot Formation. Lydekker gave its number as 1420 and Pilgrim used a later catalogue number GSI B219. A cast of the tooth, NHML M34567, and a second in the Department of Human Evolutionary Biology, Harvard University, are inscribed B220. The Harvard cast has occlusal length and breadth 31.7×27.3 mm. It has advanced a little towards hypsodonty and has a neat and simple occlusal surface devoid of any morphological approach towards Bovini.

Pilgrim (1937: 768, 1939: 198) also founded the subspecies *Pachyportax latidens dhokpathanensis* on a cranium with basal part of left horn core, GSI B488 (cast NHML M26573), from Nila in the Dhok Pathan Formation. The worn right M2 and M3 of the holotype, GSI B489, also survived (Pilgrim, 1939: 201). Pilgrim (1937: figure 51) illustrated only an AMNH tooth he had attributed to his new subspecies, and the cranium was not dealt with in print until Pilgrim (1939: figures 19a-d). Pilgrim (1939: 202) discussed in some detail another cranium GSI B245 of *P. l. dhokpathanensis* catalogued by Lydekker

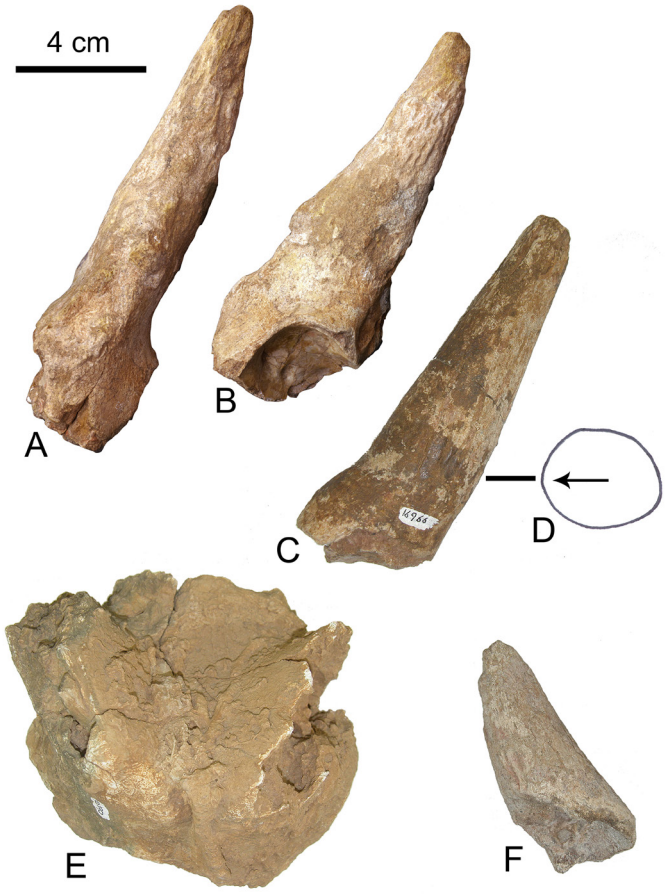

Figure 44. *Punjabameryx inflata* sp. nov. Y 3928 in A) anterior and B) left lateral views; Y 16966 in C) left lateral view and D) cross section at the base with arrow indicating anterior; Y 50790 in E) dorsal view; and Y 6842 in F) medial view. Scale 4 cm.

(1885b), but it has never been illustrated. We agree with Bibi's (2007a: 66) proposal that the lectotype tooth of *P. latidens* itself should be treated as belonging to a *nomen dubium*. The tooth has no boödont characters, so we have to assume that, as in the case of *Miotragocerus* (Table 8), there will be variation in the incidence of the more advanced characters within *Pachyportax* and that they will become commoner with the passage of time. We note that *P. latidens* has to remain the type species of the genus according to the rules of nomenclature and we propose that the name *P. dhokpathanensis* should be used as a full species. We believe that this will be advantageous in retaining both generic names *Selenoportax* and *Pachyportax* and facilitating any future suprageneric taxonomic changes.

An alleged earlier *Pachyportax* species, *P. nagrii* Pilgrim (1939: 207, figures 21a-d) has as its holotype a smaller and hornless female cranium from Nagri without a *Miotragocerus*-like rugose surface, but with a high occipital. Pilgrim (1939: 207 and 195; 1937: figure 19) added a right horn core base, AMNH 19764, to *P. nagrii*. Under our taxonomic arrangement it could be a small *Selenoportax* aff. *vexillarius*. Abbas *et al*. (2018) have attributed a very few mostly isolated teeth to *P. latidens* and one tooth to what they referred to as *P.*cf *nagrii*. These specimens are likely either *P. falconeri* or the later *P. dhokpathanensis*. Other authors (Ikram *et al*., 2016; Draz *et al*., 2020, 2021; Waseem *et al*., 2020 and Naz *et al*., 2024) have also attributed dental material to *P. latidens* or *P. nagri.*

We accept provisionally only four species of *Pachyportax*: the type species *P. latidens* containing only the lectotype tooth, the two species in our material, namely the earlier *P. falconeri* and the later *P. dhokpathanensis*, and the large *P. giganteus* of Akhtar (1995), which is not represented in our material. Following Gentry (1974) we do not regard *P. nagrii* as a valid species.

Species *Pachyportax falconeri* (Lydekker, 1886)

Boselaphus sp. Lydekker, 1884: 114, plate 13 figures 1-4,7-8, 11.

Strepsiceros(?) *falconeri* Lydekker, 1886: 8, plate 2, figs 2,2a. The name is not available from Lydekker, 1885a, being neither characterised nor illustrated therein.

Boselaphus lydekkeri Pilgrim, 1910: 70.

Selenoportax lydekkeri (Pilgrim) [in part], Pilgrim, 1937: 745, figures 55, 57-59.

Perimia falconeri Pilgrim, 1939: 165, figure 15a-d.

Holotype. NHML 37262, an immature skull, from Piram Island in the Gulf of Khambhat illustrated in Lydekker (1886) and Pilgrim (1939). It has been much rolled by water action. It is low and wide, its horn cores are at an early growth stage, and the cranial roof slopes slightly. Pilgrim's figure 15a (Pilgrim, 1939) shows the skull too slanted upwards anteriorly so that the slope of the cranial roof becomes exaggerated.

Diagnosis. Larger than *Selenoportax vexillarius* or *S.* aff. *vexillarius*, skull moderately wide and low, braincase not as short as in *S. vexillarius*. Horn cores with appreciable curvature in anterodorsal view, but shorter and less divergent than in *Selenoportax*. Cross section of the medial surface more rounded than the flatter lateral surface. The anterior keel descends to an insertion less medially positioned than in *S. vexillarius*, while the medial surface is more rounded than that of *Selenoportax*. Sinuses within frontals of restricted extent. Supraorbital pits large. Cranial roof may be slightly sloping. Shallow preorbital fossa present. Median indentation at back of palate probably extending backwards behind level of the lateral ones.

Table 9. Skull measurements on specimens of the *Selenoportax* and *Pachyportax* group. Measurements of the *Selenoportax vexillarius* holotype are means of measurments on the London cast and original in New York.

	A	B	C	D	E
Anteroposterior diameter at base of horn core	48.3	-	58.6	64.2	58.1
Mediolateral diameter at base of horn core	34.0	-	40.5	39.4	44.0
Minimum width across lateral sides of horn pedicels	c.130.0	-	-	-	c.126.0
Width across lateral edges of supraorbital pits	71.2	-	c.78.0	-	c.82.0
Length of skull top between horn bases and top of occipital	95.6	-	-	-	129.00
Braincase width	92.6	84.0	99.5	c.92.0	109.9
Occipital height at top of foramen magnum	-	42.6	45.9	c.54.0	66.7
Width across basioccipital anterior tuberosities	-	20.7	23.0	-	27.3
Width across basioccipital posterior tuberosities	-	c.37.0	40.3	44.9	44.0
Basioccipital length from front of anterior tuberosities to transverse crest of posterior tuberosities	-	22.1	47.0	-	50.1

Estimated age. 9.8 - 8.9 Ma.

Material.

Locality Y 160 (9.4 Ma)

Y 10061 Horn core pieces.

