

Miocene Bovidae (Mammalia) of the Siwaliks, Part 2: Antilopinae

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Abstract: The fluvial sediments of the Siwaliks in northern Pakistan contain a Miocene through Pliocene geologic and paleontological record. The sediments, which are thousands of meters thick, have abundant vertebrate and invertebrate fossils from multiple horizons. Renewed collecting in northern Pakistan in collaboration with the Geological Survey of Pakistan has now added over 10,000 bovid fossils to a new collection in Islamabad. The fossils include many isolated horn cores and occasional skulls, as well as teeth and postcranials. Here we discuss material belonging to the Antilopinae, recognizing fifteen species belonging to at least three tribes. Five of the fifteen have previously been named, while an additional two have cranial material suitable for defining a new species. The remaining eight taxa are known from cranial material that allows us to distinguish them from other Siwalik bovids, but in most instances they are of doubtful generic identity and we think may belong to previously recognized taxa from other geographic regions. One (*Protragelaphus* sp.) probably belongs to an unnamed species, but because the available material is inadequate for defining a new species, we do not name it at this time. In the fossil collection the Antilopini predominate among the Antilopinae, both in terms of number of species and number of specimens.

Keywords: Bovidae, Miocene; Siwaliks; horn cores

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INTRODUCTION

The Siwalik formations of northern India and Pakistan are a thick sequence of Neogene fluvial sediments having abundant remains of fossil mammals, with diverse assemblages of extinct species and especially of bovids. With fossil vertebrates first attracting scientific notice by 1832, there are now substantial collections worldwide in many museums. The Geological Survey of India in Calcutta and the American Museum of Natural History in New York notably hold the types for most of the named species, but other important collections include those of the Natural History Museum of London, Punjab University in Chandigarh, the Wadia Institute of Himalayan Geology in Dehra Dun, the Yale Peabody Museum in New Haven, the Bavarian State Collection of Palaeontology and Geology in Munich, and the Geological Institute, State University of Utrecht.

Beginning in 1973 a collaborative project between Harvard University and the Geological Survey of Pakistan (GSP) (Badgley *et al.*, 2025a), as well as with the University of Arizona and the Pakistan Museum of Natural History, has produced a new collection of Siwalik fossils which now includes more than 10,000 bovid fossils. In a companion paper (Gentry *et al.*, 2026) we discussed species of the Hypsodontinae and Bovinae. Here we discuss the Siwalik Antilopinae, recognizing 15 species belonging to three tribes. Two of the fifteen are new, both belonging to new genera. The repository of these new collections is the Vertebrate Palaeontology Collection & Research Center, Geological Survey of Pakistan in Islamabad.

Study of Siwalik bovids has been plagued by inadequate

types as well as the lack of information on the localities they came from and their ages. This makes it difficult to characterize and then compare several of the Siwalik species.

Chronological Framework

The sources and ages of earlier collections are often in question, but for the most part the newly collected material is from well dated stratigraphic sections and can be placed within a reliable chronostratigraphic framework which makes the fossils especially valuable. The chronological framework is based on paleomagnetic correlations of more than 65 stratigraphic sections. Sections included are from the Kamliyal, Chinji, Nagri, and Dhok Pathan Formations on the Potwar Plateau, as well as from the Chitarwata, Vihowa, and Litra Formations of the Sulaiman Ranges and Bugti Hills, and from the Gaj and Manchar Formations of the Lower Indus Basin. Details of the methods and documentation of this work, including procedures for determining the ages of fossil sites, have recently been reviewed in Behrensmeyer and Barry (2025) and Barry and Behrensmeyer (2025). See especially table 3.1 in Barry and Behrensmeyer (2025) for details on the sections, including published references. All age estimates are based on the Gradstein *et al.* (2012) Geomagnetic Polarity Time Scale.

A small number of localities found by Barnum Brown in 1922 (Colbert, 1935a,b; Pilgrim, 1937) are well enough documented as to location and stratigraphic horizon that their fossils can be included in this study. Unfortunately other Brown localities, as well as the extensive collections made by the Geological Survey of India and its predecessors cannot be included, because the geographic and stratigraphic data are inadequate.

Thus the holotypes and other materials described by Lydekker and Pilgrim in the late 19th and early 20th centuries cannot be incorporated in our chronological framework with any precision. Occasionally, however, it is possible to constrain the ages of Brown's localities more narrowly. One such complex of localities is noted in Table 1, together with comments on the likely age. Table 2 shows the approximate ages of the Potwar and Sulaiman terrestrial formations.

All of this work, whether collecting fossils or rock samples, measuring and describing section, running laboratory analyses, or supporting our activities in camp and field was done by a very large number of colleagues, both Pakistani and of other nationalities. A list of project participants in "Preamble to Framing Chapters" (Badgley *et al.*, 2025b) has 166 names - and is missing at least two.

We occasionally refer to the land mammal biochronological units Vallesian, and Turolian (successive Late Miocene units),

and to the numbered European Neogene mammal units. The MN units were meant to be a temporal succession of mammal faunas, with each unit having a reference faunal locality (Mein, 1999). Later studies have 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. Woodburne *et al.* (2013) present a "Chinese Standard" for the Neogene of Northern Asia.

Important localities and formations outside the Siwaliks are listed in Table 3. Dates are 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).

Table 1. Age estimates for two AMNH and PMNH localities.

The American Museum of Natural History archives contain an unpublished notebook by Barnum Brown containing a list of localities and stratigraphic notes, as well as a partial list of notable specimens found at the localities. Many fossil specimens have small paper slips with numbers and descriptions corresponding to those in the notebook. These slips are primary documents tying the specimens to the notebook list of localities and to the topographic maps recording the localities and geological information. This unpublished information allows us to insert critical bovid specimens into our chronostratigraphic framework. We prefix Brown's locality number with a "B" in order to distinguish it from other institution's localities and collections.		
Locality	Age (Ma)	Remarks
AMNH Localities B 25-37	8.3	Brown's field notebook indicates he collected isolated specimens and blocks from a single quarry one half mile (0.8 km) southwest of Dhok Pathan. Included in the fossils are the holotype and a paratype of <i>Gazella lydekkeri</i> (AMNH 19663 and 19664). Brown's quarry lies between two marker units, the Hilltop Sand and the Grey Tracer sand (Barry <i>et al.</i> 2002, fig. 4). The quarry can be placed on a paleomagnetic section determined by Noye Johnson (Barry <i>et al.</i> 2002), which shows it to be just below the transition between Chron 4r.1n and 4r.2r. It is 8.3 Ma on the Gradstein <i>et al.</i> (2012) timescale.
PMNH Locality Z 162	Late Miocene	The Litra Formation is a thick unit overlying the Vihowa Formation in the Zindapir Dome area west of Dera Ghazi Khan in southwestern Punjab. While the sediments are not highly fossiliferous and no paleomagnetic sections have been made, the presence of hipparionine equids (Raza <i>et al.</i> 2002) indicates a Late Miocene age for this locality.

Table 2. 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. ¹See Hussain *et al.* (1992) for discussion of this unit and the problem of Upper Siwalik formation nomenclature. ²In the Southern Potwar, the Kamliar and Murree Formations are not differentiated. ³The age estimate for the top of the Vihowa follows Raza *et al.* (2002). ⁴The 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
Kamliar/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

Bovidae are pecorans with horns having a keratin sheath surrounding an unbranched bony core (Bibi *et al.*, 2009). The family Bovidae has been understood as a hierarchy of subfamilies and tribes (Bibi, 2013, 2014), but molecular research on extant bovids indicates greater complexity. Adding fossil groups to the analysis of Hassanin *et al.* (2012) produces a more comprehensive, but partly conjectural arrangement of the subfamilies and tribes (Table 4).

Apart from the number of species present at different times, the importance of the Siwalik antilopines largely lies in the age and geographic origins of the tribes Antilopini, Reduncini, and Caprini, which are also present in Africa and northern and western Eurasia. The oldest Siwalik bovids are Early Miocene and include horncores and dental and postcranial fossils. Horn cores, which are necessary for recognizing species, become common only in the lowermost Chinji Formation at around 14.1 Ma, at which time our new collections show that of seven species present only one is an antilopine. An unambiguous member of the Antilopini only appears at about 13 Ma, with Reduncini and Caprini appearing much later. All the Miocene Siwalik bovids are listed in Table 5 together with estimates of their chronostratigraphic ranges in the Siwaliks. The ages given for species in that table and the text are based on the more secure identifications of the material, with horn cores given preference. Dates in parentheses have less precise estimates

and are given as possible minimum and maximum ages. The antilopine material discussed in this paper comes from 143 localities ranging between 14.1 and 6.3 Ma, with approximately 112 different stratigraphic levels.

METHODS AND MATERIALS

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

Institutional acronyms include the following: AMNH: American Museum of Natural History, New York, New York; GSI: Geological Survey of India; GSP: Geological Survey of Pakistan; MNB: Museum für Naturkunde Berlin; and NHML: Natural History Museum, London. Specimens prefixed with Y or Z are deposited in the collections of the Geological Survey of Pakistan or the Pakistan Museum of Natural History, both in Islamabad. The Brown collection is in the American Museum of Natural History. In the following we frequently refer to the collections made by the Harvard-GSP project simply as the “GSP collections.”

Abbreviations and conventions: Hypsodonty index (hyp) = height of unworn or very slightly worn m2s or m3s divided

Table 3. Important localities and formations outside the Siwaliks.

Locality	Country	Stage / MN Unit	Age (Ma)	Reference and Comments
Adu-Asa Formation	Ethiopia	Late Miocene	6.5-5.6	
Bahe Formation	China	Late Miocene	~10.8 - 7.3	Zhang <i>et al.</i> (2013)
Baode Formation	China	Late Miocene	7.2 - 5.5	Kaakinen <i>et al.</i> (2013)
Beglia Formation	Tunisia	?Middle - Late Miocene	?14 - 11	
Çandır	Turkey	Middle Miocene MN5-6	16.4 - 13.4	
Fort Ternan	Kenya	Middle Miocene	13.8 - 13.7	
Kohfidisch	Austria	Late Miocene MN10 or 11	~10.0 - ~8.0	
Langebaanweg (Varswater Formation)	South Africa	Early Pliocene	5.2-5.1	Baard's Quarry contains fossils of varying age younger than the Varswater Formation.
Lothagam (Nawata Formation to Kaiyumung Member of the Nachukui Formation)	Kenya	Late Miocene - Middle Pliocene	7.4 - ~ 4.2	
Lukeino	Kenya	Late Miocene	6.1	
Manonga	Tanzania	Latest Miocene – Early Pliocene	~ 5.3	
Maragheh	Iran	Late Miocene	8.9 - 7.4	Kostopoulos and Bernor (2011)
Mpesida	Kenya	Late Miocene	6.8	
Namurungule Formation	Kenya	Late Miocene	~ 8.5	
Ngorora Formation	Kenya	Middle - Late Miocene	13.1 - 10.5	Deino <i>et al.</i> (1990). Equids are from younger exposures at Ngeringerowa (Hill <i>et al.</i> 1985)
Paşalar	Turkey	Middle Miocene MN6	14 - 12.85	
Pikermi	Greece	Late Miocene MN12	7.4 - 7.1	Bohme <i>et al.</i> (2017)
Sahabi (Upper)	Libya	Late Miocene	6.5 - ~ 5.5	
Samos	Greece	Late Miocene MN11- 13	8.0 - 6.7	Koufos <i>et al.</i> (2009)

Table 4. A possible classification of Bovidae. Extinct taxa marked with obelisks and Siwalik Miocene taxa of known affinity in bold type.

Subfamily Bovinae	
Boselaphini	nilgai and four-horned antelope
Tragelaphini	kudu, bushbuck group. African
Bovini	cattle, buffalo
Subfamily Antilopinae	
<i>Neotragus</i>	former “Neotragini” is polyphyletic. Small, African
<i>Aepyceros</i>	impala, African
Antilopini	blackbuck, saiga antelope, gazelles
†Oiocerina	Late Miocene, includes † <i>Urmiatherium</i>
† <i>Criotherium</i>	Late Miocene, plus † <i>Palaeoreas</i>
Reduncini	waterbuck and reedbuck group plus <i>Pelea</i>
Cephalophini	duikers, African
† <i>Tethytragus</i>	Middle Miocene, not a boselaphine
Hippotragini	roan, sable antelope, oryx, addax
Alcelaphini	hartebeest and wildebeest group
<i>Pantholops</i>	chiru, Tibet. Linked with Caprini, below
Caprini	the former mainly Eurasian subfamily Caprinae
Ovibovina	muskox, serow, goral
Caprina	takin, chamois, sheep, goats

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.

In the Systematic Paleontology section only a limited number of notable specimens are listed under “Material,” while Appendices 1 through 4 contain all studied and referred specimens and include measurements. Within each taxon, the listings are ordered by age and locality. Appendix 1 has the cranial material, Appendix 2 dental, Appendix 3 astragali, and Appendix 4 other postcranial elements. (Skulls with teeth are listed in both Appendices 1 and 2.) For a new taxon the listings in the appendices form the hypodigm.

SYSTEMATIC PALEONTOLOGY

Family BOVIDAE Gray, 1821

Subfamily ANTILOPINA Gray, 1821

In most classifications the Antilopinae contain all bovids other than Bovinae and are the larger, more species rich subfamily. Early non-boselaphine bovids in the Siwaliks before the advent of *Gazella* at 13.2 Ma may best be left as tribally unclassified Antilopinae. Thereafter some tribal assignments become possible, but teeth do not evolve far enough for boödont or aegodont status to be attributed.

CHINJIKEROS new genus.

Type and only species. *Chinjikeros kanatti* nov.

Diagnosis. As for the species.

Chinjikeros kanatti new species

Holotype. GSP Y 25028 Left horn core, preserved for nearly its whole length (Figure 1). From Locality Y 478 (14.1 Ma) at 32° 41.26'N, 72° 14.31'E. Correlated to the Kanatti (Upper) section between 301.5 and 312.9 meters below the base of the upper Kanatti section of Kappelman *et al.* (1991).

Diagnosis. A small species (ca. 15-20 kg). Horn cores small, short to moderately long, maximum transverse diameter lying across the middle level of the anteroposterior diameter, no keels, little compressed, with some strong longitudinal ridges on the posterolateral corner or in the middle of the lateral side, slightly or perhaps more strongly divergent in anterior view with a barely perceptible lessening of degree of divergence at the tips, insertions moderately inclined, straight in side view or having a very slightly concave profile along the front edge, insertions wide apart and above the orbits but still leaving wide horizontal dorsal orbital rims, frontals not raised between horn core bases, sometimes a shallow postcornual fossa, front edge of pedicel at an angle to the front edge of the horn core in profile, no sinuses in pedicels, a large supraorbital foramen or a

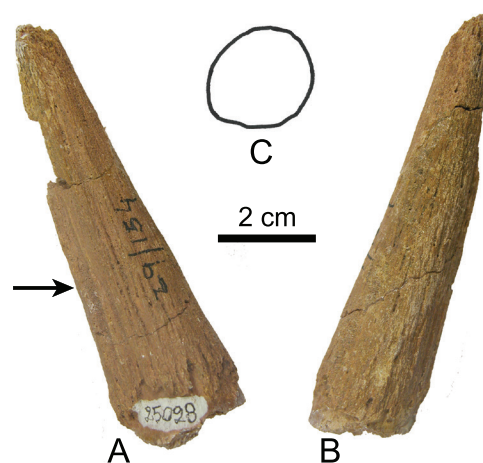


Figure 1. *Chinjikeros kanatti*. Y 25028 holotype left horn core in A) medial and B) frontal views. C) cross section with the anterior towards the right. Arrow indicates the level of the cross section on the horn core. Scale 20 mm.

Table 5. List of bovid species, with estimated ages of first and last appearances in the Siwaliks. Bracketed species = lineages. Dates in parentheses are imprecise estimates and are given as a range between the minimum and maximum dates.