Locality Y 207 (9.4 Ma)

Y 5012 Right horn core, almost complete.

Locality Y 227 (9.4 Ma)

Y 6712 Skull parts with much of right horn core and base of the left horn core.

Locality Y 343 (9.0-8.7 Ma).

Y 12525 Left horn core base.

Discussion. In the GSP collection this species ranges from 9.8 to at least 8.9 Ma, a period largely coinciding with the latest Vallesian in Europe. The medial surfaces of the horn cores Y 6712 and Y 5012 (Figures 45-46E) have become quite rounded, that on Y 11851 less so. The largest of the four horn core pieces numbered Y 10061, for which the side is unknown, also shows that the longitudinally concave side has more of a cross-sectional bulge than the opposite, presumably lateral surface. The horn core Y 5012 (Figure 45D) is definitely long but its curvature is less in anterior view than in *S. vexillarius*, that is it is less recurved towards tips, and it has a slight backward curvature in side view. Y 3517 has a large and rather compressed horn core. Torsion is strong in the *P. falconeri* horn cores Y 4606c and Y 12310, but not in other specimens and is perhaps a condition existing at only around 9.0 Ma. The basal divergence of the horn cores on Y 6712 is still strong (Figure 45B). The absence of sinuses in the horn pedicels continues to be manifested in this species in Y 5012, Y 3517, Y 11851, Y 4606c and Y 12310. The identity of the much-rolled horn core Y 12303 as *P. falconeri* is suggested by its large size and the position of the supraorbital pit well lateral and anterior to the apparent line of the top/front of the pedicel. The basioccipital Y 12294 has more of a triangular than a rectangular shape, the anterior tuberosities are upstanding, close and localised, there is a valley between the posterior tuberosities, and no central longitudinal groove or ridge.

The large size of the species of *Pachyportax* makes it possible to identify isolated teeth and skeletal elements. There is additional skeletal and dental material of *P. falconeri* from the localities listed in the Appendices as well as from another 17 localities within its documented chronological range that are not listed.

Comments. It is unfortunate that the type specimen of *P. falconeri* is both immature and water-rolled. The skull has low and wide proportions, its horn cores are not very divergent and are inserted widely apart. The divergence might have been greater in an adult specimen, but decreased divergence in *P. falconeri* as a whole compared with *S. vexillarius* would be compatible with shorter horn cores. The anterior keel descends to an insertion less medially positioned than in *S. vexillarius*. The wide insertions are probably primitive in bovids and unchanged from *S. vexillarius*. The supraorbital pits are large, perhaps a juvenile character, and wide apart from one another, and there are very slight surface depressions where otherwise there might have been preorbital fossae. The braincase is not as short as in the holotype of *S. vexillarius* and the cranial roof is more sloping in profile. The median indent at the back of the palate probably extends behind the lateral ones. The occlusal lengths of the holotype's teeth would have been close to dP2-dP4 56.8, dP2 16.5, dP3 20.6, dP4 19.8, M1 22.2, M2 (erupting)

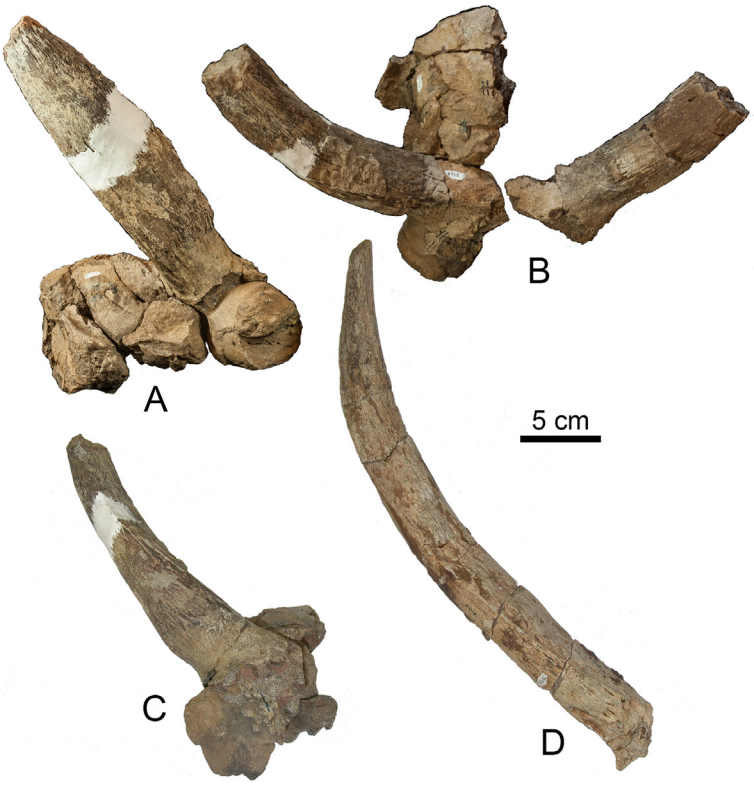

Figure 45. *Pachyportax falconeri*. Y 6712, skull with right horn core and detached base of left horncore in A) right lateral; B) dorsal; and C) anterior views. Y 5012 right horn core in D) anterior view. Scale 5cm.

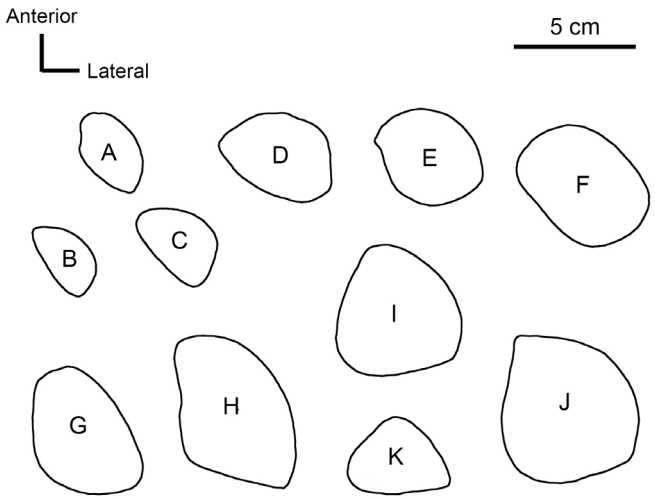

Figure 46. Horn core cross sections near the bases for some boselaphines and an early bovine. All are shown as of the left side with the anterior direction towards the top of the illustration and lateral side towards the right. Scale 5 cm. A) *Sivoreas eremita*, holotype, MNHL cast M43977, right horn core reversed. B) *Helicoportax praecox*, Y 25153. C) *Helicoportax tragelaphoides*, holotype, MNHL cast M43976, reversed. D) *Selenoportax vexillarius*, holotype, MNHL cast M15755. E) *Pachyportax falconeri*, Y 5012, reversed. F) *Pachyportax falconeri*, MNHL M2402a. G) *Pachyportax dhokpathanensis* , MNHL cast M26573. H) *Pachyportax giganteus*, after Akhtar (1995). I) *Parabos cordieri*, Institut de Paléontologie, Paris. J) *Proamphibos lachrymans*, holotype, MNHL cast M26576. K) *Boselaphus tragocamelus*, MNHL (Zoology) 1891.8.7.49, right horn core reversed.

24.0. The length of its deciduous premolar row suggests a species the size of a larger *Miotragocerus*, but bovid upper deciduous premolar rows are difficult to measure accurately and vary much according to the state of wear. Moreover, the two molars are compatible in size with the *Pachyportax* teeth in the time interval 9.8 - 8.9 Ma (Figure 47).