?Family Bovidae	
Subfamily Hypsodontinae	
<i>Palaeohypsodontus zinensis</i> Métais et al., 2003	?28.3 - 18.2 Ma
?Hypsodontinae sp.	15.2 Ma
<i>Kubanostragus sokolovi</i> Gabunia, 1973	14.1- 12.1 Ma
<i>Hypsodontus pronaticornis</i> Köhler, 1987	13.7 - 12.8 Ma
Family Bovidae	
Subfamily indet.	
?Bovidae sp. 1	16.0 - 15.1 Ma
Subfamily Bovinae	
Tribe Boselaphini	
<i>Eotragus noyei</i> Solounias et al., 1995	17.9 - 16.8 Ma
<i>Carinameryx lindsayi</i> Gentry et al., 2026	(18.3 - 17.9 Ma)
<i>Elachistoceras khauristanensis</i> Thomas, 1977	14.1 - 8.5 Ma
[<i>Strepsipterax meyeri</i> Gentry et al., 2026	14.1 - 12.4 Ma
[<i>Strepsipterax gluten</i> Pilgrim, 1937	12.4 - (11.2 - 10.8) Ma
[<i>Sivaceros antecedens</i> Gentry et al., 2026	14.1 - 13.4 Ma
[<i>Sivaceros gradiens</i> Pilgrim, 1937	13.0 - (11.3 - 11.0) Ma
?(<i>Sivaceros</i>) <i>vedicus</i> Pilgrim, 1939	9.8 Ma
<i>Sivoreas eremita</i> Pilgrim, 1939	14.1 - 12.1 Ma
<i>Helicoportax praecox</i> Pilgrim, 1937	13.4 - (11.2 - 10.8) Ma
[<i>Selenoportax vexillarius</i> Pilgrim, 1937	(11.2 - 10.8) Ma
[<i>Selenoportax</i> aff. <i>vexillarius</i>	10.2 - 9.8 Ma
[<i>Miotragocerus pilgrimi</i> (Kretzoi, 1941)	?10.5 - 8.8 Ma
[<i>Miotragocerus punjabicus</i> (Pilgrim, 1910)	8.7 - 6.4 Ma
<i>Tragoportax salmontanus</i> Pilgrim, 1937	8.4 - 7.2 Ma
<i>Punjabameryx inflata</i> Gentry et al., 2026	?9.4 - 7.3 Ma
<i>Ruticeros pugio</i> Pilgrim, 1939	?
Tribe ?Bovini	
[<i>Pachyportax falconeri</i> (Lydekker, 1886)	9.8 - 8.9 Ma
[<i>Pachyportax dhokpathanensis</i> Pilgrim, 1937	9.0 - 7.2 Ma
[<i>Pachyportax giganteus</i> (Akhtar, 1995)	?
Subfamily ?Bovinae	
<i>Rectacornis mirabilis</i> Gentry et al., 2026	9.6 - 9.0 Ma
Subfamily Antilopinae	
Tribe undifferentiated	
<i>Chinjikeros kanatti</i> new genus and species	14.1 - 11.7? Ma
Tribe Antilopini	
[? <i>Gazella</i> sp.	13.2 - 11.7 Ma
[<i>Gazella lydekkeri</i> Pilgrim, 1937	10.2 - 6.3? Ma
<i>Prostrepsiceros vinayaki</i> (Pilgrim, 1939)	8.4 - 7.9 Ma
? <i>Prostrepsiceros</i> , large sp.	8.2 - 7.9 Ma
<i>Nisidorcas planicornis</i> (Pilgrim, 1939)	9.0 Ma
? <i>Protragelaphus</i> sp.	10.8 Ma
<i>Spiraliscornis inopinata</i> new genus and species	8.8 Ma
Tribe Reduncini	
[<i>Kobus</i> sp.1	9.4 - 8.2 Ma
[<i>Kobus porrecticornis</i> (Lydekker, 1878)	8.1 - 7.7 Ma
[<i>Kobus</i> sp.2	7.4 - (7.2 - 6.6) Ma
Tribe Antilopini or Caprini	
<i>Tethytragus</i> sp.	13.4? - 12.4 Ma
? <i>Caprotragoides</i> , sp. indet.	10.2 - 8.6 Ma
? <i>Dorcadoryx</i> sp.	9.7 - 9.4 Ma
Tribe Caprini	
<i>Protoryx</i> aff. <i>solignaci</i> (Robinson, 1972)	11.3 Ma

small supraorbital pit, but not forming a *Gazella*-like triangular depression.

Chinjikeros kanatti horn cores differ from those of *Homiodorcas tugenium* by being longer, less compressed, and lacking a posterior keel. They differ from *Gazella* in being shorter, straighter, and less compressed. The large triangular depression around the supraorbital foramina of *Gazella* is absent in *C. kanatti*.

The species is named for a small Punjab village known for its fertile orchards and lush surroundings. A very pleasant place to visit with several remarkable fossil sites nearby.

Estimated age. 14.1 - 11.7? Ma

Material.

Locality Y 478 (14.1 Ma)

Y 25018 Left horn core.

Y 25028 Left horn core. Holotype.

Y 25208 Left horn core base, part of frontal and of right pedicel.

Locality Y 878 (14.1 Ma)

Y 47045 Right horn core base with part of frontal.

Locality Y 507 (11.7 Ma)

Y 25134 Left mandible with m1 and m3.

Y 42307 Right mandible with damaged p4 and m1, m2-m3.

Discussion. Both horn cores and dental remains are known from 14.1 to 13.0 Ma, but we have also referred four mandibles to *Chinjikeros kanatti* that are younger (12.8 to 11.7 Ma), although they possibly belong to the species we refer to as *?Gazella* sp.

Chinjikeros kanatti is best represented at Locality Y 478. The absence of backward curvature of the horn cores (Figure 1, Figure 2 A), absence of a gazelle-like triangular depression or pit around the supraorbital foramen as seen in Y 25018 and Y 47045 (Figure 2B and E), the wide insertions of the horn cores in relation to rather a narrow braincase, as in Y 25208 (Figure 2F), and unraised frontals between the horn bases are

all primitive characters. The likely shortness, straighter course, and lack of compression of Y 26783 (Figure 2 G) preclude it being assigned to *Gazella* despite it being the youngest horn core listed for this species and falling within the temporal range of *?Gazella* sp

The horn cores of *Chinjikeros kanatti* differ from *Hypsodontus sokolovi*, also present at Locality Y 478, in shorter length, straightness, stronger longitudinal grooving, less smoothly rounded cross section, less upright in side view, and more divergent in anterior view. If a large and shallow postcornual fossa is characteristic of *H. sokolovi*, this would make another difference. If torsion is present in *C. kanatti* (Y 25020) it would be in the same homonymous direction as in *H. sokolovi*. Additional horn cores of doubtful identity from Locality Y478 are Y 25041, Y 25170, Y 28084, and Y 46296, but these are not part of the *Chinjikeros kanatti* hypodigm.

The tooth remains listed (Figure 3) in Appendix 2 span 13.1-11.7 Ma but only the poorly preserved upper molars from Locality Y 725 (13.0 Ma) are associated with horn cores of *Chinjikeros kanatti*. The other teeth are concentrated around 13.0 Ma, but four of them are 12.8 Ma or younger. It should be noted that the youngest horn cores of *C. kanatti* are 13.0 Ma, while three horn cores attributed below to a similarly-sized possible species of *Gazella* occur at 13.2, and 11.7 Ma. If teeth of both species were present in the collection it is very likely that we are unable to tell them apart. No dental characters have been given in the diagnosis.

The molars are low-crowned and show somewhat late joining of crests on the occlusal surface. Upper molars have small styles, a flat labial wall of the metacone, and a small posterior part of M3. Lower molars show tiny basal pillars on m3 (less reduced on m1), slight to moderate development of an anterolabial cingulum not reaching the stage of becoming a goat fold, and slight outbowings of ribs on their lingual walls. The basal pillar on the m3 of Y 42307 is tall despite its tiny diameter and that on m2 is more robust. The m1 and m3 of Y 25134 are larger than earlier teeth of this species (Appendix 2). Neither m3 of Y 26377 nor Y 25134 have central fossettes on their hypoconulid lobes, but Y 26433 did. No expansion is seen at the lingual end of the p4 metaconid. The fairly flat labial wall of the metacone on upper molars may be unique but the other characters are frequently seen in early bovids. The two specimens (Y 42307 and Y 25134) from Locality Y 207 (11.7 Ma) are associated with a horn core we attribute below to *?Gazella* sp. and while possibly belonging to *?Gazella* sp. the two specimens do not have gazelle-like attributes.

Separation of the teeth of small antilopines from very small boselaphines is difficult. We have listed specimens (Appendix 2) for *Chinjikeros kanatti* from a long time range which are intermediate in size between teeth assigned to *Elachistoceras khauristanensis* Thomas 1977 and those of *Gazella lydekkeri* Pilgrim 1937 (Figure 4). Teeth of *C. kanatti* differ from those of *E. khauristanensis* in that: 1) the rear central fossettes of upper molars lack a spur from the lingual wall and their lingual lobes do not turn forwards in later wear, 2) The p4 parastylid and paraconid are not differentiated, 3) the metasyllids on lower molars are absent or very small, and 4) the m3 hypoconulid has the lingual wall generally offset labially and not enclosing a central fossette.

The metacarpal Y 1466 from Locality Y 70 (13.8 Ma) is about the size to go with *C. kanatti*, but is not associated with horn cores. It has distal condylar ridges which reach high on the posterior surface. It is too long to belong to the same species as

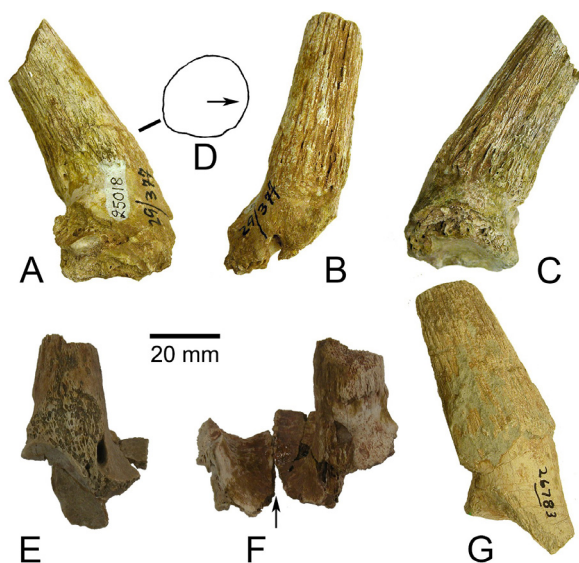


Figure 2. *Chinjikeros kanatti*. Y 25018 left horn core in A) medial, B) anterior, and C) lateral views. D) cross section with arrow indicating anterior. Y 47045 right horn core in E) anterior view. Y25208 frontlet with left horn core in F) medial view with arrow marking the midline. Y 26783 right horn core in G) lateral view. Scale 20 mm.

the incomplete metatarsal Y 45979 assigned to *Elachistoceras kauristanensis* and dated at 9.4 Ma. Its length $\times$ minimum shaft width of $125 \times \sim 10$ mm may be compared with values of 89.5×8.5 mm for the late Early Miocene Namibian bovid *Namacerus garipeensis* (Morales *et al.*, 2003, plate 3 figure 5), 159×13.0 mm for a Pikermi *Gazella capricornis* NHML M11469, and a mean of 125×8.7 mm for 8 examples of the extant steinbok, *Raphicerus campestris*. According to these figures the *Chinjikeros* metacarpal would be longer and less thick than in the very early bovid *Namacerus*, about as long but thicker than in living *Raphicerus*, and not long enough to fit a Late Miocene *Gazella*.

Remarks. This species is not a boselaphine. Although about the same size, it differs from contemporary Middle Miocene boselaphines, which have mediolaterally compressed horn cores, usually with demarcations and anterior and sometimes posterior keels. Middle Miocene boselaphines also usually show signs of anteriorwards growth or modification of horn core bases or their pedicels (Solounias, 1990). These are all features absent in *Chinjikeros kanatti*.

Species of *Eotragus* and *Namacerus* are usually grouped with boselaphines and seen as possibly ancestral (Solounias *et al.*, 1995) - a view not accepted by all (Gentry 2010, Van der Made 2012). *Eotragus* and *Namacerus* differ from *Chinjikeros kanatti* most notably in size, but also in having short and more spike-like horn cores with an incipient anterior keel that may form a continuous, although subdued, keel in some species. *C. kanatti* has deep longitudinal grooves on the posteriomedial face of the horn core, which are not present in either *Eotragus* or *Namacerus*.

The only early member of the Antilopinae in Africa well enough known to have been named is *Homoiodorcas tugenium* Thomas 1981. It is from the Ngorora Formation in Kenya, with other possible occurrences of *Homoiodorcas* under various names from Libya, Saudi Arabia, Israel, and Thailand (Thomas 1983, Tchernov *et al.*, 1987, Mein and Ginsburg 1997, Gentry

2010). *Chinjikeros kanatti* horn cores differ from *H. tugenium* in being slightly larger and probably longer, cross section less narrowed posteriorly, no posterior keel, without a rather sudden distal diminution in anteroposterior diameter (Thomas, 1981), no twisting of the axis at the base whereby the lateral surface is turned to face partly anteriorly and partly upwards (a condition seen in several extant Neotragini and some fossil species), not having a somewhat flattened medial surface, not curved backwards, no gazelle-like triangular supraorbital pit, and a shallow rather than a variable postcornual fossa. In the past *Homoiodorcas* has been taken as a neotragine, but we believe now that it is better not to differentiate tribes within Antilopinae before the appearance in the record of *Gazella* as a definite member of the Antilopini. *Chinjikeros kanatti* is of similar geological age to the supposed *Gazella* sp. at Fort Ternan (Gentry 1970, plate 15, plate 16 figures 1-3). It could be seen as a possible ancestor or relative of *Gazella* or *Kobus*.

Tribe ANTILOPINI Gray, 1821

Living Antilopini comprise on the one hand the gazelles and several other mainly African genera and on the other the heteronymously spiral-horned type genus, *Antilope* Pallas, 1766, now including only *Antilope cervicapra* (Linnaeus 1758), the blackbuck of India. Molecular and genetic studies endorse the relationship between *A. cervicapra* and non-spiral horned Antilopini (Hernández Fernández and Vrba, 2005; Hassanin *et al.*, 2012; Bärmann *et al.*, 2013). *Gazella* and several extinct spiral-horned antilopines, the latter bearing many names, are found in the Miocene of the Siwaliks. Spiral-horned antelopes with homonymously curved horn cores have been placed in the separate subtribe Oiocerina Pilgrim by Kostopoulos (2014).

Genus GAZELLA Blainville, 1816

Type species. *Gazella dorcas* (Linnaeus, 1758).

Diagnosis. Small to moderate sized bovids. Moderate to long

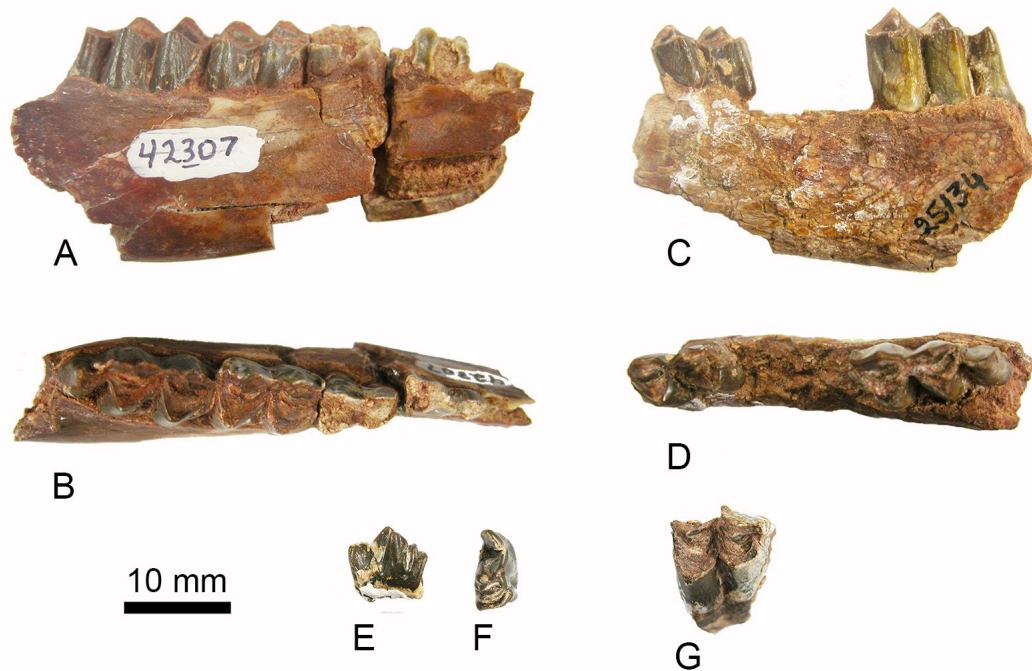


Figure 3. *Chinjikeros kanatti* Y 42307 right mandible with p4-m3 in A) labial and B) occlusal views, Y 25134 left mandible with m1 and m3 in C) labial and D) occlusal views, Y 31422 right p4 in E) labial and F) occlusal views, Y 31967 left M3 in G) occlusal view. Scale 10 mm.

horn cores, the level of maximum mediolateral width lying at or just behind the anteroposterior midpoint, without keels or torsion, subcircular or elliptical cross section, lateral surface often flatter than the medial, little or moderate divergence, inserted above the back of the orbits, moderately upright insertions, backwardly curved, moderately wide insertions, moderate to strong postcornual fossa, limited incidence of sinuses within the frontals, frontals between the horn bases not rising above the level of the dorsal orbital rims, large triangular supraorbital pits around the supraorbital foramina, braincase neither shortened nor its roof greatly angled downwards on the axis of the face, occipital surface with each half facing partly laterally as well as backwards, moderate to large auditory bullae, median indentation at the back of the palate lies anterior to the level of the paired lateral indentations. Teeth with a restrained level of hypsodonty, basal pillars non-existent on upper molars and confined to m1 if present at all on lower molars, moderate styles and stylids, and limited development of ribs. Sometimes incipient transverse goat folds appear on the front of lower molars. The m3s probably lengthen in relation to m1s or m2s and in living species often have an enlarged third lobe. The p4s do not develop closed antero-lingual walls between the paraconid and metaconid. Most extant species with horned females.