It is even more unfortunate that the nomenclature of this and the next species became tangled with that of the younger name *Selenoportax lydekkeri* (Pilgrim) 1910. Seven specimens with large teeth from the "Punjab" and not known to be associated with each other were described by Lydekker (1884) as *Boselaphus* sp. and named *B. lydekkeri* by Pilgrim (1910: 70). Subsequently Pilgrim (1937: 745) transferred his species into *Selenoportax* and chose as lectotype a left maxilla with dP2-M2, GSI B213 (Lydekker, 1884: plate 13 figure 1, our Figure 48). Pilgrim's measurements of the teeth he referred to *S. lydekkeri* (Pilgrim, 1937: 851-2) suggest that they were about 14% bigger in linear dimensions than those of *S. vexillarius*. The M1 and M2 on the *lydekkeri* lectotype, being recently erupted, have especially large lengths of 28 and 29 mm. Such measurements agree with those within the time span of *P. dhokpathanensis* in our collection. Pilgrim (1937: 746, 1939: 174) also extended *S. lydekkeri* to include teeth in the AMNH and two horn cores from Piram Island, GSI B790 and NHML M2402a. The latter horn core (Lydekker, 1886: plate 3 figure 5, at the time wrongly thought by Lydekker to be of the right side) has been rolled by wave action, is bigger than any GSP *Selenoportax* or *Pachyportax* horn cores, and has an index of 59.4×46.7 (79%). It has an anterior keel descending to an anteromedial insertion (Figure 48) and there are posterolateral and posteromedial rounded corners at the base (Pilgrim, 1939: plate 7 figure 11), (Figure 46F). The posterior keel is more evident distally and looks as if it would have descended to become the posterolateral rounded corner basally. We have chosen to regard *S. lydekkeri* as a junior synonym of *P. falconeri* and consequently can retain the name *dhokpathanensis* for the following species. The M1 and M2 lengths of the *lydekkeri* lectotype are the largest *P. falconeri* measurements on Figure 47.

Species *Pachyportax dhokpathanensis* Pilgrim, 1937

Pachyportax latidens dhokpathanensis Pilgrim, 1937: 768.

Pachyportax latidens dhokpathanensis Pilgrim, 1939: 198, figures 19a-d.

Selenoportax giganteus (Akhtar, 1995; Gentry *et al*., 2014: table 2).

?Pachyportax sp. Gentry *et al*., 2014: table 2.

Holotype. GSI B488 (cast NHML M26573), a cranium with basal part of left horn core, from Nila in the Dhok Pathan Formation. The worn right M2 and M3 of the holotype were recorded under the number GSI B489 (Pilgrim, 1937: 768, 1939: 199). Pilgrim (1937: figure 51) illustrated only an AMNH tooth he had attributed to his new subspecies, and the cranium was not described or illustrated until Pilgrim (1939: figure 19a-d, and plate VII figure 5).

Diagnosis. Larger than *Pachyportax falconeri*. Skull moderately wide and high. Level of maximum transverse width of cross-section of horn core lies centrally rather than posteriorly. Horn cores sometimes with flattening of the lateral surface, more inclined backwards than in holotype of *Selenoportax vexillarius*. Supraorbital pits small. Braincase moderately long and high, cranial roof almost horizontal behind horn cores and sloping posteriorly as it approaches top of occipital, rugose surface on cranial roof behind horn bases. Basioccipital with low thin longitudinal ridges or crests on long somewhat swollen anterior tuberosities, a short median longitudinal crest between anterior and posterior tuberosities. Median indentation at back of palate extending backwards behind level of the lateral ones.

Estimated age. **9.0 - 7.2 Ma.**

Material.

Locality Y 980 (8.9 Ma)

Y 52773 Right horn core base.

Locality Y 444 (8.6 Ma)

Y 15411 Palate and part of cranium. Very damaged base of right horn core. Left dP2-M2 with erupting M3, right dP4-M2.

Locality Y 17 (8.0 Ma)

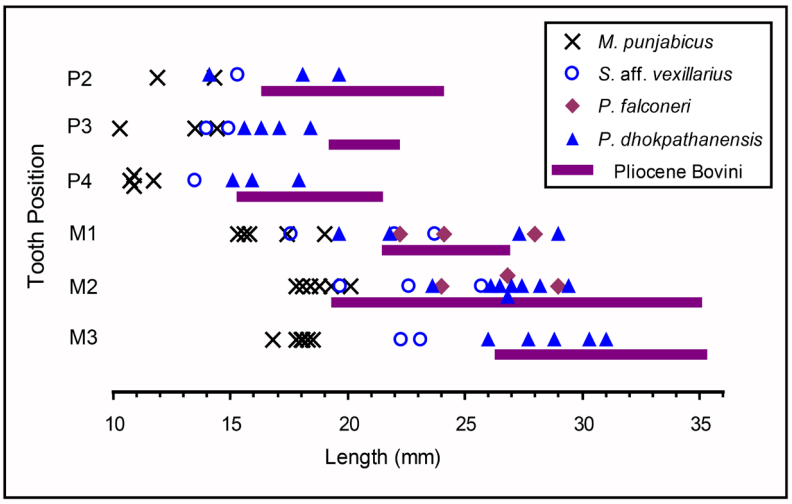

Figure 47. Occlusal lengths of upper cheek teeth in some Late Miocene Siwaliks Boselaphini. Horizontal lines denote ranges for combined measurements for the Early Pliocene Bovini *Proamphibos lachrymans*, *P. kashmiricus*, *Ugandax demissum*, and *Alephis lyrix* (Data from original measurements by AW Gentry; Pilgrim, 1939; Gentry, 1980; and Gromolard, 1980).

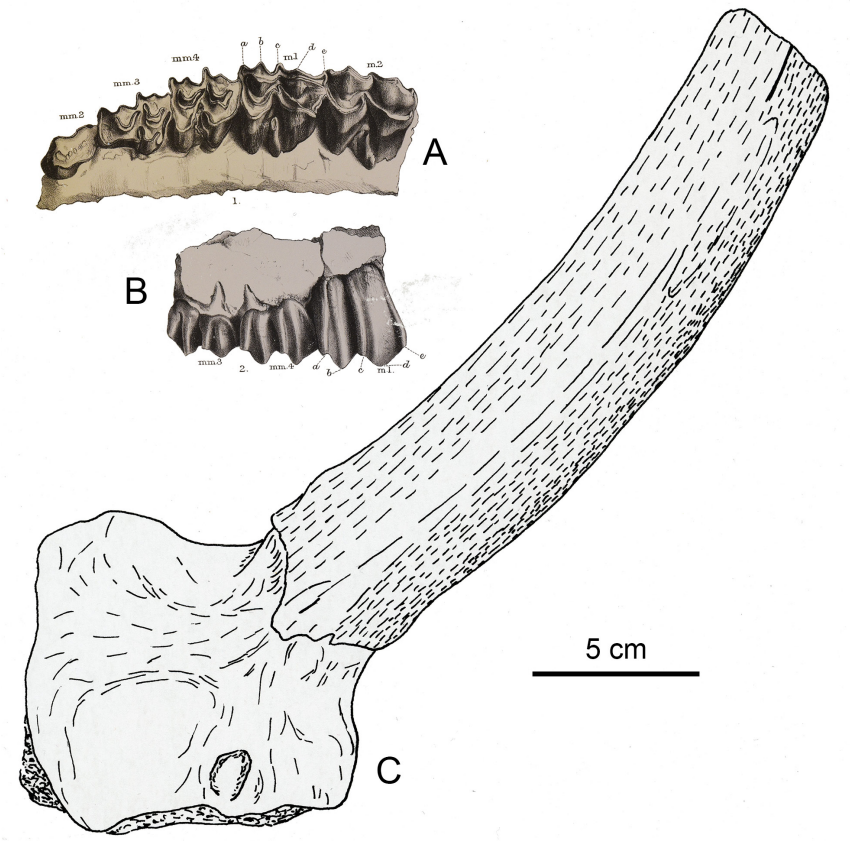

Figure 48. *Pachyportax falconeri*. A) GSI B213 lectotype left maxilla of *Selenoportax lydekkeri* with dP^2-M^2 and B) left maxilla with dM3-M1 from the same site. From Lydekker 1884, pl. 13 fig.1. Letters a, b, c, d, e indicate the costae. Measurements from Pilgrim 1939:850 - M2 length 29 mm and unworn height 45 mm. C) MNHL M 2402a, left horn core and part of frontal of *Pachyportax falconeri* from Piram Island, in anterodorsal view. Scale 5 cm.

Y 207 Paired mandibles with p2-m3.

Locality Y 399 (8.0 Ma)

Y 14914 Cranium with left pedicel base.

Y 14915 Left base and other horn core pieces.

Collecting Level KL 8 (7.8 Ma)

Y 15276 Base of (presumed) left horn core.