Remarks. The 14 or so living species of *Gazella* are now often split into many more species and the sub-Saharan African ones placed in two additional generic names, *Nanger* and *Eudorcas* (Groves and Grubb 2011). Gazelles graze and browse in semiarid and arid open regions and are cursorially adapted. The skulls, horn cores, and dentitions, however, are not very distinctive, and identifying Miocene fossils as definitely *Gazella* or not *Gazella* is difficult.

Many names have been proposed for extinct gazelles. The first-discovered fossils were the Late Miocene *Gazella capricornis* (Wagner 1848) of Pikermi, *G. deperdita* (Gervais 1850 [in Gervais 1848-52]) in France, revised by Heintz (1971), and *G. pilgrimi* Bohlin (1935) of Samos. *Gazella mytilinii* Pilgrim 1926 and *G. longicornis* Andree 1926 are older names for Samos gazelles than *G. pilgrimi*, and Kostopoulos (2009a)

believed *G. mytilinii* to be valid as an additional species. The first-studied gazelles in China were *G. gaudryi* and *G. dorcadooides*, both of Schlosser (1903) and based on isolated teeth of unknown provenance. In early studies of what came to be known as the Baodean fauna or land mammal age, Bohlin (1935, 1941) extended these names to cover cranial material. Kurtén (1952) used the names for two Baodean ecological assemblages: the more southeasterly *gaudryi* or forest faunas and the more northwesterly *dorcadooides* or steppe faunas. Later on Zhang *et al.* (2002) announced an earlier fauna from the Bahe Formation containing a new gazelle said to be like *G. lydekkeri*, the Siwaliks gazelle. It would have lived during the first half (~10.0-8.0 Ma) of the time span of *G. lydekkeri*.

The name *Antilope deperdita* first appeared in Gervais and de Serres (1847), Sur les Mammifères fossiles des sables marins tertiaires de Montpellier. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences* Paris 24, pp. 799-801. Their description is insufficient to make the name available. The use of a footnote and of the future tense in the final sentence implies that the formal naming was to be postponed until a later date. The wording of the description is equally inadequate in 1850 (*in* Gervais, 1848-52) but the illustration does make the name available.

The following Siwalik species of doubtful generic identity comes from the Middle Miocene.

?*Gazella* sp.

Estimated age. 13.2 - 11.7 Ma

Material.

Locality Y 850 (13.2 Ma)

Y 41593a Right horn core base, also a longer piece (Y 41593b) of a left damaged horn core.

Locality Y 498 (11.7 Ma)

Y 25149 Left horn core base.

Locality Y 507 (11.7 Ma)

Y 25154 Right horn core base.

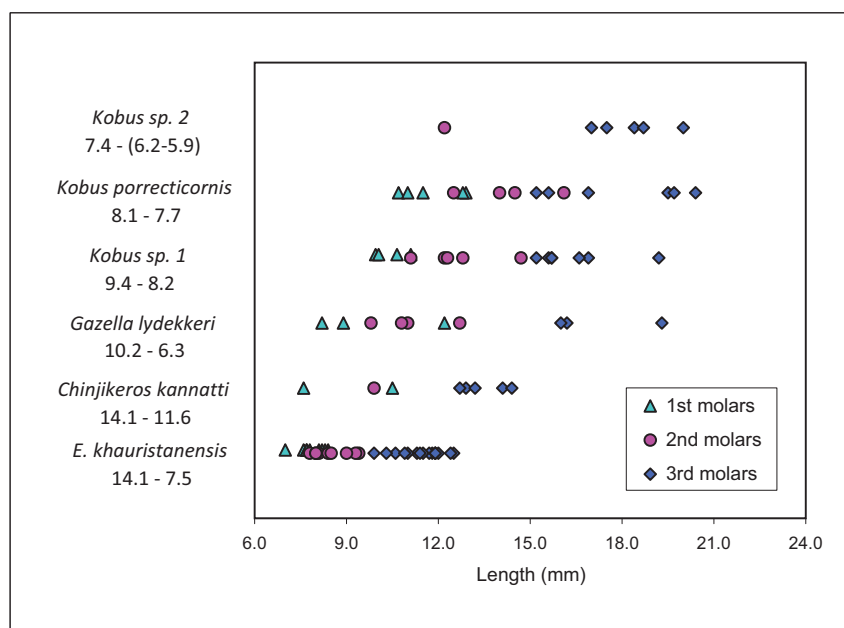


Figure 4. Scatter plots of lengths of m1, m2, and m3 of *Elachistoceras khauristanensis* and five Middle and Late Miocene Siwalik antilopines.

Discussion. The main difference of the little-compressed horn cores Y 41593 and Y 25154 from those of *Chinjikeros kanatti* lies in their being very slightly curved backwards along the posterior edge and more strongly so along the anterior edge (Figure 5). They also show a less irregular cross section and some flattening of a more definitely developed lateral surface (Figure 5A). The incipient backward curvature of Y 25154 (Figure 5C) at 11.7 Ma precludes an identification of it as the latest *C. kanatti*. It would be very interesting to know if these horn cores had lost the primitive wide insertions which seem to be present in *C. kanatti*. The more compressed Y 25149 is very

like a gazelle with a flatter lateral surface than the medial surface and a moderate backwards inclination. However, what may be the supraorbital pit is small for a *Gazella*. It may be related to the narrow condition seen in *G. lydekkeri* or it could be related somehow to the earlier and larger Siwaliks *Tethyragus* sp. A poorly preserved partial base of a right horn core (Y 26673) with part of the orbit from Locality Y 726 (13.1 Ma) may also be a ?*Gazella* sp. Figure 6 shows the basal diameters of horn cores of *Chinjikeros*, *Gazella* sp., and *G. lydekkeri*. There is considerable variation amongst the three, but in comparison to the Middle Miocene species, horn cores of the Late Miocene *G. lydekkeri* are both larger and more compressed.

Thomas (1984) identified a horn core (Y 1491) and two lower molars (Y 1707 and Y 2295) as *Gazella* sp. The specimens range in age from 13.5 to 13.3 Ma, but we have not seen the material. Several horn cores in the Brown collection could also be this species, including AMNH 29865, AMNH 29976, and AMNH 29980 which were identified by both Thomas (1984) and Pilgrim (1937) as *Gazella* sp. However, at 14.0, 13.8, and 14.1 Ma respectively, these specimens all lie outside the chronostratigraphic range established by the GSP specimens for *Gazella* sp. and instead might be *Chinjikeros kanatti*. A fourth specimen, a pair of horn cores (GSI K 16/343) discussed and figured by Thomas (1984, Plate 4, figure 4a,b), is very likely the same species as the GSP material listed here. The distances and directions from nearby villages given by Thomas (1984), if correct, would place it in the upper Chinji Formation with an age somewhere around 12.3 Ma.

We have not identified any teeth as this species, but it is quite likely that some of those listed under *Chinjikeros kanatti* could belong to it. Khan *et al.* (2013, 2021) referred a collection of upper and lower bovid dentitions and a fragment of a horn core from the Chinji Formation to *Gazella* sp., but we have not seen the material. Some specimens might belong to *Chinjikeros kanatti* sp. nov.

Much more remains to be learned about the relationship in the Siwaliks between this species and *Chinjikeros kanatti*, and the three genera *Gazella*, *Kobus* and *Tethyragus*. *Gazella* is common from the Late Miocene onwards in Europe and China.

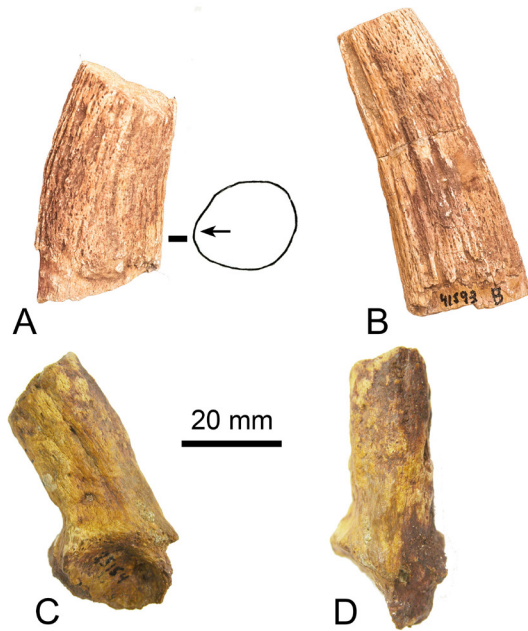


Figure 5. ?*Gazella* sp. Y 41593a base of a right horn core in A) medial view with cross section with the anterior towards the left and a longer piece of the left horn core Y 41593b in B) lateral view. Y 25154 in C) lateral and D) frontal views. Scale 20 mm.

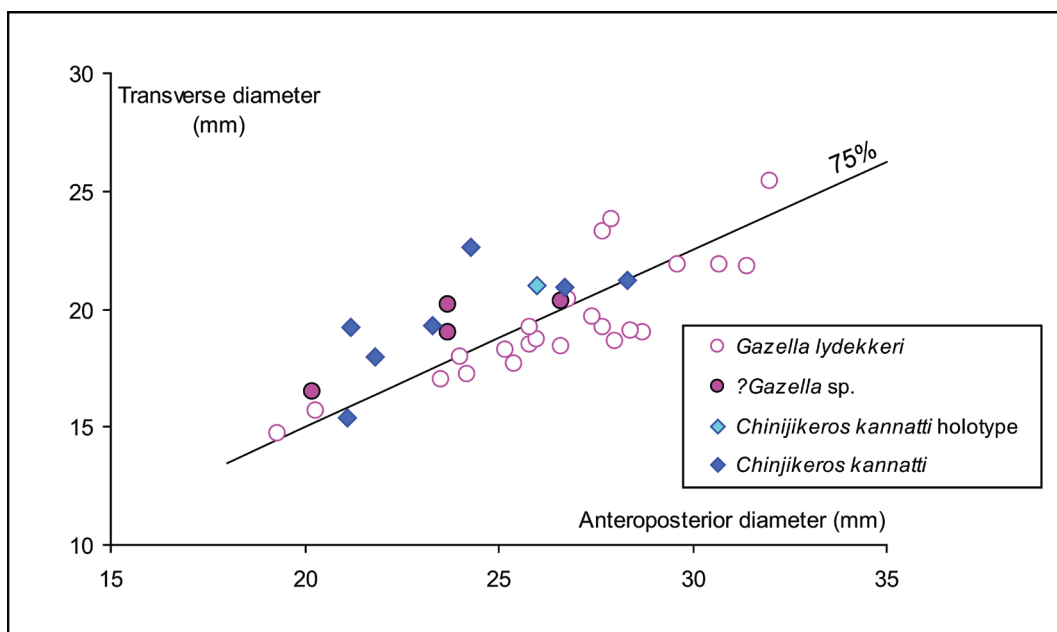


Figure 6. Basal diameters of horn cores of three Middle and Late Miocene Siwalik antilopines. Measurements are given in Appendix 1. The diagonal line is that along which transverse diameter is 75% of anteroposterior diameter. Horn cores with more transverse compression lie towards the right and base of the diagram.

Its first appearance in the Siwaliks, and for that matter in Africa, may be earlier than in Europe or China, but it is difficult to be sure (Thomas, 1984). It is possible, for example, that the Middle Miocene *Gazella* claimed at Fort Ternan (Gentry 1970) may belong to an early genus equally related to *Aepyceros* and other Antilopinae, if not to Caprini as well. Similar caveats apply to supposed gazelles in early Late Miocene localities in western Eurasia where the remains are rather sparse (Gentry 2003, 2004; also see remarks in Azanza *et al.*, 1998).

Species *Gazella lydekkeri* Pilgrim, 1937

Holotype. AMNH 19663, skull and conjoined mandible from a quarry one half mile (0.8 km) southwest of Dhok Pathan. The locality is probably one of the B 25-37 complex with a date of 8.3 Ma (Table 1).

Diagnosis. A small gazelle (ca 10-20 kg) with long horn cores, compressed elliptical cross section, lateral surface flatter than medial, slight to moderately divergent horn cores, degree of divergence may lessen distally, no sinuses within pedicels, females hornless (AMNH 19664, Pilgrim, 1937), narrow supraorbital pits, narrow and sloping dorsal orbital rims, long nasals, premaxilla contact on the nasals, and a cranial roof showing relatively little downturning posteriorly in profile. The teeth are those of a fairly generalised bovid. Rugosity of the enamel is not seen, unlike contemporaneous Boselaphini. There is a low degree of hypsodonty. Small basal pillars (ectostylids) are still present on the labial side of the lower molars, diminishing in size backwards. Incipient transverse goat folds are detectable on the front of lower molars. Styles and stylids are moderately developed and vertical ribs between them are poorly or moderately developed. The m3 hypoconulid may be a small flange offset labially but becoming a lobe later in wear and it seems not to have had a central fossette. The length of premolar rows relative to molar rows is less shortened than in some fossil or most living gazelles. The P2s are larger than the P4s.

Estimated age. 10.2 - 6.3? Ma

Material.

Locality Y 450 (10.2 Ma)

Y 18026 Right horn core base.

Y 16836 Right mandible with p2-m3r.

Y 50615 Left lower molar.

Y 50616a Left upper molar.

Also postcranial remains of a small antelope, suitable for *Gazella*.

Locality Y 258 (10.2 Ma)

Y 9435 Right horn core.

Y 9460 Right upper molar.

Y 46513 Distorted left m3.

Also postcranial remains of a small antelope, suitable for *Gazella*.

Locality Y 311 (10.1 Ma)

Y 6563 Left horn core base with pedicel preserved anteriorl and medially.

Y 47522 Left horn core with supraorbital pit and part of orbit.

Y 47629 Left horn core, almost complete.

Also dental and postcranial remains of a small antelope, suitable for *Gazella*.

Locality Y 337 (9.7 Ma)

Y 5973 Right upper molar.

Locality Y 315 (9.4 Ma)

Y 11024 Right horn core with part of orbit and frontal.

Locality Y 314 (9.3 Ma)

Y 10953 Right horn core.

Locality Y 196 (9.0 Ma)

Y 4688 Right horn core.

Locality Y 177 (8.5 Ma)

Y 4104 Right lower molar, probably m2.

Locality Y 10 (7.9 Ma)

Y 21950 Right horn core.

Locality Y 109 (7.9 Ma)

Y 2900 Left P3-M3.

Locality Y 374 (7.3 Ma)

Y 14089 Right m1-m3.

Locality Y 956 (6.3 Ma)

Y 52547 Left horn core.

Discussion. This is an abundant species, occurring at many localities. There are many additional unlisted skeletal and dental remains from the localities listed above and especially from Localities Y 450, Y 258, and Y 311. Other unlisted localities within the established chronologic range also have both dental and skeletal material that is likely to belong to this species. The species ranges from at least 10.2 to 7.9 Ma and perhaps to 6.3 Ma, so it is likely that if we had a more complete knowledge of morphology it would be seen to have changed over such a long span. The teeth are fairly generalised and for the purpose of identifying teeth the holotype is of great value simply because of the certainty that its upper and lower teeth do belong to this species. As we move into younger levels it becomes safer to ignore *Chinjikeros kanatti* and ?*Gazella* sp. as alternative identifications, but it also becomes more hazardous to distinguish the fossils from reduncines. The first reduncine horn core in the Siwaliks appears at 9.3 Ma and seems to be from a species about the same size as *G. lydekkeri*.

The first occurrence of *Gazella lydekkeri* is at 10.2 Ma, but this follows a significant gap between 10.2 and 11.4 Ma in the productivity of the sediments - as shown in figure 3.3 in Barry and Behrensmeyer (2025). It would be of much interest to have material from this poorly fossiliferous interval as it is preceded by the disappearance of ?*Gazella* sp and might help us understand the relationships between the two taxa. This is of course not the only major gap in the Siwalik sequence as there are others associated with major faunal events that occur between 18 and 17 Ma and between 15 and 14 Ma (Barry and Behrensmeyer, 2025). Behrensmeyer *et al.* (2025) have discussed Siwalik taphonomy and its relation to the varying lithologies of the sediments.