Locality Y 457 (7.4 Ma)

Y 13921 Right maxilla with P2-M3.

Locality Y 907 (7.4 Ma)

Y 49754 Base of (presumed) left horn core.

Locality Y 927 (7.4 Ma)

Y 50764 Base of (presumed) right horn core, left horn core and a distal piece.

Locality Y 386 (7.2 Ma)

Y 14258 Left m3.

Discussion. The GSP/Harvard collection comprises a great many teeth and skeletal elements and a few horn cores of this species. They range from between 9.0 to 7.2 Ma with a brief period of overlap with *P. falconeri*, perhaps on the order of 50,000 to 100,000 years. The damaged cranium and palate Y 15411 (Figure 49) is of a large-sized species with teeth considerably larger than in specimens of *Selenoportax* aff. *vexillarius*, such as the female skull Y 12150 at Locality Y 311 (10.1 Ma). This species could be seen as continuing from a state like that of the skull of *Pachyportax falconeri* (Y 6712) if the anterior keel of the latter's horn cores became more robust basally while the posterior keel remained unchanged. The horn cores Y 49754 (Figure 50) and Y 15276 look as if they are mostly larger and probably more compressed than in *P. falconeri* (Figure 51**)**, but there are only two others in the collection (Y 14915 and Y 52883) that are measurable**.** Of these two Y 14915 is small but insufficiently compressed to be a *Miotragocerus*. The back of the base of the very damaged right horn core on Y 15411 fails to show enough of a keel to match *Selenoportax*, but also has insufficient keel to be entirely satisfactory within *Pachyportax*. The partial cranium Y 14914 looks narrower and higher than the earlier *Selenoportax* aff. *vexillarius* specimen Y 46750. The immature partial cranium and palate Y 15411 (Figure 48) has an extensive preorbital fossa which is poorly delimited and not very deep (compare the fossa's condition in the *P. falconeri* holotype). The median palatal indent lies behind the level of the lateral ones.

Y 49754 is the best specimen of a putative *P. dhokpathanensis*. It is the base of a large and possibly long horn core (Figure 50A-C), which we believe to be of the left side and in which the anteroposterior position of the level of maximum mediolateral width of cross section lies well back, although the maximum width is more central in the other horn cores (Y 15276, Y 52883, and Y 50764). Y 49754 has a rounded edge instead of a sharp keel anteriorly, a sharp posterolateral keel (Figure 50A), and is slightly compressed. However, the horn core Y 50764 has a strong anterior keel. The supposed lateral surface of Y 49754 is flattened and does not curve round in its anterior part as it approaches its anterior limit. The medial surface is well rounded. The degree of divergence lessens as the horn core rises from its base. The horn core may have had a slight backwards curvature and it shows clockwise torsion. It is not possible to assess the presence or absence of sinuses within the pedicel, but Y 15276, Y 52883 and Y 50764 all have an anterior sinus at the top of their pedicels, while Y 14915 has no visible sinus in its pedicel. The flattening of its lateral surface, the rounded edge rather than a keel anteriorly, the sharp posterolateral keel and possibly slight backward curvature all make Y 49754 satisfactory as a *Pachyportax*, and the line of the medial pedicel wall suggests a continuing substantial basal

divergence.The horn core piece Y 52617 has a blunt keel on one side. In general signs of torsion may be more apparent in less lengthened horn cores.

Teeth of *Pachyportax dhokpathanensis*, like those of *Selenoportax*, are more hypsodont than those of the Siwalik *Miotragocerus*, as exemplified by both m2s and m3s (Table 7). In addition, although samples are small, *P. dhokpathanensis* also appears to be more hypsodont than *Selenoportax* aff. *vexillarius*. Samples are also too small to reliably assess relative lengths of individual teeth of the species of *Pachyportax*. It may be that P4 is not as small relative to neighbouring teeth as in *Miotragocerus* (Figure 47) and that m2 and m3 are relatively longer.

At about 8.6 Ma the teeth of *Pachyportax dhokpathanensis* become larger. This is shown in the teeth of the cranium and palate Y 15411 (8.6 Ma). The cranium is subadult and no bigger than the earlier *Selenoportax* aff. *vexillarius* Y 46750, but its teeth are definitely much larger and are large even among later *Pachyportax*.

In their morphology *Pachyportax* teeth show a decidedly bovine aspect interpreted by Bibi (2007a) as marking the actual first appearance of Bovini. The characters in the generic diagnosis are more pronounced than the boödont trends already described in *Miotragocerus* (Table 6). In the upper dentition of Y 13921 and the partial upper molar Y 16775 (Figure 49C, D), both from Locality Y 547 at 7.4 Ma), bovine characters of the teeth are enhanced by being labiolingually wider and with larger basal pillars although the specimens are in late and later middle wear respectively. The lower molars of Y 207 (Figure 50) at 8.0 Ma have basal pillars that while not bigger are more integrated with the body of the teeth, while the vertical lingual ribs are more localised. The molars on the mandible Y 16965 at 8.1 Ma are large and show slight pinching of the labial lobes similar to that of the lingual lobes of a few upper molars, for example the maxilla Y 17884 at 8.1 Ma.

Developments not seen in *Miotragocerus* are: lower molars of *Pachyportax dhokpathanensis* often with stronger lingual ribs (Appendix 3, character 40) and the central fossettes of the lower molars sometimes having a constriction across their centres (character 42). The boödonty in *Miotragocerus* or *Tragoportax* underlines the necessity of using both large size and boödonty as identity markers for early bovine teeth.

Some characters of *Miotragocerus* are less common in *Pachyportax*. For instance a transverse front wall of p3 and p4 may be less frequent (Appendix 3, character 47), and the lingual end of the p4 metaconid does not protrude more forwards (character 50). Other differences may come up occasionally such as the somewhat irregular outline of the walls of p3-p4 on the notably bovine-looking Y 207 or different relative sizes of paraconid and parastylid on p3-p4. It must be stressed that all these dental characters vary much among individuals and may also change according to state of wear.

The metacarpal Y 31407 is certainly too large to belong to a *Miotragocerus*. It is quite short and relatively robust with a large unciform facet, and the posterior surface has a shallow hollowing towards the top. Distally none of the tiny hollows above the condyles, front or back, are deep, and the condylar ridges are poorly defined. The articular surface of the proximal metatarsal Y 52888 is wider than it is anteroposteriorly long, a characteristic generally found in larger bovids such as Bovini.

There is additional skeletal and dental material of *P. dhokpathanensis* both from localities listed in the Appendices and from another 44 localities not included in the Appendices. This includes eighty-four specimens collected by G.E. Lewis and now in the Yale Peabody Museum collections. Some of the YPM material was identified by Bibi (2007a,b) as indet. Bovini.

Comments. It is likely that as early as 9.8 Ma *Pachyportax* had evolved from an ancestry close to *Selenoportax vexillarius* and had become more heavily built. Our small sample spanning

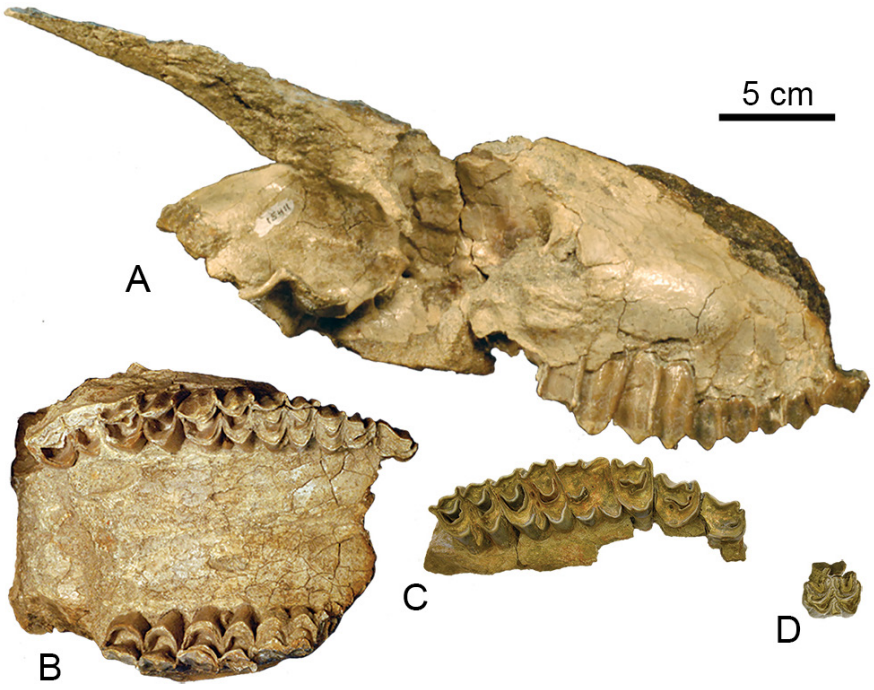

Figure 49. *Pachyportax dhokpathanensis*. Y 15411 cranium with very damaged horncore and dP2-M2 with erupting M3 in A) lateral and B) occlusal views. Y 13921 right maxilla with P2-M3 in C) occlusal view. Y 16775 broken right upper molar in D) occlusal view. Scale 5 cm.

more than two million years shows glimpses of changes whereby *Pachyportax* acquired increased size, a change in the horn cores from a flatter medial to a flatter lateral surface, a decreasing degree of basal divergence of the horn cores, and the occipital edge less smoothly rounded.

The relationship of *Pachyportax* to later Siwaliks Bovini has still to be elucidated. The Tatrot type skulls of the bovines *Proamphibos lachrymans* and *P. kashmiricus* (Pilgrim, 1939: 270, plates.5-7 and figure 32) date from ca. 3.5-2.6 Ma in the Pliocene (Patnak, 2013: figure 17.11). They have strongly crushing teeth (molars with a large occlusal area, a more complicated outline of the central fossettes, large basal pillars, strong labial ribs of upper molars, and outbowed lingual walls of lower molars). They also show strong rugosity of the cranial roof behind the horn core insertions, a character seen in the holotype *Pachyportax dhokpathanensis* and reminiscent of modern *Boselaphus* and Miocene *Miotragocerus* but not known in early bovines of Europe and Africa. Pilgrim (1939: 153, plate 8) related *Proamphibos* to later *Hemibos* and *Bubalus*. The position and relative strengths of the keels on the horn cores of *Pachyportax* resemble *Proamphibos* (Figure 46E-H, J) and raise the possibility that it could be an earlier part of the evolution of the *Bubalus* group.

The relationship of *Pachyportax* to bovines beyond the Siwaliks is even more uncertain. The boselaphine or bovine *Parabos cordieri* in the southern European lower Pliocene is about the same size as *Pachyportax dhokpathanensis* but has some character differences such as horn cores less compressed (Figure 46I) and more upright in side view, and cranial roof more inclined. It shows no dental advances towards the boödonty of Bovini (Gromolard and Guérin, 1980: plate 1 d-h) although the studies of Michaux *et al*. (1991) and Montoya *et al*. (2006) suggest the possibility of a smooth transition from *P. cordieri* to the southern European bovine *Alephis lyrix*. Teeth of *A. lyrix* and of the early Pliocene *Ugandax demissum* in Africa are about the same size or larger than those of *Pachyportax dhokpathanensis* and are at more or less the same level of morphological change or even lagging behind (Gentry, 1980: figure 10; Gromolard, 1980: plate 1 figures 2-3; Bibi, 2007a: figure 2). As would be expected, all these early forms fall short of modern bovine teeth in a lower degree of hypsodonty, less enlarged basal pillars, the central fossettes of upper molars still in the shape of a V rather than a wide U, and labial ribs and styles and lingual stylids less pronounced. An African bovine at Toros-Menalla, Chad (Vignaud *et al*., 2002) may be as early as 7.0 Ma, but its teeth have not been described. Placing a single boundary between Boselaphini and Bovini still looks like being a tricky operation and the Bovini could yet be polyphyletic.

A note on Pachyportax giganteus Akhtar, 1995

Pachyportax giganteus was founded on a cranium with a left horn core. The specimen is in the Pakistan Museum of Natural History, Islamabad, no. 87/323 (Akhtar, 1995: figure 1). It is said to be from near Dhok Pathan, Chakwal district, Pakistan. According to his measurements (Akhtar, 1995: table 1) it would be larger in linear dimensions than the *P. dhokpathanensis* holotype by about 12%. The horn core is short with strong anterior and posterolateral keels. The maximum mediolateral width is positioned centrally along the anteroposterior axis of the cross section mainly because of a well-defined medial keel (Akhtar, 1995: figure 1e) perhaps reminiscent of *Boselaphus*. There is of course a possibility that the medial keel is a neomorph and not linked with the old posteromedial keel of *Helicoportax* and *Selenoportax*. The horn core shows a limited degree of smooth curvature in anterior or posterior view as the degree of divergence diminishes from base to tip. The illustrations show a demarcation on the horn core. The frontals have a weak to

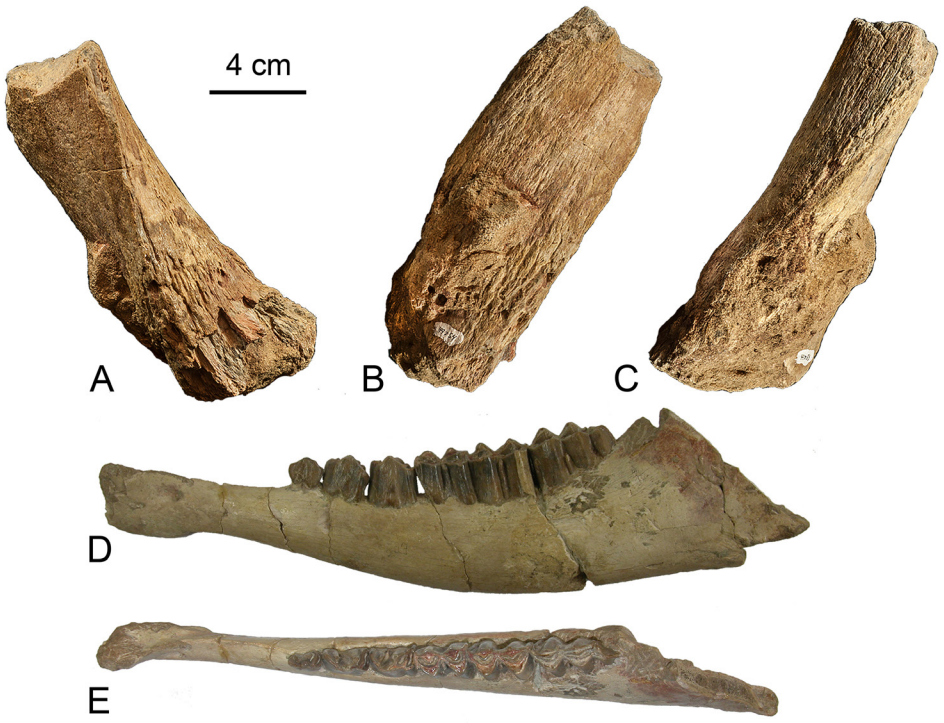

Figure 50. *Pachyportax dhokpathanensis*. Y 49754 left horn core in A) posterior; B) lateral; and C) anterior views. Y 207b left mandible with crowns of p3-m3 in D) labial and E) occlusal views. Scale 4 cm.

moderately rugose surface behind the horn bases and seeming to pass anterior to them, the posterior part of the cranial roof turns downwards as it approaches the occiput, and the occipital surface is without a rounded outline in posterior view.

Akhtar (1995) doesn't give details on where the specimen came from, other than the vague «Dhok Pathan,» by which he was probably refering to the area south of the Soan River near the Dhok Pathan Resthouse. The rocks there range in age from 8.6 to 7.8 Ma, which would place it within the temporal range of *Pachyportax dhokpathanensis*. Note also that some of the horn cores of *P. dhokpathanensis* are nearly as large as those of *P. giganteus*, especially in the transverse diameter (Y 15276, Y 49754, Appendix 4). Nishioka *et al*. (2019, 2020) referred specimens from Myanmar and Thailand to *P giganteus*. As noted previously the ages of the Thai and Myanmar fossils are not clearly known and could be from the latest Late Miocene or even the Pliocene (Nishioka *et al*., 2019).