Abbas *et al.* (2018) attributed a modest sample of Upper Miocene cheek teeth to *Gazella lydekkeri*, as have Draz *et al.* (2020, 2021); Khan *et al.* (2024); Naz *et al.* (2024); and Saeed *et al.* (2018), while Middle Miocene teeth have been identified by Khan *et al.* (2013, 2021) and Rafeh *et al.* (2018) as *Gazella* sp. and by Samiullah *et al.* (2020) as *G. lydekkeri*. As noted in our later discussion of the first appearing species of *Kobus*, early reduncines are difficult to distinguish from gazelles, both in their dentitions and in their horn cores. It is likely that some of the Late Miocene materials discussed in these papers are

reduncines not *Gazella*. The horn core discussed by Naz *et al.* (2024) in particular has characters suggestive of *Kobus*.

The first listed *G. lydekkeri* horn core, Y 18026 (Locality 450, 10.2 Ma) (Figure 7A), has a suggestion of faint keels and had been considered as a *Helicopotax*, but the age and the small size are wrong for *Helicopotax*. It is here taken as an early, large, and not completely satisfactory example of *Gazella lydekkeri*. The slightly younger Y 9435 (Locality Y 258, 10.2 Ma) (Figure 7B, C) is the oldest definite *Gazella* horn core in the Siwaliks showing nearly all the characters of the generic diagnosis. It is less compressed than are most of the horn cores at 10.1 Ma (Appendix 1).

The assemblage of horn cores shows fairly wide variation, as seen in specimens from Locality Y 311 (Figure 8). Y 6563 (Figure 8A) has a narrow cross section rounded both posteromedially and posterolaterally rather like a small *Caprotragoides*. Y 47522 (Figure 8B) has an extensive postcornual fossa which is quite deep in its central part. Y 47504 has a slightly wider but still triangular supraorbital pit (Figure 8C), while Y 47629 (Figure 8D, E) shows that divergence increases slightly in its distal parts. Y 11024 (Figure 7D, E) is quite long in the anterior-posterior dimension, less compressed than most other *Gazella lydekkeri*, the maximum transverse diameter lying rather posteriorly, with quite an extensive posterior surface, the posterolateral edge becoming almost a keel higher up from the base (as is also seen in Y 47629). Other characters are less different from other *G. lydekkeri*, and Y 11024 does show a

gazelle-like narrow and triangular supraorbital pit (Figure 7E). The horn cores Y 11024, Y 10953 and Y 4688 (9.4 to 9.0 Ma) are longer in the anteroposterior diameter than most horn cores from 10.1 Ma (Appendix 1).

The late-occurring Y 52547 (6.3 Ma) (Figure 9A, B) is a small-diameter horn core without appreciable compression and showing backward curvature. It might be a female, which would contrast with the hornless female skull AMNH 19664 mentioned by Pilgrim (1937). It has been omitted from Figures 5 and 6. If it is not a *Gazella lydekkeri*, then the age range for *G. lydekkeri* would be 10.2 - 7.3 Ma.

While not listed in Appendix 1 a left horn core, Y 3093 from Locality Y 7 (8.3 Ma), should be mentioned. It is quite small (Figure 9C, D) and with an index of 21.4×17.0 mm (79%) less compressed than usual in *Gazella lydekkeri*, but the lateral surface is flatter than the medial surface as befits a gazelle. The horn core looks as though it has been thrust medially and slightly backwards so as to lie against the frontals, a character also seen in *Dorcadoryx* sp. but here very extreme and undoubtedly due to postmortem distortion. The frontal bone is thin and plate-like more like a female individual or a species smaller than a gazelle.

The dental and postcranial remains listed for Locality Y450 are most probably of *Gazella lydekkeri*. The upper molar Y 50616a (Figure 9E, F) is high crowned for an early Late

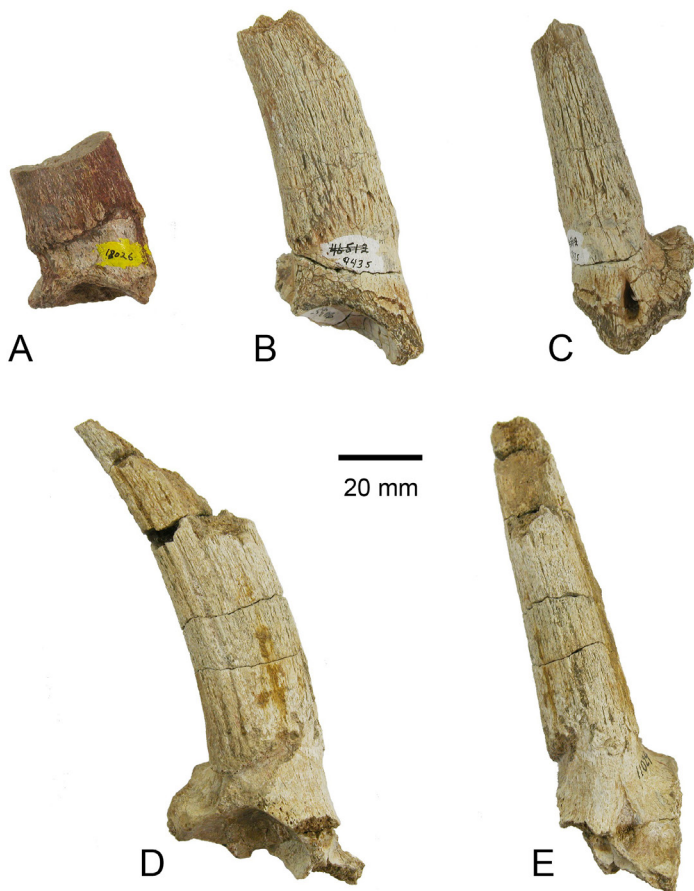


Figure 7. *Gazella lydekkeri*. Y 18026 right horn core in A) lateral view. Y 9435 right horn core in B) lateral and C) anterior views. Y 11024 right horn core in D) lateral and E) anterior views. Scale 20 mm.

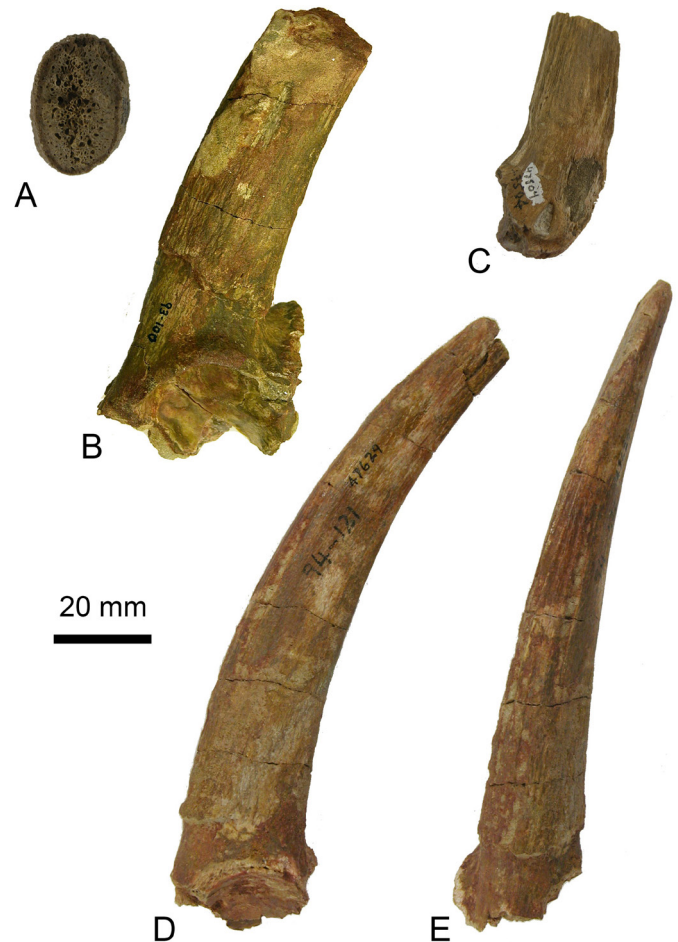


Figure 8. *Gazella lydekkeri*. Y 6563 left horn core in A) dorsal view. Y 47522 left horn core with supraorbital pit and part of orbit in B) lateral view. Y 47504 left horn core and part of orbit in C) anterior view. Y 47629 left horn core in D) lateral and E) anterior views. Scale 20 mm.

Miocene species and the proximal metatarsals do not have so large a naviculocuboid facet as to make *Gazella* an unlikely attribution. It is of interest that the upper molar shows a strong labial rib on the paracone, has a slightly convex metacone wall, a crest in the posterior fossette, and no basal pillars. The lower molar Y 50615 (Figure 9G, H) has a goat fold and a small basal pillar which are reduncine-like characters and unlike Turolian gazelles in the west. The mandibular dentition Y 16836 in late wear has a premolar row length 65% of the molar row length and the AMNH holotype *G. lydekkeri* has a value of 59%. These values compare with means of 57% and 63% respectively for small samples of the European MN12 *G. deperdita* and *G. capricornis* (Gentry, 2003, table 15.3). A sample of the living *G. dorcas* gave 52% but an unusually high value of 65% was found in two African sub-Saharan *G. rufifrons*.

Figure 4 shows that the m3 is lengthened markedly in *G. lydekkeri* compared with *Elachistoceras* and *Chinjikeros*. Using values plotted on the diagram the mean ratios for m3 as a percentage of m2 is 155% in *G. lydekkeri*, 135% in *E. khauristanensis* and 136% in *C. kanatti*. A similar result followed from comparing m3s with m1s, but samples are small. We should acknowledge the shortcomings of our *Gazella* and *Kobus* identifications and the desirability of a comprehensive survey of these ratios in bovids as a whole.

At Locality Y 258 the upper molar Y 9460 has small styles and a strong anterior labial rib, but the modern reduncine character of narrowly-pointed lingual lobes is lacking. The m3 Y 46513 from the same locality has lingual walls widely outbowed, labial lobes widely pointed, a slight goat fold, and the third lobe without a central fossette and with its lingual wall slightly offset lingually. The labial rib of the upper molar and the outbowed lingual walls and goat fold of the m3 could be considered reduncine-like. A lower molar Y 4104 also has a goat fold.

The upper molar Y 5973 has rather flat labial walls between the styles in contrast with the previously mentioned ones. The P4s on Y 2900 and the AMNH holotype (Pilgrim, 1937) are still anteroposteriorly asymmetrical teeth and differ from some *G. capricornis* and from the *G. deperdita* shown in Heintz (1971, plate 4, figure 1b).

Nothing in our collection adds significantly to the known morphological information about *Gazella lydekkeri*. In general Miocene gazelles differ from living ones in slightly smaller size, horn cores inserted more widely apart and often less compressed in transverse cross-section, cranial roof coming forward in profile at a high level relative to the top of the face (Andree, 1926, plate 16 figure 7; Pilgrim, 1937, figure 35; this is perhaps a primitive pecoran character surviving in Late Miocene gazelles), longer nasals, shorter basioccipitals with smaller and less widely separated anterior tuberosities, lower-crowned teeth, less reduced basal pillars in lower molars, less enlargement of the back lobe of m3, and longer premolar rows. *Gazella lydekkeri* differs from the existing Indian gazelle, *G. bennetti*, by not having such an inflated auditory bulla and in being slightly smaller. Roberts (1977) reports that female gazelles in Pakistan normally have horns, but some populations may have hornless females.

Western fossil gazelles are mainly of Turolian (MN 11-12: 8.9 - 7.1 Ma) age (Bouvrain, 1996) while Fortelius and Zhang (2006, figure 2) show the Baode Formation in China as temporally equivalent to MN 13 (7.1 - 5.3 Ma) in Europe and the Bahe Formation as temporally equivalent to MN 10 (9.9 - 8.9 Ma). Hence any of the gazelle species mentioned

above in the summary survey under the heading *Gazella* will be contemporaneous with one part or another of the long *G. lydekkeri* time span. *Gazella lydekkeri* seems to be an unremarkable Late Miocene gazelle. Even in rather rarely preserved face characters the holotype skull resembled a Samos *G. pilgrimi* skull in the New York collection (AMNH 20570) in long nasals, moderate-large sized ethmoidal fissures and preorbital fossae, and premaxillae contacting the nasals. A limited number of other comparisons can be made among Late Miocene gazelles.

The mediolateral compression of *G. lydekkeri* horn cores is comparable with that of *G. deperdita* and stronger than in *G. capricornis*, *G. pilgrimi*, *G. gaudryi*, or *G. dorcadoides*.

Flattening of the lateral surface of the horn cores is not pronounced in Miocene gazelles but may be less obvious in *G. capricornis* than in others including *G. lydekkeri*.

The degree of divergence alters little along the course of gazelle horn cores. A slight increase distally seems to be visible

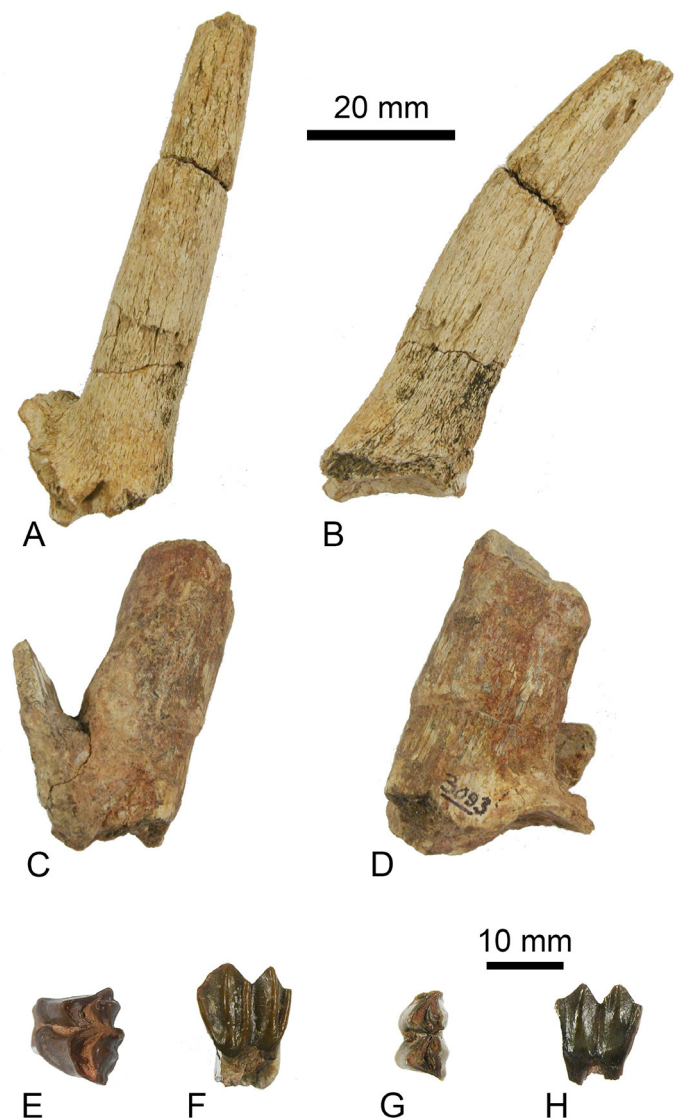


Figure 9. *Gazella lydekkeri*? Y 52547 left horncore in A) anterior and B) lateral views. Y 3093 left horncore in C) anterior and D) lateral views. Scale 20 mm. Y 50616a upper left molar in E) occlusal and F) labial views. Y 50615 left lower molar in G) occlusal and H) labial views. Scale 10 mm.

in the *G. deperdita* specimen of Heintz (1971, plate 2 figure 2) in contrast to the *G. lydekkeri* holotype.

The Chinese Baodean gazelles have enlarged postcornual fossae, and *G. dorcadoides* and possibly other species (Li and Chi, 1964, plate 1; Bohlin 1941, figure 27) possess wide horizontal dorsal orbital rims, and differ thereby from western gazelles and *G. lydekkeri*.

The supraorbital pits are narrower in *G. lydekkeri* than in other gazelles.

The cranial roof looks less downturned posteriorly in *G. lydekkeri* than in other gazelles, for example the Samos lectotype of *G. mytilinii* shown by Andree (1926, plate 16 figure 7).

The anterior tuberosities of the basioccipital in *G. lydekkeri* are large with longitudinal ridges behind them flanking a central groove. In examples of *G. deperdita* and *G. pilgrimi* (Heintz, 1971, plate 1 figure 2; AMNH 20570), and in the Chinese gazelles the anterior tuberosities are more localised

Gazella gaudryi may have the median indentation at the back of its palate situated more posteriorly than in other gazelles.

In western sites (for example Cucuron in France and Samos in Greece) the labial wall of the metacone on the upper molars may be flatter than in *G. lydekkeri*, the third lobe on m3 is not flange shaped, goat folds on lower molars are rare and central fossettes may be straighter.

The premolar row of the holotype *G. lydekkeri* is as short in relation to the molar row as in *G. pilgrimi* and *G. dorcadoides* and shorter than in *G. capricornis* and *G. gaudryi*. However the premolar row is relatively longer in the early mandible Y 16836.