Subfamily ?BOVINAE Gray 1821

RECTACORNIS genus nov.

Type and only included species. *Rectacornis mirabilis* species nov.

Diagnosis. A large species (ca. 150 to 250 kg?) with moderately long, straight horn cores, subdued anteromedial keel descending medial to large supraorbital pit, and stronger posterolateral keel that becomes more salient distally. Horn core with no torsion, very little or no compression, and flat medial and very rounded lateral surfaces. At the base maximum mediolateral width positioned anteriorly along the anteroposterior cross section. Horn cores inserted widely apart with only slight divergence (approximately 15°), no distal diminution in degree of divergence, inclined in side view, no backward curvature, and no sign of a demarcation. The long axis of the anteroposterior cross section is at a large angle to the midline of the skull. Very small frontal sinuses are posterolateral to the supraorbital pit and do not extend into the pedicel. The postcornual fossa is shallow, large, and narrow and there is no rugosity on the cranium behind the horn insertions. This species is similar in size to *Selenoportax* and species of *Pachyportax*. However, it differs from the slightly older *Selenoportax* in having straight and much less compressed horn cores which have flat medial and very rounded lateral surfaces, a subdued anteromedial keel, and a salient posterolateral keel. The angle of divergence is very low with neither torsion nor distal diminution in the angle of divergence so that there is no appreciable curvature in anterodorsal view. The species differs from contemporaneous *Pachyportax* in having straight and less compressed horn cores with flat medial and more rounded lateral surfaces, a subdued ridge-like anteromedial keel, a salient posterolateral keel, maximum mediolateral width of cross section positioned anteriorly, no torsion around the axis, and no distal diminution in the very low angle of divergence.

The generic name refers to the very straight horn core.

Rectacornis mirabilis species nov.

Holotype. GSP Y 15339, a broken frontlet with much of the left horn core, the base of the right horn core, and fragments of the skull (Figure 52). From Locality Y 439 (9.3 Ma) at 33° 10.20'N, 72° 26.43'E. Correlated to the Dinga Kas section between 19.0 and 9.0 meters above the base. (Behrensmeyer and Tauxe, 1982; Tauxe and Opdyke, 1982). Horn core index 40.8×38.3 (94%).

Diagnosis. As for the genus.

The trivial name is in reference to being remarkable because of the holotype size and age.

Estimated age. 9.6 - 9.0 Ma.

Material.

Locality Y 217 (9.6 Ma)

Y 15744 Left horn core base.

Locality Y 439 (9.3 Ma)

Y 15339 Broken frontlet with much of left and base of right horn core and fragments of the skull. Holotype.

Locality Y 193 (9.0 Ma)

Y 16008 Left horn core base.

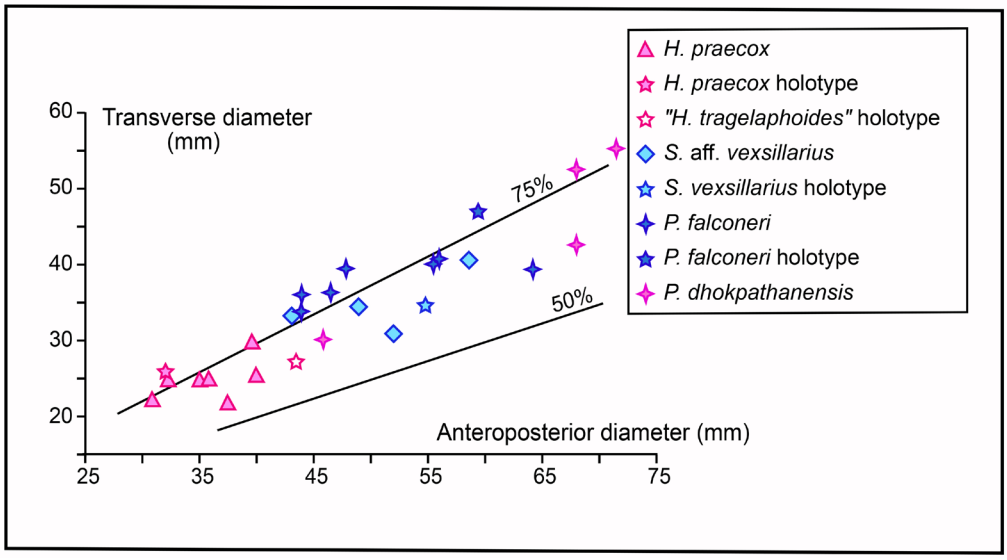

Figure 51. Basal diameters of horn cores of *Helicoportax*, *Selenoportax*, and *Pachyportax*. Measurements are given in Appendix 4. The upper diagonal line is that along which the transverse diameter is 75% of the anteroposterior diameter and the lower line is 50%. Horn cores with more transverse compression lie towards the right and towards the base of the diagram.

Discussion. This mysterious Late Miocene (9.6 to 9.0 Ma) species has long straight horn cores. There is a sharp medially-inserted "anterior" keel and a posterolateral keel. The horn cores are little compressed, and between the keels the posteromedial surface is no more than slightly convex and the anterolateral surface shows a considerable bulge. Divergence (approximately 15-20°) and backward inclination are both moderate and constant and the insertions quite wide apart. The horn cores are remarkably straight with very slight torsion (apparent only for the distal posterolateral keel), but no spiralling nor backward curvature. The horn cores are inserted above the back of the orbits. Sinuses are visible low down where the front of the pedicels merges with the frontals. The frontals between the horn bases are not higher than the dorsal orbital rims, and these dorsal orbital rims are probably only narrow.

The dentition is not known, but an upper fourth premolar and a damaged upper molar (Y 6051a,b) from the same locality as the horn core Y 15744 could belong to this species. Both are similar to boselaphines, with weak styles and a weak labial rib on the molar.

Comments. Apart from the remarkably straight horn cores, distinctive features of this species are the very slight torsion and the relatively rectangular cross section of the base of the horn cores, which becomes more triangular distally (Figure 52D, E). In addition, the subdued anteromedial keels on these horn cores are nearer to being narrow ridges on the body of the horn core than markers of the intersections between surfaces in different planes. In this they remind one of Tragelaphini, a resemblance which is contradicted by the absence of torsion or spiralling. The insertion above the back of the orbits looks more posterior than in the boselaphines described in this paper.

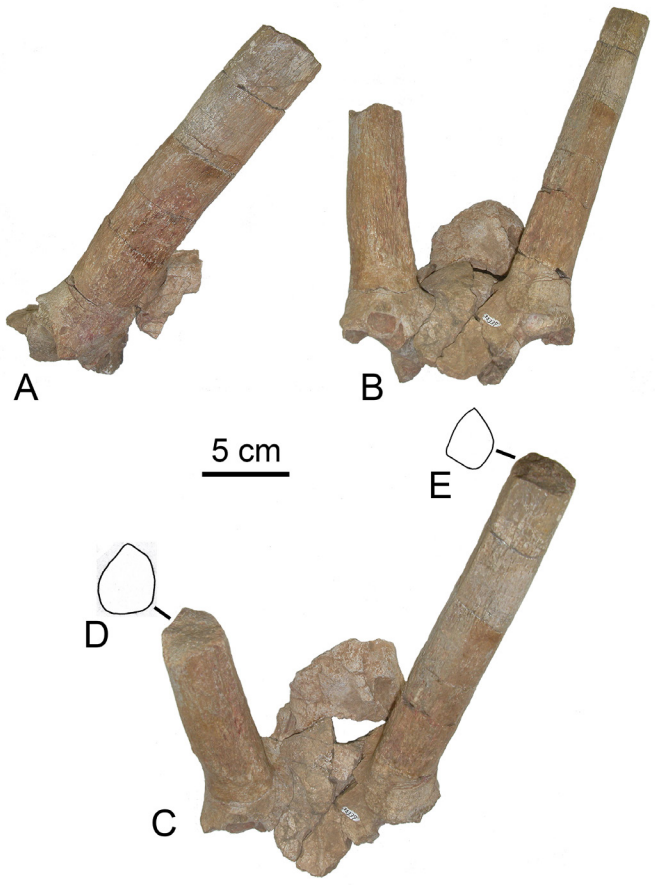

Figure 52. *Rectacornis mirabilis* new genus and species**.** Y 15339. Broken frontlet in A) lateral, B) frontal, and C) dorsal views. D) cross section of right horn core at 105 mm above base. and E) cross section of left horn core at 190 mm above base. Scale 5 cm.