The P4s of some Chinese gazelles (including the one in the Bahe Formation) show an approach to the lingual fusion of paraconid and metaconid (Teilhard de Chardin and Young, 1931 figure 5; Bohlin, 1941 figs 1-8) seen in present day east Asian gazelles of the *Procapra* subgeneric group, but this is not present in *G. lydekkeri* or other Miocene gazelles, and one would have to be certain of having distinguished the Chinese examples from *Dorcadoryx*.

Thus *Gazella lydekkeri* does have a small number of possible differentiating characters but more complete knowledge of infraspecific variation among Miocene gazelles is needed in order to make reliable comparisons. The relatively longer premolar row in the early *G. lydekkeri* mandible Y 16836 warns us of possible evolutionary change over its 4 million year time-span in the Siwaliks. At around 8.0 Ma it became markedly less common in the Siwaliks and the reduncine more common.

The remaining antilopines described below have spiral horns that are heteronymously curved (anticlockwise on the right). The terms used to refer to keels and other structures in spiral-horned antilopines are confusing as sometimes different terms are applied by different authors to the same structure in a species. For example, “posterior,” “posterior-external,” and “postero-lateral” for the most prominent keel in *Protragelaphus skouzesi* (Theodorou *et al.*, 2010; Bouvrain and de Bonis, 1986; Geraads and Gülec, 1999). Or occasionally the same term may be applied to what are possibly non-homologous structures, as for example the “posterior keel” of *Nisidorcus planicornis* and *Protragelaphus skouzesi* (Theodorou *et al.*, 2010). In what follows we use the term most commonly employed or that seems most descriptive, but without implying homology among different species.

Genus *PROSTREPSICEROS* Major, 1891

Type species. *Prostrepsiceros houtumschindleri* (Rodler and Weithofer, 1890).

Diagnosis. Moderate to long horn cores, heteronymous torsion (anticlockwise on the right); anterior and posterolateral keels; fairly open spiralling; cranial roof slightly to moderately inclined.

Remarks. *Prostrepsiceros* is the main genus among a number of Late Miocene spiralhorned antilopines, overlapping and exceeding the size of contemporaneous gazelles. Three long standing generic names in this group are *Palaeoreas* Gaudry, 1861, *Protragelaphus* Dames, 1883, and *Prostrepsiceros* Major, 1891. All three were originally placed in the African tribe Tragelaphini, but later recognized as Antilopini or members of other tribes. More genera and species were described in the later 20th century and onwards (Bouvrain, 1979, 1992; Kostopoulos, 2004, and others).

Prostrepsiceros is mainly known from the Turolian of southeast Europe and southwest Asia. Four lineages or stocks following the small *P. vallesiensis* of the late Vallesian were: (1) *P. houtumschindleri* with a posterolateral keel and a weaker anterior one, and also with a facial morphology like modern *Antilope cervicapra* (Gentry, 1971, plate 5 figure 1); (2) *P. axiosi*, *P. elegans* and *P. zitteli* with more emphasis on the anterior keel; (3) *P. rotundicornis* and *P. fraasi* with poor or no keels and with more open spiralling, but perhaps not a natural group; and (4) *P. vinayaki*, a Siwaliks species known only by small horn cores. The anteroposterior axis of the cross section of the horn cores in group (3) evolved a more transverse alignment in relation to the anteroposterior axis of the whole skull, and the anterior keel (or traces thereof) may descend to a more medial insertion basally. This weakens the reliability of comparing measurements by different authors of horn core basal diameters and compression.

Species *Prostrepsiceros vinayaki* (Pilgrim, 1939)

Gazellinae(?) gen.indet.(aff. *Helicotragus*) *vinayaki* Pilgrim, 1939, plate 1 figures 10, 10a.

Prostrepsiceros vinayaki (Pilgrim). Thomas, 1984, figure 16, plate 3 figure 7a-b.

Holotype. GSI B799 (cast NHML M42957), left horn core from near Nila, (33°10'N 72°37'E), Dhok Pathan Formation (Late Miocene). The holotype is 25.8×19.1 mm (index 74%).

Diagnosis. Small horn cores, well compressed, having an anterior keel and a weaker posterior one, a flatter lateral than medial surface, maximum thickness is central or posterior, rather weak spiralling, and quite a large supraorbital pit.

Estimated age. 8.4 - 7.9 Ma

Material.

Locality Y 174 (8.4 Ma)

Y 4082 Right horn core (Thomas, 1984, figure 16, plate 3 figures 7,7a).

Locality Y 98 (7.9 Ma)

Y 2631 Right horn core base.

Discussion. Thomas (1984) noted that Pilgrim's type horn core was not linked with the boselaphine *Sivoreas* (correcting Gentry, 1970) and placed it in *Prostrepsiceros*. It has an anterior keel, maximum thickness is central or posterior, a less open spiral, a weaker posterior keel, but it does have a flatter lateral surface although still remaining curved, and quite a large supraorbital

pit. Y 2631 (Figure 10) looks as if it possesses an anterior keel, but this appearance may have been caused by damage to the front of the anteromedial surface. Y 4082 had a posterolateral keel and a weaker anterior keel (Thomas, 1984, figure 16). The level of maximum transverse thickness lies centrally, lateral surface flatter than the medial, a posterolateral keel, inserted above the back of the orbits, with backward curvature, and no sinuses visible at the base of the pedicel.

Two older horn cores, possibly of *Prostrepsiceros*, are Y 12438 a right horn core base from Locality Y 328 (9.4 Ma) and Y 14654 right and left horn core bases together with a third horn core piece without its base, from Locality Y 366 (9.0 Ma). The Locality Y 366 specimens show a more or less oval cross section (25.1×19.8 mm [79%]), a long axis probably angled on the mid-line of the skull, possible keels front and back, probably a curved course, and no sinuses in the vicinity of the supraorbital pits. They may not be conspecific with Y 12438. We have not assigned with any certainty teeth to this or other spiral-horned antelopes in the Siwaliks.

Gentry (1999, figures 22.18, 19) described possible material of this species from localities of the Late Miocene (ca. 7.9 – 6.9 Ma) Baynunah Formation, United Arab Emirates. The index of the horn core there was 29.6×20.9 mm (71%) and it had an anterior keel and an approach to a posterolateral one, thereby agreeing with the *P. vinayaki* holotype. *Prostrepsiceros vinayaki* was extant within the time span of many other spiral-horned antilopines in western Eurasia and if the first occurrence of this species in the Siwaliks was as old as 9.4 Ma, it would be approximately 600,000 years younger than occurrences at Sinap in Turkey (Gentry, 2003).

?*Prostrepsiceros* large sp.

Estimated age. 8.2 - 7.9 Ma

Material.

Locality Y 97 (7.9 Ma)

Y 2530 Left horn core and part of frontal including part of the orbit.

Locality Y 24 (8.2 Ma)

Y 49568 Right horn core.

Locality Y 600 (8.1 Ma)

Y 17889 Right horn core with part of top of orbit.

Y 17890 Left horn core with part of orbit.

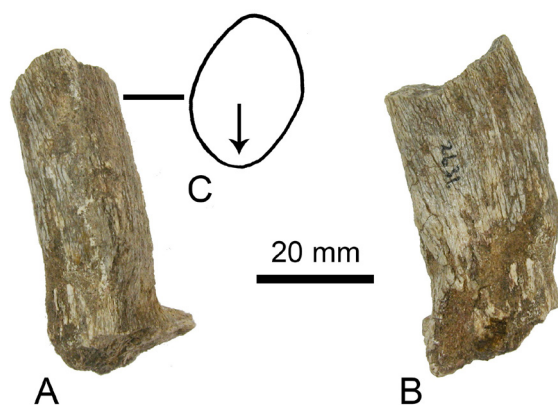


Figure 10. *Prostrepsiceros vinayaki* Y 2631 right horn core base in A) anterior and B) lateral views with C) cross section from about 3 cm above the base with arrow indicating anterior. Scale 20 mm.

Discussion. These horn cores are larger than *Prostrepsiceros vinayaki*, but well compressed, having an anterior keel and a weaker posterior one, a flatter lateral than medial surface, weak spiralling, and a large supraorbital pit.

Y 2530 (Figure 11A, B) preserves the midline and much of the orbit with the bases of the horn cores being about 3 cm apart. At the base the anteroposterior axis of the horn core cross section is very oblique to the midline, twisting distally to create a weak heteronymous spiral. The horn core is strongly divergent and inserted at a steep angle. The supraorbital pit is large and reduncine-like. The weak anterior keel becomes more pronounced distally and has an anteromedial insertion. The horn core's surface is smooth.

The supraorbital pit is small, but not gazelle-like in Y 17889, while Y 17890, a left horn core found at the same locality as Y 17889, has a moderate-sized and fairly shallow postcornual fossa and the front of the pedicel is quite high.

Although poorly preserved, Y 49568 (Figure 11C, D) is of some interest. A sharply keeled edge down one side has the appearance at its base of being posterior. If the downward facing smooth surface below one side of the horn core is part of the orbit and not a sinus, then the horn core will be of the right side. Given this orientation we have a posterolateral keel showing anticlockwise torsion, a more rounded anterior edge, a flattened lateral surface, divergence decreasing from the base upwards and slight backward curvature. Part of the transverse frontals suture has survived close to the horn core base and there is a sinus in the frontals immediately lateral to the pedicel but not penetrating into it (Figure 11D). If there had been an anterior keel it would have descended to an anteromedial insertion as in *Nisidorcas planicornis*.

Y 49568 is about the same size as ?*Protragelaphus* sp. described below, but the torsion is weaker and the lateral surface is noticeably flatter. It looks similar to Samos *Prostrepsiceros*

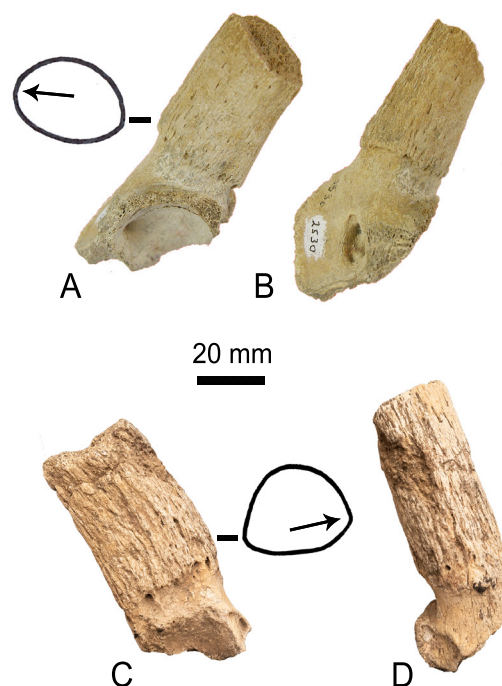


Figure 11. ?*Prostrepsiceros* large sp. Y 2530. Left horn core with cross section at base in A) lateral and B) anterior views. Y 49568 right horn core with cross section at base in C) lateral and D) anterior views. Arrows indicate anteriors of the cross sections. Scale 20 mm.

fraasi and to Sahabi *P. libycus* (Lehmann and Thomas, 1987; genus for latter species changed to *Dytikodorcas* nov. by Bouvrain and de Bonis, 2007 and then to *Afrotragus* nov. by Geraads, 2017). The Baynunah Formation *Afrotragus* aff. *libycus* (Gentry, 1999) agrees well with Y 49568 in its degree of compression and an approach to a posterior keel.

Genus *NISIDORCAS* Bouvrain 1979.

Type species. Gazellinae gen.indet. (cf. *Antilope*) *planicornis* Pilgrim, 1939, plate 1, figures 7. 7a.

Diagnosis. As for the type species, *Nisidorcas planicornis*.

Nisidorcas planicornis is reported from Turolian (MN11 and 12) localities in SE Europe and SW Asia (Bouvrain, 1979; Köhler, 1987; Kostopoulos, 2006, 2016). Geraads and Gülec (1999) suggested some of this material could be separated as a second species but this was doubted by Kostopoulos and Bernor (2011). We question whether any of the non-Siwalik material belongs with the Siwalik species.

Species *Nisidorcas planicornis* (Pilgrim, 1939)

Antilope cervicapra Lydekker 1885 Catalogue of the fossil Mammalia in the British Museum (Natural History), vol.2:52.

Gazellinae gen.indet. (cf. *Antilope*) *planicornis* Pilgrim, 1939 plate 1, figures 7, 7a.

Antilospira incarinatus Tekkaya, 1969, plate I, fig. 1; plate II, fig. 1; plate III, fig. 1.

Holotype. NHML 37264, a water-rolled right horn core collected in the 1830s. It is probably from Piram (formerly Perim) Island in the Gulf of Khambhat (formerly Cambay) and Late Miocene. (see Pilgrim, 1939, pp. 40-41 for a discussion of its origin. Lydekker, 1885 listed it as from northern India and of Pleistocene age.) The holotype is 27.9×21.3 mm (76%). These measurements differ slightly from those given by Pilgrim (1939), which were 29×21.5 mm.

The holotype was the only known specimen of Pilgrim's

species until Bouvrain (1979) referred specimens from Greece, Turkey, and Macedonia to it and created the genus *Nisidorcas*. Gentry (2003) suggested that the holotype immature female cranium of *Cambayella watsoni* (NHML M3683, Pilgrim, 1939, plate 3 figures 6-8), also from Piram Island, might be conspecific with Pilgrim's species but this was doubted by Kostopoulos (2006).

Diagnosis. Spiral horned Antilopini slightly bigger than the *Gazella* of the Late Miocene. Moderately long horn cores in which maximum thickness is central or posterior, anterior keel blunt or absent, posterolateral keel present and stronger distally, slightly or quite well compressed, lateral surface flatter than the medial one, moderate divergence, rather weak spiralling (anticlockwise on the right), well-inclined, insertion above the back of the orbits, little backwards curvature in holotype, quite a large supraorbital pit.

Estimated age. 9.0 Ma

Material.

Locality Y 979 (9.0 Ma)

Y 52732 Left horn core.

Locality Z 162 (Late Miocene, see Table 1)

Z 2589 Left horn core.

Z 2590 Left horn core.

Discussion. These horn cores are the first new specimens from India or Pakistan since the holotype was found. Y 52732 (Figure 12A, B, C) is a somewhat long (preserved length ca. 150 mm) and delicate horn core. Its level of maximum transverse thickness lies centrally, it shows a rounded surface in place of an anterior keel proximally (Figure 12C), although more distally there is a wide shallow groove which would have lain alongside an anterior keel, while a posterolateral (or "postero-external") keel is present with its basal end above and somewhat lateral to the postorbit bar of the frontal. Mediolateral compression is modest (77%), the lateral surface is flatter than the medial. The degree of divergence increases above the base and is then followed by a slight liration, the

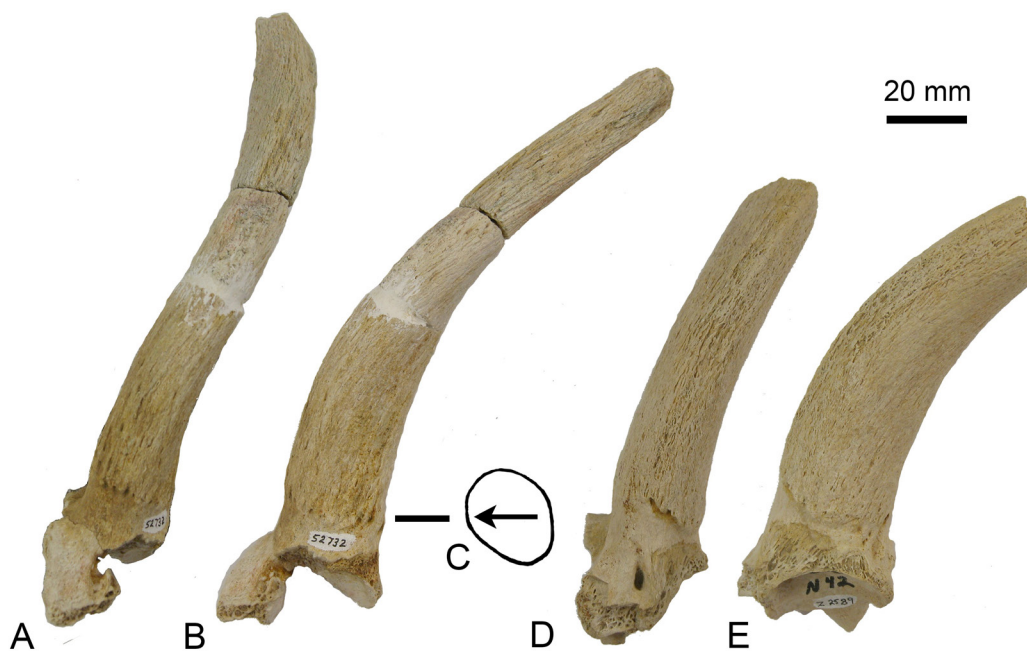


Figure 12. *Nisidorcas planicornis*. Y 52732 left horn core in A) anterior and B) lateral views, C) cross section with arrow indicating the anterior. Z 2589 left horn core in D) anterior and E) lateral views. Scale 20 mm.

insertion being above the back of the orbits. In contrast to the holotype the horn core shows backward curvature, but it only becomes evident in the distal portion (Figure 12B). The long axis of the horn core cross section is at quite a large angle (ca 45 degrees) to the skull mid-line and thus, had an anterior keel existed, it would have descended to an anteromedial insertion. The horn cores were not inserted widely apart. There is only a shallow and narrow postcornual fossa in the preserved surface area behind the horn core, and no sinuses are visible at the base of the pedicel. The supraorbital pit is quite large. The slope of the cranial roof is unknown.