CONCLUSIONS

We recognize twenty-three bovine and four hypsodontine species (or probable species) from the Oligocene and Miocene deposits of Pakistan. Nineteen of these have previously been named, while another five have cranial material suitable for defining a new species. Two species, referred to as ?Hypsodontinae sp. and Bovidae sp. 1, are distinctive, but because the available material is not adequate for defining a new species, we refrain from naming them at this time. A third potentially new species, *Selenoportax* aff. *vexillarius*, has also been left unnamed at this time because we are not certain it is distinctive from *Selenoportax vexillarius*. Of the ninteen previously named species, the Harvard-GSP collection contains specimens of all but three or possibly four: *Ruticeros pugio, Pachyportax latidens, Pachyportax giganteus,* and *Selenoportax vexillarius* if it is distinct from what we refer to as *Selenoportax* aff. *vexillarius*.

Boselaphini predominate in the GSP collections, both in terms of number of species (15 or 16) and number of specimens (~75%). Most of the boselaphine genera are endemic to the Siwaliks and Southeast Asia (*Elachistoceras, Strepsiportax, Sivaceros, Helicoportax, Selenoportax, Tragoportax, Ruticeros,* and most likely *Sivoreas*), as are also the hypsodontine *Palaeohypsodontus* and the possible bovin *Pachyportax*. Our new species *Rectacornis mirabilis* and Pilgrim's *Ruticeros pugio* are also known only from the Siwaliks. The predominance of boselaphines plus the number of endemic taxa gives the Siwalik bovid fauna a characteristic aspect and collectively comprise the best-known Miocene record of the subfamily.

The distal width of the astragalus provides a measure of size from which equivalent body masses can be calculated using regressions based on extant species (Morgan, 1994) (Appendix 6). Weights based on regressions of femoral and metapodial dimensions (Kappelman, 1986; Scott, 2004) are compatible with these data.

Figure 53 shows the astragalus distal width plotted against time for 419 bovines, plus two hypsodontines and twenty-seven antelopines. As can be seen from the figure, throughout the Miocene the size of the largest species steadily becomes larger, although very small species persist. Eventually by the Late Miocene this produces a range of sizes similar to extant bovids, with the smallest individuals weighting just over 5 or 6 kgs and the largest more than 250 kgs; a range in size from species the size of neotragines to species the size of a greater kudu.

There is a noticeably abrupt increase between 11.4 and 10.5 Ma (Figure 53 and Appendix 6). At that time (except for *Hypsodontus pronaticornis* which on the basis of teeth we estimate had a body mass near 160 kg) individuals over 55 kg appear for the first time. This body mass increase occurs at the same time as a major turnover of species, with the increase being due to the appearance of both *Selenoportax* aff. *vexillarus* and *Miotragocerus pilgrimi*. After this abrupt increase, the general trend toward ever larger sizes accelerates with the appearances

of species of *Pachyportax*. The apparent loss of large bovids and a more restricted size range after 7 Ma are the result of a sparse fossil record.

A weaker, but also abrupt increase is apparent between 15.2 and 14.1 Ma when five species in five different genera appear, an increase apparently accompanied by an expansion of the range of sizes. However, the sudden appearance of so many additional species is most likely partly an artifact of preservation as the sediments older than 14.1 Ma are poorly fossiliferous. The complete turnover of species and expansion in size between 11.2 and 10.5 Ma is not an artifact, although how rapidly and exactly when it took place are uncertain (Figure 53).

The overall trend of size increase over at least ten million years (Figure 53) is in accord with "Cope's Rule, " the general observation that body size tends to increase in linages over time (Stanley, 1973). The question is why did this happen? And the answer in the case of the bovids must be related to environmental and vegetative changes and shifting diet and predation (Badgely *et al*., 2008; Bibi, 2007a,b; Cerling *et al*., 2025; Gentry *et al*., 2025). The same data, however, show size increases among Siwalik giraffoids, tragulids, and, although the data is more sparse, among suids and anthracotheres. So the bovid story is only part of a larger phenomenon, the specifics of which should be of future research interest.

It is reasonable to think of the first bovids as animals like the boselaphine *Eotragus* in Europe or *Namacerus* in Africa. Wherever horn cores or sometimes teeth of *Eotragus* have been found, they have generally been referred to new species. This is probably correct, given the wide distribution and the age span of the records, but scope for horn core variation is limited, so convincing differences between the species are unlikely to be demonstrable.

The earliest named and well dated *Eotragus* in the Siwaliks is *E. noyei* at around 17.9 Ma, although specimens of *Eotragus* from Dera Bugti may be between 22 and 20 Ma (Antoine *et al*., 2013). There is a second small boselaphine (*Carinameryx lindsayi*) present in the Vihowa Formation of Zinda Pir (ca. 18.1 Ma) that documents the existence of two divergent boselaphine lineages by 18 Ma. A third yet larger species (Bovidae sp. 1) appears by 16.0 Ma.

This situation is complicated by the Hypsodontinae, a group probably anciently present in China. They were already present in our area of southern Asia before the end of the Oligocene and perhaps as far as Saudi Arabia in the Early Miocene. They acquired horn cores at about the time *Eotragus* appeared. In the Middle Miocene a single horned species looking like *Hypsodontus sokolovi* may precede a more diverse array of species in different regions. The very limited Siwaliks occurrences are compatible with this view. Many teeth of Middle Miocene Hypsodontinae are found to be in later wear and with misshapen occlusal surfaces suggesting a difficult feeding regime. Hypsodontines disappeared before the end of the Middle Miocene. The suggestion that they may have been an Old World branch from the same stem as Antilocapridae is attractive (Janis and Manning, 1998) and needs further investigation, but see Kostopoulos (2014) on the possibility of an *Oioceros* and Antilopinae relationship.

Little is known about the phylogenetics of any of the Siwalik bovines. Among the boselaphines there are several earlier and later species pairs that could be ancestor and descendent species, but we have not undertaken a phylogenetic analysis. It is very likely that Boselaphini arose from an *Eotragus*-like ancestor and as noted by 18 Ma species of *Eotragus* are joined by *Carinameryx lindsayi.* With compressed, keeled horn cores this latter species appears to belong to a linage similar to the species of the Middle Miocene. Subsequently, the Siwaliks have what is probably the best Middle through Late Miocene record of diverse and abundant boselaphines. Between 17 and 14.1 Ma the record is sparse, containing mostly dental and skeletal remains with only two horn cores, that while too incomplete to identify are not like either older or younger horn cores.

The fauna from 14.1 Ma until about 12.5 Ma contained two newly recognized species in the separate genera *Strepsiportax* and *Sivaceros* with low and wide and high and narrow skull proportions respectively. *Sivaceros* also showed a rugose surface behind the horn bases, and the early presence of a demarcation. There was also a species of *Sivoreas* which probably evolved to

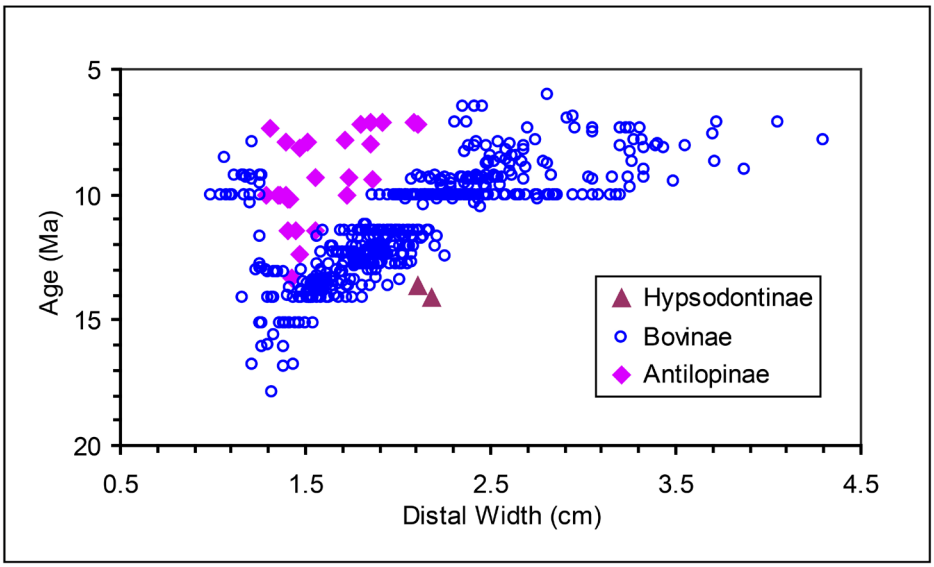

Figure 53. Measurements of the distal width (cm) of the astragalus (Appendix 6) plotted against geologic age. Data include 2 hypsodontines, 519 bovines, and 27 antilopines.

attain a larger size than the other two boselaphines and which had strong torsion of the horn cores and short premolar rows. Its horn cores may have remained small relative to overall skull size. The short premolar row, if it continues to be corroborated by later finds, must have an ecological significance and opens the possibility that Boselaphini of the Middle Miocene may have been more diversified than would be possible when other bovid groups had evolved further.