We have restricted our diagnosis of this species to features of the horn core, unlike other recent diagnoses that include many features of the skull and are based on referred material not the holotype (for example, Bouvrain, 1992). Y 52732 compares well to the holotype horncore, except for the appearance of greater backward curvature and slight but distinct liration. It is compressed to the same degree with flattened lateral and rounded medial surfaces, it has a distinct posterior keel, but no anterior keel, and a weak open spiral. The horn core is inserted above the rear of the orbit and inclined at about a 45 degree angle, features not apparent in the holotype. The minimal backward curvature of the holotype is also seen in the lower two-thirds of Y 52732. The holotype is too truncated to show liration if it existed.

Y 52732 is clearly different from the Greek and other material that has been referred to *Nisidorcas planicornis*. For example the widely spaced horn cores of NIK1848 from Nikiti 2, Greece (Kostopoulos, 2016, fig. 9) are straight without spiralling or liration as are those of PER-781 from Perivolaki, Greece (Kostopoulos, 2006, Plate 1, figures 5 and 6). We believe reference of these non-Siwalik specimens to *N. planicornis* is mistaken.

We tentatively attribute to this species two other horn cores (Z 2589 and Z 2590) from the Litra Formation in the Zinda Pir area of central Pakistan (Raza *et al.*, 2002). These are only known to be of Late Miocene age (Table 1). Z 2589 (Figure 12D, E) has a preserved length of almost 100 mm and an index of 30.3×22.4 mm (74%). The level of maximum transverse thickness lies centrally along its anteroposterior cross-sectional axis, neither lateral nor medial surface is flattened. An anterior keel with a wide groove laterally to it starts about 20 mm above the base, posterolaterally there is an intersecting edge rather than a definite keel between the lateral and medial surfaces. Divergence increases rapidly above the base and heteronymous torsion is present, inclination is moderate in side view, while backward curvature is quite strong. There is a very shallow, indistinct postcornual fossa. A small supraorbital pit is at the base of the pedicel, no sinuses are visible on either side of the supraorbital pit or along the broken top of the orbital rim.

Z 2589 is unlike Y 52732 in that the lateral surface is not flattened and an anterior keel is present at least distally and descends to an anterior rather than an anteromedial insertion. A second Litra Formation horn core base Z 2590 (basal index 81%) is similar, but has a more distinct postcornual fossa.

While the holotype of *Nisidorcas planicornis* does not have an anterior keel, it bears some resemblances to species of *Prostrepsiceros*, including the weak spiralling and moderate degree of compression, flatter lateral than medial surfaces, the position of maximum thickness, the large angle between long axis of the horn core and mid-line, and the large supraorbital pit. Except for the absence of an anterior keel, Pilgrim's species might more properly be attributed to *Prostrepsiceros*.

Our *Nisidorcas planicornis* horn cores differ from *Prostrepsiceros vinayaki* by having no anterior keel and a central or slightly anterior level of maximum transverse thickness. Both *N. planicornis* and *P. vinayaki* differ from most *Prostrepsiceros* species by being rather small and with quite compressed horn cores, but they do resemble in these characters the early Greek *Prostrepsiceros vallesiensis* of Bouvrain (1982) studied anew by Kostopoulos (2009b). Moreover the 9.0 Ma date of Locality Y 979 makes Y 52732 an early record of *N. planicornis* and probably of equivalent age to the late Vallesian in the west.

The absence of flattening of the lateral surface of Z 2589 is unlike either *Prostrepsiceros vinayaki* or other *N. planicornis*, and the anterior keel is unlike the *Nisidorcas* holotype and Y 52732. This horn core opens the possibility of a link to *Antilospira*, a Pliocene and younger Asian genus with many supposed species.

There are many cross-connections between the Late Miocene species of spiral horned antilopines and it looks as if too many generic names must be in use. The variability of keel expression and other horn core characters in the Siwalik material of *Nisidorcas planicornis* and *Prostrepsiceros vinayaki* suggest that there must be doubt about the validity of the generic separation. If it were further possible to sink *Prostrepsiceros* in *Antelope*, one might regard Y 52732 as marking the appearance of *Antelope* in the Indian subcontinent. If, however, the direct line of descent to *A. cervicapra* emanates from *P. houtumschindleri*, then the loss or absence of an anterior keel in Y 52732 and the *N. planicornis* holotype would be a parallel to the same loss or absence in *A. cervicapra*.

Genus *PROTRAGELAPHUS* Dames, 1883

Type species. *Protragelaphus skouzesi* Dames, 1883

Diagnosis. Moderate to long horn cores tightly twisting around a straight or nearly straight axis without open spiralling. Torsion is anticlockwise on the right. Horn cores slightly compressed transversely with a strong posterior keel and no anterior keel. The lateral surface flattened and the medial rounded. Horn cores moderately separated, divergence moderate (ca. 25 degrees) and constant, insertion inclined backwards, backwards curvature none or very slight. Extensive sinuses in pedicel not extending into base of horn core. The cranium is short with small supraorbital pits.

Remarks. *Protragelaphus skouzesi* is a western species of Turolian (largely MN12) age. The holotype from Pikermi was not illustrated by Dames (1883) but Kostopoulos (2022) has figured what is mostly likely Dames' holotype (MNB Ma.42647). Other Pikermi specimens have been illustrated by Wagner (1857, plate 7 figure 18), Gaudry (1865, plate 53 figure 4), and Pilgrim and Hopwood (1928, plate 9 figures 2-3).

?*Protragelaphus* sp.

Estimated age. 10.8 Ma

Material.

Locality Y 779 (10.8 Ma)

Y 31935 Part of a right? horn core.

Discussion. This is the earliest-dated fossil of a spiral horned antilopine in the collection. The horn core (Figure 13) is somewhat like *Sivoreas eremita*, but the locality carries the remains of a hipparionine horse and the neatness of the keel on the anterior face of the horn core, the lack of any sign of its spread downwards on to the front of the pedicel,

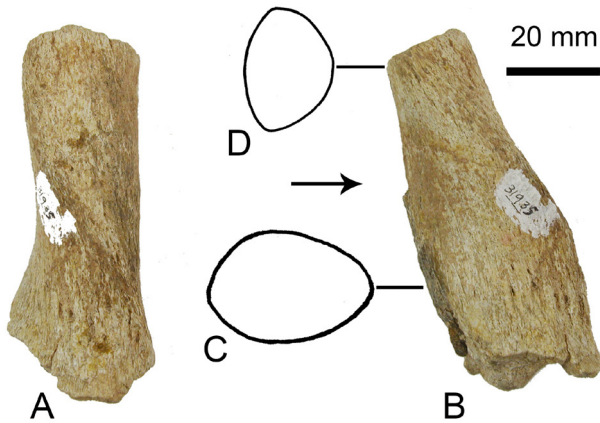


Figure 13. *Protragelaphus* sp. Y 31935 part of horn core, probably the right side, in A) anterior and B) lateral views with cross sections C) at base and D) about 5 cm above the base. Arrow indicates anterior of the cross sections. Scale 20 mm.

and the presence of sinuses in the pedicel all make *Sivoreas* an unsustainable attribution. If it belongs to a spiral-horned antelope its anticlockwise torsion would make it a right horn core. Assuming this, we see the “anterior” keel (Figure 13) is sharper than the “posterior” one. (The specimen number on its white background is positioned next to this putative “anterior keel” which, while it is difficult to determine the orientation of the horn core, may descend to a more medial than posteromedial insertion. This keel is what is referred to as a “posterior keel” by Theodorou *et al.*, 2010.) The horn core is well compressed (70%) with the lateral surface flattened and the medial rounded. The axis is straight, but the keels are quite tightly twisted. A large sinus extends more than half way up the pedicel. The lack of open spiralling makes it comparable with *Ouzocerus*, *Protragelaphus*, or *Palaeoreas* among western Late Miocene antilopines, but species of these genera have strong true posterior keels. It is slightly larger and more compressed than *Protragelaphus skouzesi*, and does not have such a tight twist or strong posterior keel as *Palaeoreas lindermayeri*. It is slightly bigger and more compressed than the Pentalophos (Vallesian of Greece) *Ouzocerus* of Bouvrain (1997). Both *Helladorcas* and *Majoreas* have horn cores with more open spiralling.

With no adjacent skull fragments that show how it is inserted, this is a difficult specimen to identify. The straight, tightly twisted, and compressed horn core with flat lateral and rounded medial surfaces suggest *Protragelaphus*. However, the keel on the anterior face descends to a more medial rather than a posteromedial insertion and the posterior one does not have the exaggerated form and nearly 180 degree rotation of the posterior keel of *Protragelaphus* (Roussiakis, 2009, fig. 4; Theodorou *et al.*, 2010, fig. 10; Kostopoulos, 2022, fig. 26). With an estimated age of 10.8 Ma the specimen is significantly older than occurrences of *Protragelaphus* in the region around the Black Sea. While different, this is too poor a specimen to base a new taxon on.

ANTILOPINAE?

SPIRALISCORNIS new genus

Type and only species. *Spiraliscornis inopinata*, genus and species nov.

Diagnosis. A large spiral horned bovid (ca. 100 – 250 kg?), horn cores robust and long, with keels tightly twisted about a straight axis without open spiralling, torsion heteronymous (anticlockwise on the right), maximum thickness central, prominent posteromedial and weaker posterolateral keels present, no mediolateral compression (basal index exceeds 100%), posteromedial surface flattened, anterolateral rounded, divergence very slight and constant, in side view probably slightly to moderately inclined, with very slight backwards curvature, insertions very close, postcornual fossa elongated and shallow, sinuses present in the frontals but not reaching into pedicels.

Differs from the similar sized species of *Selenoportax* and *Pachyportax* in the very marked twisting of the horn cores with prominent posteromedial keel and a subdued posterolateral keel, no mediolateral compression, minimal and constant divergence with horn core rising almost vertically from very closely placed insertions. Differs from the similar sized *Rectacornis mirabilis* of Gentry *et al.* (2026) in having more tightly twisted horn cores with prominent posteromedial keel and a subdued posterolateral keel, minimal divergence, and with horn cores rising from very closely placed insertions.

Among Late Miocene spiral horned antilopines the absence of open spiralling at the base makes this taxon comparable with *Protragelaphus*, *Palaeoreas*, or *Stryfnotherium*. In these the shape of the horn core is generally similar, although usually much more compressed. In addition, apart from differences in size and the degree of compression, species of these genera have horn cores that are set far part and more widely diverging, as well as having a strong posterior keel (variously “postero-external” or “postero-lateral” and equivalent to our “posterolateral keel”) that inserts posterolaterally above the frontal postorbital bar and is the most prominent keel, while (except for *Palaeoreas*) the anteriomedial keel is absent or merely a trace (Bouvrain, 1978, 1980, and 1997; Bouvrain and de Bonis, 1986; Geraads and Gulec, 1999; Köhler, 1987; Kostopoulos, 2004, 2022; Kostopoulos and Koufos, 1999; Kostopoulos and Soubise 2018, Roussiakis, 2009; Theodorou *et al.*, 2010). These taxa are also all younger than the material of this species.

Among the spiral horned antilopines, the species of *Ouzocerus* are an exception to some of these generalizations. Most significantly the new taxon differs from *Ouzoceru* in the absence of any mediolateral compression and the very minimal divergence, with the horn cores rising almost vertically from very close placed insertions. Its horn cores are more loosely twisted and, because the horn core is not compressed, the posterolateral keel appears in its proximal portion to be more subdued. The frontals were elevated and lacked the depression noted in *Ouzocerus* by Kostopoulos and Koufos 1999.

The generic name refers to the shape of the horn core.

Spiraliscornis inopinata new species

Holotype. GSP Y 49547 Right horn core with attached portions of the skull and separated lower part of left horn core (Figure 14). From Locality Y 609 (8.8 Ma) at 33° 19.679'N, 72° 39.873'E. Correlated to the Ratha Kas section between 939.7 and 926.6 meters above the base (Tauxe and Opdyke 1982 – as “Rhata” Kas).

Diagnosis. As for the genus.

The trivial name refers to the unexpected or unforeseen occurrence of this species.

Estimated age. 8.8 Ma

Material.

Locality Y 609 (8.8 Ma)

Y 49547 Much of right horn core and lower part of left, with some internal elements of skull and basicrania. Holotype.

Locality Y 166 (8.8 Ma)

Y 3589 Distal part of left horn core. Tentatively included in this species.

Discussion. A large, mysterious, and very rare species. The holotype includes the right horn core with parts of the skull having the interfrontal suture marking the midline. The robust horn cores of the holotype (Figure 14) are not mediolaterally compressed (basal index: 107%) and were probably long. They show anticlockwise (heteronymous) torsion around a straight axis, possibly making one full 360° turn along the course of an intact horn core.

Two keels are present, a prominent posteromedial and a weaker posterolateral keel. The posterolateral keel originates above the post-orbital bar of the frontal, forming a low, roughened ridge that approximately 8.5 cm distally becomes a narrow and shallow spiralling groove. The posteromedial keel is sharper and more crest-like, originating posteromedially near the junction of the interfrontal and frontal-parietal sutures and wrapping around the anterior face of the horn core. The posterolateral part of the horn core base is more posteriorly placed than the posteromedial part and maximum thickness is central. A somewhat flattened and narrow posteromedial surface basally (Figure 14C) probably becomes the prominent and wide groove flanked by the two keels which can be seen distally on Y 3589 (Figure 15A). A coalesced, presumed anteriomedial surface is rounded (Figure 15C). The horn cores are nearly vertical at their bases and, although partially masked by the curved keels, diverge 8-9 cm above the base at a very slight (ca. 10°) and probably constant angle. In side view the horn cores are moderately inclined and very slightly curved backwards. The insertions are very close together, perhaps as little as 10 to 15 mm apart, and above the orbits. The pedicels

lack internal sinuses, and the frontals, which do contain sinuses, are elevated between the horn core bases. There is a shallow, elongated postcornual fossa. Only the top of the supraorbital pit is preserved and its size and shape are not known.

We include the distal horncore Y 3589 in this species with some hesitation, as it has a much more open spiral than the holotype. It is, however, of a size to match the holotype and the axis of the spiral is straight with what we take to be the posteromedial face rounded (Figure 15C). Although from a different locality, is of the same age as the holotype. If not of this species, then it documents yet another large spiral-horned antilopine in the later Miocene Siwaliks, this one with an open spiral.

Nothing suggests that this is a boselaphine species. The only large non-boselaphine Miocene antelope with anticlockwise torsion, keeled horn cores, and no open spiralling in western Eurasia at this period is *Criotherium argalioides* from Samos and Turkey (Kostopoulos *et al.*, 2023). It shows no resemblance to our species. *Criotherium* horn cores are not very long, compression is strong distally, the posterolateral keel is the stronger one, torsion is stronger, the horn cores are less closely inserted, and the insertions are definitely postorbital. Our best suggestion is that we have a local (south Asian) large spiral-horned member of the Antilopinae or Antilopini.

Tribe REDUNCINI Kottnerus-Meyer 1907

Present-day reduncines contain the African *Redunca*, reedbucks, and *Kobus*, kob, lechwes and waterbuck. They live in habitats near water and females are hornless. Their horn cores are without keels or torsion, but often with transverse ridges. Horn cores may be set at a low inclination in side view with upwards and forwards curvature or they may have a more upright insertion and backward curvature. Postcornual fossae are present. Frontals have few or no internal sinuses and fail to become appreciably elevated between the horn insertions. Temporal ridges on the cranial roof approach closely posteriorly, a maxillary tuberosity is prominent in ventral

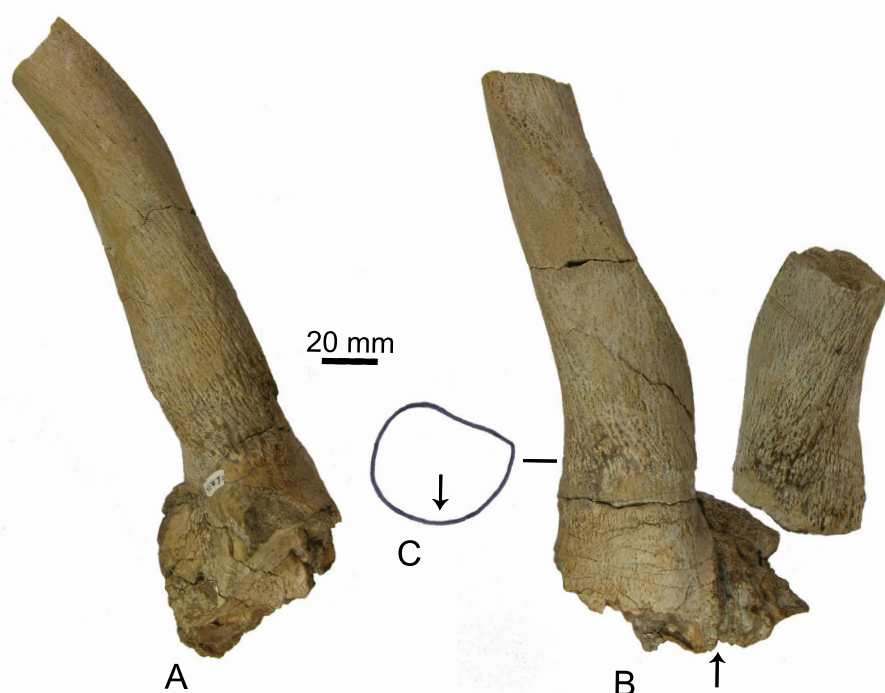


Figure 14. *Spiralicornis inopinata* new genus and species. Y 49547 holotype skull fragment with right horn core in A) lateral view and B) skull fragment with right horn core and detached lower part of left horn core in anterior view with paired arrows indicating the interfrontal suture. C) cross section at base of right horn core with arrow indicating anterior. Scale 20 mm.

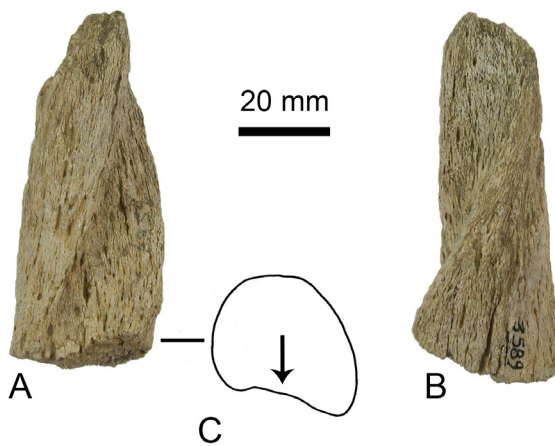


Figure 15. *Spiraliscornis inopinata* new genus and species. Y 3589 distal end of left horn core in A) anterior? and B) lateral? views and C) cross section of proximal end of the fragment with arrow indicating presumed anterior. Scale 20 mm.

view of the skull, the infraorbital foramen is placed low and anteriorly, palatal ridges on the maxillae in front of the tooth rows come close together, the basioccipital has large anterior tuberosities. Teeth of living species are rather small in relation to skull and mandible size, moderately hypsodont, upper and lower molars with basal pillars, upper molars with small but marked ribs between the styles, lingual lobes of upper molars and labial lobes of lower molars constricted, lower molars with goat folds, upper and lower P2s small, and lower premolars with the appearance of anteroposterior compression. Lower p4s are without paraconid-metaconid fusion to form a closed lingual wall and p3-p4 have strongly projecting hypoconids and often a deep and narrow labial valley in front of them. The boödont-like complexity of reduncine molars evolved gradually and was not fully present until the Pleistocene.

Reduncines have long been known in the Siwaliks. Those from the Pinjor Formation (ca. 2.6 - 1.7 Ma) are reminiscent of lechwes or kobs, but have rather strong *Boselaphus*-like temporal ridges on their cranial roofs unlike African reduncines. These ridges led Gentry and Gentry (1978), but not Pilgrim (1939), to favour a relationship with Boselaphini. Gentry (1980) compared the teeth of early Pliocene reduncines at Langebaanweg with the aegodont and not very hypsodont teeth of Tragelaphini and not with Antilopini which later turned out to be the more relevant comparison, and thus the simpler and Antilopini-like characters (such as very small or no basal pillars, occlusal simplicity, much weaker labial ribs on upper molars, flat lingual walls of lower molars) were unexpected. Eventually Gentry (1992) moved Reduncini away from Boselaphini and Bovini, while molecular and other studies (Gatesy *et al.*, 1997; Vrba and Schaller, 2000; Matthee and Davis, 2001; Marcot, 2007; Hassanin *et al.*, 2012) led to the view that Reduncini should go into Antilopinae.

Reduncines earlier than the Pinjor ones were found in the Siwaliks of the Dhok Pathan Formation of the Hasnot area (~7.4 Ma) and possibly earlier (Pilgrim, 1939). Among them is *Dorcadoxa porrecticornis* (Lydekker, 1878 - here referred to *Kobus*), which is similar to forms in Africa (Gentry, 1970, 1980, 1997, 2010). The GSP/Harvard collection now reveals that a small reduncine species or lineage occurred in the Siwaliks as early as 9.4 Ma, although it is not known whether there was a continuous record from the Late Miocene to the

Late Pliocene. In Africa early reduncines come from sites such as the Middle Awash Adu-Asa Formation, Lothagam, Mpesida and others from around 7.0 Ma onwards (Haile-Selassie *et al.*, 2009; Harris, 2003; Thomas, 1980; Kingston *et al.*, 2002), but two possibly reduncine horn cores from Ngorora (Thomas, 1981, plate 3 figures 4-5) might give a first appearance of the tribe in Africa of up to 9.4 Ma.

Various claims for Late Miocene reduncines elsewhere in Eurasia (not mentioned in Gentry 2010) are mistaken or as yet uncertain. A horn core from Gravittelli, Sicily, subsequently lost in an earthquake, was first thought to be a gazelle but later a possible reduncine (Seguenza, 1902; Hooijer, 1946; Thomas *et al.*, 1982). Another claim is for two genera from Moldavia, *Procobus* Khomenko, 1913 and the earlier and smaller *Moldoredunca* Lungu, 1979. *Procobus* contains *P. melania* and *P. brauneri*, the first being the type species (Pilgrim and Hopwood, 1928). *Moldoredunca* contains the one species *M. amalthea* on which Korotkevich and Krakhmalnaya (1983) and Krakhmalnaya (1996) give more information. Neither genus is convincingly reduncine, as Kostopoulos and Merceron (2024) have shown that *Procobus* is probably a caprine, while Kostopoulos (2022) has suggested *Moldoredunca amalthea* is based on horn cores of a female *Miotragocerus*. A p2-p3 from an MN13 level in Turkey (Köhler, 1987) is also uncertain as a reduncine and "*Redunca*" *eremopolitana* of Erdbrink (1982) from Maragheh was thought by Gentry (2000) to be wrongly oriented *Pachytragus* or *Norbertia* horn cores.

Genus *KOBUS* A. Smith, 1840

Dorcadoxa Pilgrim, 1939

Type species. *Kobus ellipsiprymnus* (Ogilby, 1833)

Kobus is difficult to diagnose other than that living species are larger than *Redunca*. Horn cores are sometimes like *Redunca* in being set at a low inclination in side view with upwards and forwards curvature, but sometimes with a more upright insertion followed by backward curvature. They are often longer than in *Redunca*. Other characters are given under Reduncini above.

The main Miocene species in the Siwaliks is *Kobus porrecticornis*, to which we add two doubtfully separate species, the earlier *Kobus* sp.1, and the later *Kobus* sp. 2. *Kobus porrecticornis* was for long taken as an antilopine and Pilgrim (1939) founded *Dorcadoxa* for it. Subsequently Gentry (1970) suggested it was a reduncine and Thomas (1980) placed *Dorcadoxa* in *Kobus*. It is very like some of the early African reduncine fossils.

Kobus sp. 1

Estimated age. 9.4 - 8.2 Ma

Material.

Locality Y 226 (9.4 Ma)

Y 6943 Left mandible with p4-m1.

Locality Y 269 (9.4 Ma)

Y 14596 Left m3.

Locality Y 211 (9.3 Ma)

Y 5223 Left M3, with small posterior half.

Y 47110 Right m3.

Locality Y 317 (9.2 Ma)

Y 11641 Right horn core base in two non-joining pieces.

Locality Y 158 (8.7 Ma)

Y 3450 a,b Left and right horn cores.

Locality Y 30 (8.4 Ma)

Y 645 Left mandible with p4-m2.

Locality Y 24 (8.2 Ma)

Y 459 Right mandible with m3.

Y 461 Left mandible, p4-m3.

Discussion. The first reduncine to appear in the Siwaliks is a gazelle-sized species at 9.4 Ma with the earliest horn core accepted as a reduncine being Y 11641 at 9.2 Ma (Figure 16A, B). The species lasted to around 8.2 Ma. Its horn cores have no clear-cut reduncine characters but show small differences from the contemporaneous *Gazella*. Basically they have pedicels which look broader and shorter, and the main cause of this appearance seems to be a more pronounced anteromedial thickening near the base. No horn cores are sufficiently well preserved to link this character with a greater backwards inclination than in *Gazella* but Y 51698, listed below as the later species *Kobus porrecticornis*, suggests that this could be the case.

It is hard to be consistent and objective in making identifications. The paired horn cores of Y 3450 (Figure 16C-E) are backwardly curved, their maximum thickness lies centrally along the anteroposterior axis, they have a flattened lateral surface, an approach to a posterolateral keel, degree of divergence lessening very slightly from the base upwards (also seen in a *K. porrecticornis* Y 31408), no sinuses at the base of the pedicels, and a small supraorbital pit on the left side with a narrow and shallow groove in front of it. These characters could fit *Gazella*, and the last is not reduncine-like, but the pedicel does broaden, and the more regular grooving on the front of the horn cores is also like early reduncines. The horn core Y 21950 from Locality Y 10, listed above as *G. lydekkeri*, also has the expanded pedicel of the reduncine species, but is rather small for *Kobus* sp. 1.

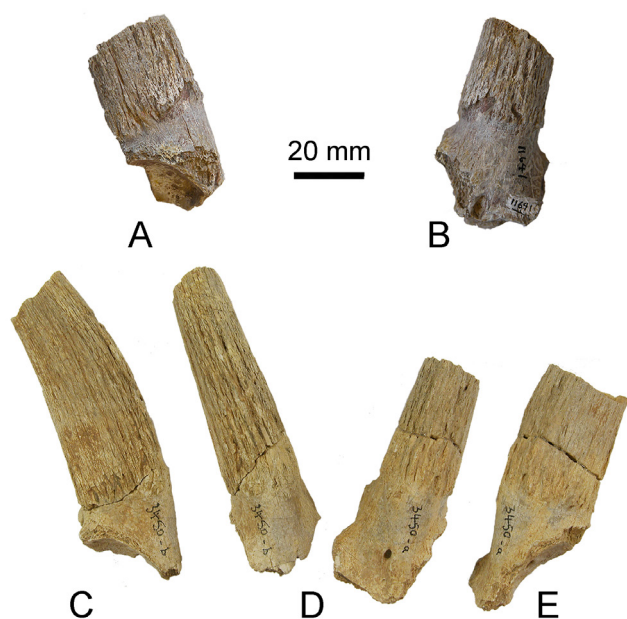


Figure 16. *Kobus* sp. 1. Y 11641 right horn core base in A) lateral and B) anterior views. Y 3450 right and left horn core bases in C) right lateral, D) anterior, and E) left lateral views. The paired right and left horn cores of D are approximately positioned as in life, although the distance between the pair is unknown. Scale 20 mm.

As with horn cores so too with teeth it is hard to tell Miocene reduncines from *Gazella*. Their teeth show few characters of the modern boödont reduncines and the relationship of Reduncini to other Antilopinae is still very uncertain (Bibi, 2014). *Kobus* sp. 1 has much overlap in size with *G. lydekkeri* (Figure 4), its upper molars may have better-marked ribs between the styles on their labial walls, particularly on the paracone, a basal pillar on m1 might be of moderate rather than small size, goat folds are perhaps more frequent and more prominent on lower molars, front and rear outbowings on the lingual walls of the lower molars may be stronger particularly on the metaconid, the increasingly transverse orientation of the front and back edges of the lower premolars can give an appearance of anteroposterior compression, the metaconid ridge on p4 may be transverse rather than diagonal, and p4s may show a strongly projecting hypoconid and a deep and narrow labial valley in front of it. When these characters occur we can see them as deviating from gazelles but we cannot be certain of their homology with the same states in later reduncines. For example we might expect basal pillars to decline as Antilopini evolved, but would they also be doing this in early Reduncini and then reappearing in later ones? The condition of the third lobe of m3 is variable and the uncertainty of our tooth identifications prevents us finding reliable differences from gazelles.

These Siwaliks teeth are like the early Reduncini at African sites such as Manonga and Sahabi. Their acquisition of reduncine-like characters is starting to make them more different from Antilopini than are the Langebaanweg reduncines (Gentry, 1980, 1997, 2008). Langebaanweg reduncines have fewer signs of labial ribs or changes in the simple outlines of the central fosses on upper molars, while on the lower molars they show smaller basal pillars, almost no signs of goat folds, and flatter lingual walls.

The earliest teeth listed under *Kobus* sp. 1, Y 6943 and Y 14596 (both 9.4 Ma), show hints of a non-gazelline morphology in the enhanced size of the paraconid and lingual end of the metaconid ridge in p4 (Figure 17A,B), a slight goat fold in m1, and a moderate sized basal pillar in m3. On Y 5223 (Figure 17C) the M3 shows the primitive character of a small posterior half and on the m3 Y 47110 from the same locality (Figure 17D) the third lobe is a narrow flange directed posterolabially and bent labialwards at its tip. Y 5623 (Figure 17E) is an m2 on which the strength of the goat fold and the twin outbowings of the lingual walls are notable. The p4-m1 of Y 645 (Figure 17 B) are fairly small but the p4 shows transverse front and back walls and a transverse metaconid ridge.

Reduncine teeth get bigger through time in the Siwaliks (Figure 4) and the larger ones at Locality Y 24 at 8.2 Ma could signal the appearance of *Kobus porrecticornis*. Indeed the m3 Y 459 at that locality was originally assigned to *Kobus* sp. 1 and the partial lower tooth row Y 461 to *K. porrecticornis*. For the time being we can avoid ambiguity by taking the 8.1 Ma horn core Y 51698 as the earliest occurrence of *K. porrecticornis* and put all older reduncines in our collection into *Kobus* sp. 1.

Species *Kobus porrecticornis* (Lydekker, 1878)

Antilope porrecticornis Lydekker, 1878, plate 25 figure 4.

Gazella porrecticornis Lydekker, 1886, figure 2.

Dorcadoxa porrecticornis Pilgrim, 1939, plate 1 figure 9.

Gazellinae gen. indet. (?*Gazella*) *superba* sp.nov. Pilgrim, 1939, plate 1 figures 4, 4a,b.

Reduncini gen. indet. (cf. *Indoredunca*) *theobaldi* Pilgrim, 1939, plate 3 figures 10, 10a.

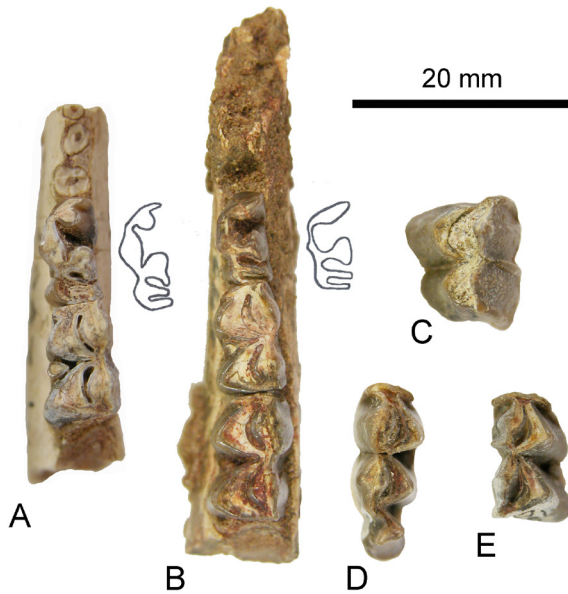


Figure 17. *Kobus* sp. 1. A) Y 6943 with p4-m1, B) Y 645 with p4-m2, C) Y 5223 M3, D) Y 47110 m3 and E) Y 5623 m2. All in occlusal view. An outline of p4 is shown for Y 6943 and Y 645. Scale 20 mm.

Reduncinae(?) gen. indet. (cf. *Kobikeryx*) sp. Pilgrim, 1939, plate 3 figures 4, 5, 5a.

Kobikeryx atavus Pilgrim, 1939, figure 14.