After 12.5 Ma and for the rest of the Middle Miocene both *Strepsiportax gluten* and *Sivaceros gradiens* were more advanced than their predecessors and likely ancestors. *Sivoreas eremita* disappeared by about 12.0 Ma and was overlapped and outlasted for a short spell by *Helicoportax praecox*. If *Helicoportax* were closely related to or congeneric with *Sivoreas*, it must have been an independent lineage starting as early as *Strepsiportax* and *Sivaceros*. Its more remote ancestry might have been close to *Strepsiportax,* but uncertainty about dates and the identifications of horn core bases make all this conjectural.

The earliest boselaphines outside the Siwaliks are in East Africa (Fort Ternan, 13.8 Ma) and Russia (Belometchetskaja, MN5 or 6?, perhaps as old as 16.4 Ma). In both locations they overlapped with the Hypsodontinae, as did *Strepsiportax*, *Sivaceros* and *Sivoreas* in the Siwaliks. *Kipsigicerus labidotus* at Fort Ternan is coeval with *Strepsiportax meyeri,* but morphologically closer to the younger *S. gluten* from which it differs by more advanced horn cores, by shorter premolar rows, and by molar teeth which were rather high crowned for a boselaphine. Less is known of the Belometchetskaja *Paratragocerus* but it might be closer to *Sivaceros* and *Miotragocerus*. *Sivoreas* may also have lived in East Africa, but, if it did, it may not have appeared until about 12.0 Ma. Two boselaphines appeared in Europe late in the Middle Miocene; one was *Austroportax* with resemblances to *Strepsiportax* and perhaps *Helicoportax*, and a second was *Miotragocerus*, probably related to *Sivaceros*.

After about 10.2 Ma the common fossil boselaphine in the Siwaliks alongside hipparionine horses becomes *Miotragocerus pilgrimi*, first analysed by Thomas (1984a). It is larger than the Middle Miocene *Sivaceros* and probably descended from an unknown small species of *Miotragocerus* soon after the genus had split from *Sivaceros*. It shows good differences from Vallesian species further west in Eurasia such as *Miotragocerus pannoniae* and *M. leskewitschi*, but looks closer to *M. rugosifrons*, a Turolian species of which the Pikermi *M. amalthea* is probably a derived variant.

In the Siwaliks *Miotragocerus pilgrimi* was succeeded by *M. punjabicus* at around 8.8 Ma. The change appears to have been gradual. An additional Siwaliks species, *Tragoportax salmontanus*, is also present in this period. By 8.0 Ma either the *Miotragocerus* or *Tragoportax* had developed some boödont-like features in their teeth similar to those of early bovines and later reduncine and hippotragine antelopes. *Miotragocerus rugosifrons* is the closest species in the west to *M. pilgrimi* or *M. punjabicus* but lacks any suggestion of boödonty in its teeth. Around the end of the Miocene *Tragoportax* and *Miotragocerus* became extinct or at least are not recorded in the fossil record.

Also present in the Late Miocene of the Siwaliks is the larger *Selenoportax*, seemingly replacing *Helicoportax* and probably related to it, and soon replaced by the related *Pachyportax* which began to acquire bovine-like teeth. If we see *Pachyportax* as a stem bovine, it could be linked with the Tatrot *Proamphibos* with decidedly boödont teeth and then to later *Hemibos* and *Bubalus*. More study is needed to assess tribal level classification among these bovids, and the extent of parallel evolution.

The position of *Boselaphus* itself within Boselaphini needs study. Besides the extant *B. tragocamelus* the genus also includes the cranium NHML 36851 of the slightly less advanced Pleistocene *B. namadicus* (Rütimeyer, 1878: plate 6 figures 7-8). The living nilgai is a large boselaphine characterised by short little-divergent horn cores laid-back and inserted behind the orbits. The teeth are about the size of those of early *Pachyportax* but with longer molar rows relative to premolar rows. Some characters are bovine-like such as well-marked styles and some emphasis on the ribs of upper molars, lingual lobes less narrowly pointed, and central fossettes in more the shape of a wide U. Pilgrim (1939: plate 8) placed *Boselaphus* closer to bovine origins than to *Miotragocerus* and subsequent authors have not offered contrary opinions. Yet there are similarities to *Miotragocerus*. The short horn cores narrow abruptly in the antero-posterior plane immediately above the base, and narrow lines or ridges continue forwards from the base of the anterior keel on to the frontal bone, all of which prompts the thought that the entire horn core could be just a distal end above the surviving top of a demarcation. The cranial surface behind the horn cores is also rugose as in *Miotragocerus*. Admittedly demarcations can occur in Group (A) boselaphines and a rugose surface is present in the *Pachyportax dhokpathanensis* holotype and in *Proamphibos*. Also this rugosity in *Boselaphus* passes forwards of the horn insertions (Solounias, 1990: 432, figures 12-14), presumably because the absence of raised frontals between the horn bases allows it to do so. Even so, the possibility remains that *Boselaphus* is close to or descended from *Miotragocerus* and that this group of Boselaphini may not be extinct.

Duboisia santeng has been little noticed since Hooijer's paper of 1958. It lived on Java and nearby parts of Malaysia in the Pleistocene, is smaller than *Boselaphus*, and specialised by having prominent precornual ridges bordering rugose raised areas which just fail to meet anteriorly (Stremme, 1911: plate 19 figure 4) and which must have been surmounted by some kind of keratinous structure. It is apparent from this feature, from Solounias's discussion of the precornual area in *Boselaphus*, from the four horns of *Tetracerus*, and from the condition of *Punjabameryx inflata* new species, that Boselaphini are prone to develop a diverse range of structures in this area of the skull supplementing or modifying the main horn cores. Nishioka and Vidthayanon (2018) have discussed a skull from Thailand that they refer to as *Duboisia* aff. *santeng,* which may be latest Miocene. Geraads (1979) described four teeth also from Java under the name *Duboisia(?) sartonoi.*

ACKNOWLEDGMENTS

Our research is a result of a long collaboration with the Geological Survey of Pakistan, and we are grateful to the various Directors General and members of the Survey who have over the years supported our project, as well as to the local people of Pakistan who for many years have been so kind to strangers camped in the midst of their homes.

We also thank our many Siwalik Project colleagues who have greatly enlivened our time in the field and lab, to say nothing of their direct contributions to our understanding of Siwalik geology, stratigraphy, and the other fauna. AWG thanks Nikos

Solounias and David Pilbeam for inviting him to participate in this study; the Department of Human Evolutionary Biology, Harvard University, for the provision of facilities, encouragement, advice, and much hospitality.

Financial support has come through a number of grants from the National Science Foundation, Smithsonian Foreign Currency Program, the Wenner-Gren Foundation for Anthropological Research, and the American School for Prehistoric Research. We also gratefully acknowledge the abiding support of Ms F. Berkowitz of the Smithsonian Office of International Relations and Ms Ernelle Ross of the Smithsonian Travel Office. Without the efforts of such people projects like ours cannot prosper.

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