Holotype. GSI B229, left horn core with frontal, perhaps from Hasnot, in the upper part of the Dhok Pathan Formation (Late Miocene). Pilgrim (1939) mentions a right horn core, GSI B230, which may be the same individual as the holotype frontlet. The dimensions given by Lydekker (1878) (converted to mm) are anterior-posterior diameter: 40.6, transverse diameter: 29.2, length: 114.3, with the basal index being: 72%. It is the largest specimen of the species (Figure 18).

Diagnosis. Horn cores probably quite long, central or slightly posterior level of maximum transverse thickness, front edge rounded in cross section with no approach to a keel, posterolateral keel often present, poor mediolateral compression, lateral surface flatter than medial one, transverse ridges poor, longitudinal grooving on the surface, quite strong divergence becoming weaker distally, inclined insertions, curving backwards, a deep localised postcornual fossa, and low pedicels. Frontals between horn bases perhaps slightly above level of dorsal orbital rims. No sinuses lateral to pedicel or medial to supraorbital pit. Supraorbital pits quite deep.

Estimated age. 8.1 - 7.7 Ma

Material.

Locality Y 599 (8.1 Ma)

Y 51698 L *Kobus porrecticornis* Left horn core with part of orbit and frontal.

Locality Y 606 (8.1 Ma)

Y 49550 Left mandible with p4-m2.

Locality Y 998 (8.1 Ma)

Y 51533 Left horn core.

Locality Y 17 (8.0 Ma)

Y 2817 Right mandible, p4-m3.

Locality Y 547 (8.0 Ma)

Y 31408 Right horn core.

Locality Y 953 (7.9 Ma)

Y 50932 Right horn core.

Y 50937 Right m3.

Locality Y 948 (7.8 Ma)

Y 50864 Left horn core.

Locality Y 949 (7.8 Ma)

Y 50881 Left p4.

Locality Y 900 (7.7 Ma)

Y 49740 Left maxilla with P3-M3; right M3; left mandible with roots of p3 and p4 and crowns of p2 and m1-m2 and part m3; right m2 and part m3.

Y 49742 Left horn core and right horn core base and distal piece.

Discussion. In the interval 8.1-7.7 Ma a good deal of variation in size is encountered, with some reduncine horn cores larger than *Kobus* sp. 1 and looking something like a small *K. kob*, while others, e.g. Y 51533 or Y 2536, can still be small (Figure 18, data in Appendix 1). However, they have become recognisably *K. porrecticornis* and it turns out to be a common antelope within its rather short time range, apparently superseding *Gazella lydekkeri* in that role.

Divergence and inclination were both quite strong (Figure 19A, B) with the degree of divergence lessening distally in what might have been quite long horn cores (Figure 19C, E, and G). No sinuses can be seen in the preserved parts of the pedicels and the maxilla of Y 307 has the infraorbital foramen low above P2. The supraorbital pits are triangular in Y 51698, and narrow in Y 142. Y 50864 (7.8 Ma, Figure 19C, D) is larger than earlier horn cores such as Y 51698 (8.1 Ma, Figure 19A, B) and looks much like an example of the later and larger African *Kobus sigmoidalis* Arambourg 1941, but lacks the transverse ridges.

Compared with *G. lydekkeri* the horn cores may have been longer, the level of maximum transverse thickness less posterior, the anterior edge more rounded, an approach to a posterolateral keel more frequent, transverse compression slightly weaker, the divergence stronger, the inclination greater, as suggested in Y 51698 for example, and the postcornual fossa larger. The pedicels remain short as in earlier *Kobus* but their medial spread as they descend becomes less important.

For comparison Figures 6 and 18 show the basal diameters of horn cores in Siwalik Antilopinae. *Chinjikeros*, *Gazella* sp. and *Kobus* sp. 1 tend to be small and nearly all lie above the 75% line making them not only smaller, but also less compressed than their successors *G. lydekkeri* and *K. porrecticornis*. Figure 20 shows the changes in degree of compression over time. We see here that *G. lydekkeri* and *K. porrecticornis* have the most compressed horn cores, that the earliest *Kobus*, *Kobus* sp. 1, is later than *Chinjikeros* or *Gazella* sp., that *Kobus* sp. 2 loses the compression seen in *K. porrecticornis*, and that the record diminishes or ceases after about 7.0 Ma.

With the exception of Locality Y 900, none of the teeth assigned to *Kobus porrecticornis* have been found in close association with skull or horn core material, but teeth with varying degrees of difference from supposed gazelle teeth continue to be found as in the earlier period when *Kobus* sp. 1 was extant. Most of them are lower teeth. The mean ratios for reduncine m3/m2 lengths derived from values on Figure 4 are 130% in *Kobus* sp. 1 and 128% in *K. porrecticornis* so it looks as if their m3s remained shorter than in *Gazella lydekkeri*

(155%). The *Kobus* sp. 2 value of 153% is based on only one m2 so is obviously unreliable.

The upper teeth of Y 49740a at 7.7 Ma (Figure 21E) have smooth enamel and show moderate hypsodonty. There are no basal pillars on the upper molars but there is a small one on m2 and a very small one on m3. The metacone labial wall is slightly convex on upper molars, the rear crest of the protocone is not joined to the rest of the tooth until middle wear, there are no cingula, the posterior part of M3 is not small, premolars are small relative to molars, P3 does not have a symmetrical central fossette.

The basal pillars on *K. porrecticornis* lower molars may be larger than in *Kobus* sp.1. The mandible Y 49550 (Figure 21A, B) at 8.1 Ma looks satisfactory as a reduncine with its large size, strong goat fold on m2, p4 metaconid swollen at its lingual end, and its parastylid turned to lie in a transverse rather than a diagonal plane. The slightly later Y 2817 at 8.0 Ma is also a good reduncine lower dentition. The molars have goat folds, basal pillars declining in size from small-moderate on m1 to tiny on m3. Their labial lobes are well rounded and bluntly pointed, the central fossettes well-curved, lingual walls with slight outbowings, and the rear lobe of m3 offset labially. The back lobe of the m3 Y 50937 has a forward hook resulting in a gap on its lingual side. The p4 is anteroposteriorly compressed and its hypoconid projects labially. The paraconid on the p4 of Y 50881 and Y 2840 (Figure 21 D) projects quite far lingually. Nevertheless there is considerable variation among dentitions we assign to *K. porrecticornis*. The p3 or p4 on Y 16498, also at 8.0 Ma, has little or no approach to an appearance of anteroposterior compression, only a slight forward expansion at the lingual end of the metaconid ridge, and no labial projection of the hypoconid and looks very unlike the p4 on Y 2817. However, the two horn cores at the same locality have been identified as *K. porrecticornis*.

The fossils described by Pilgrim (1939) under the three ornate names Gazellinae gen.indet. (?*Gazella*) *superba* sp. nov., Reduncini gen.indet. (cf. *Indoredunca*) *theobaldi*, and Reduncinae(?) gen. indet. (cf. *Kobikeryx*) sp. look as if they could be examples of *Kobus porrecticornis*. We have insufficient material to make comparisons with our own *Kobus*

spp. 1 and 2, and (?*Gazella*) *superba* and Reduncini gen.indet. (cf. *Indoredunca*) *theobaldi* can remain as synonyms of *K. porrecticornis* for the present. We have also listed *Kobikeryx atavus* as a synonym. This name is based on a cranium (GSI B 798), probably male but broken just behind the horn pedicels, from 2 miles west of Kotal Kund and of uncertain stratigraphic level (Pilgrim, 1939). We agree with Pilgrim that it is a reduncine. The cast in London (M35389) is a little larger than the cranium of the *Gazella lydekkeri* holotype with a more sloping and less curved roof in profile and has much larger anterior tuberosities of the basioccipital. These tuberosities are wider apart and further forward than in the gazelle and each has crests or flanges emanating anteriorly and posteriorly from its highest point. The poorly marked temporal ridges come close together in their posterior parts, possibly more so than in gazelles although this is very uncertain. Again and for the present, *Kobikeryx atavus* need not be taken as a species additional to *Kobus porrecticornis* or its likely predecessor and successor species *K. spp. 1* and 2.

Kobus porrecticornis is a common species within its time range. This may reflect some ecological factor, especially if *Gazella* became rare shortly after 8.0 Ma. By this date *Miotragocerus punjabicus* had replaced *M. pilgrimi*. In East Africa *K. porrecticornis* or a very similar species is known from about 7.0 Ma onwards at Mpesida, Lukeino, the Adu-Asa Formation, and the Ibole Member at Manonga (Thomas, 1980; Gentry, 1997; Haile-Selassie *et al.*, 2009). A claim for Baard's Quarry at Langebaanweg (Gentry, 1980) is temporally anomalous and perhaps based on a later different small kob species. Six or more additional reduncine species have been named in the African time interval 7.0-5.0 Ma (Gentry, 2010, figure 38.11). The most similar one to *K. porrecticornis* is *K. presigmoidalis* Harris, 2003 with a long time range in the Nawata and Nachukui Formations at Lothagam, but it is larger and with incipient lamination of the horn cores (Harris, 2003). *Zephyreduncinus oundagaisus* Vrba and Haile-Selassie, 2006 is a second species in the Adu-Asa Formation and has larger and more compressed horn cores. *Redunca ambae* Haile-Selassie *et al.*, 2009 from low in the Middle Awash Sagantole Formation (5.2 Ma) has larger horn cores with weaker backward curvature. *Kobus subdolosus* Gentry, 1980 at Langebaanweg has

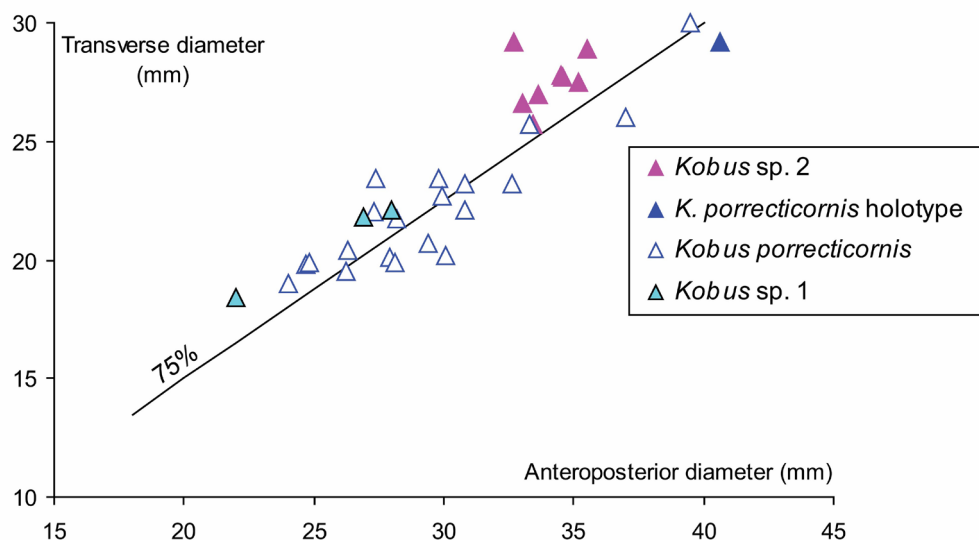


Figure 18. Basal diameters of horn cores of three Middle and Late Miocene Siwalik species of *Kobus*. Measurements are given in Appendix 1. The diagonal line is that along which transverse diameter is 75% of anteroposterior diameter. Horn cores with more transverse compression lie towards the right and base of the diagram.



Figure 19. *Kobus porrecticornis*. Y 51698, left horn core with parts of orbit and frontal in A) anterior and B) lateral views. Y 50864, left horn core in C) anterior and D) lateral views. Y 2541, Left horn core in E) anterior and F) lateral views. Y 49742b, left horn core in G) anterior and H) lateral views. Scale 20 mm.

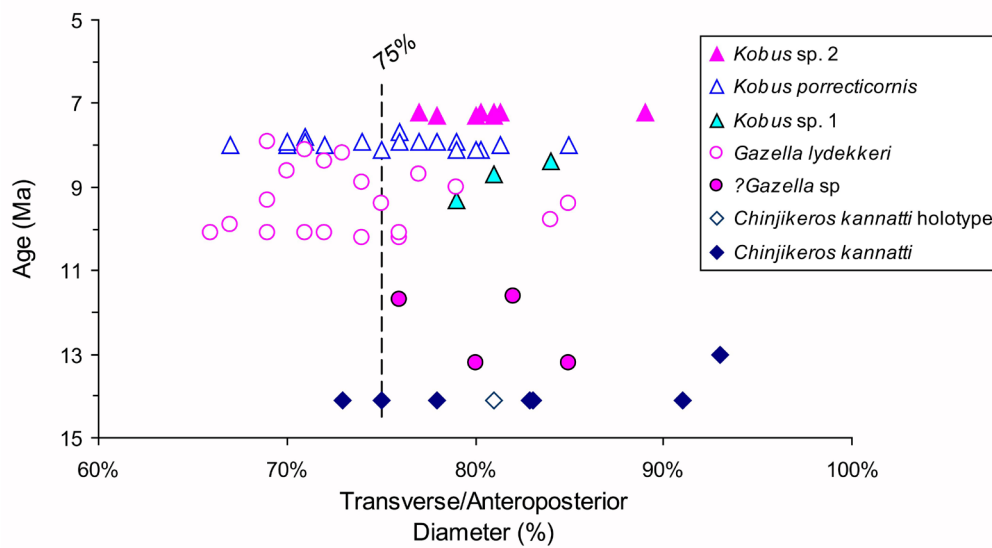


Figure 20. The combined data of Figures 6 and 18, plotted as the ratio of anterior to transverse diameters against age of the specimen (Ma).

larger horn cores that are relatively shorter, probably wider in basal cross section, and without backward curvature, and *Kobus ammophi* Geraads *et al.*, 2009 from Kossom Bougoudi, Chad (~5.5 Ma) is similar and with very advanced teeth. *Menelikia leakeyi* Harris, 1991 at Lothagam (Harris, 2003, figure 11.11) goes back to the Lower Nawata Formation (7.4-6.5 Ma), but has long horn cores with increasing distal divergence. It is evident that there is more morphological diversity and probably speciation in Africa than has come to light in the Siwaliks in the same 2 million year time interval. It may be noted here that the longitudinally-crested basioccipital anterior tuberosities of Pilgrim's *Kobikeryx atavus* in the Siwaliks are similar to those in *Kobus* at Langebaanweg (Gentry, 1980, figures 19, 27 [top right]), but the auditory bulla is not so hugely inflated as in the specimen Gentry (1980, figure 19) assigned to *K. subdolos*. Haile-Selassie *et al.* (2009) describe the basioccipital of their *Redunca ambae*, close in date to Langebaanweg, as not having such splayed anterior tuberosities as some other reduncines, so there may be specific differences among early reduncines in this character.

Kobus sp. 2

Estimated age. 7.4 - (7.2 - 6.6) Ma

Material.

Locality Y 452 (7.3 Ma)

Y 50817 Right M3.

Y 50958 Right horn core with parts of frontal.

Locality Y 581 (7.2 Ma)

Y 16792 Right horn core base.

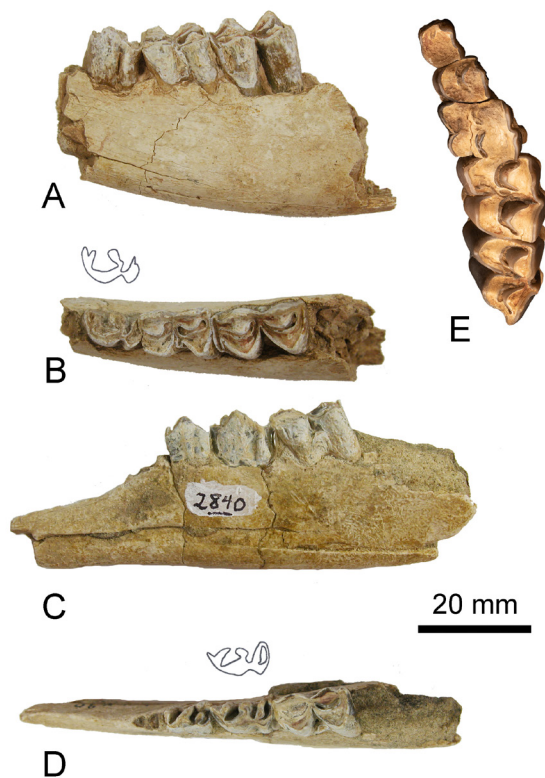


Figure 21. *Kobus porrecticornis*. Y 49550, left p4-m2 in A) buccal and B) occlusal views. Y 2840, left p3-m1 in C) buccal and D) occlusal views, and Y 49740a, left P3-M3 in E) occlusal view. An outline of p4 is shown for Y 49550 and Y 2840. Scale 20 mm.

Y 47018 Left horn core.

Locality Y 922 (7.2 Ma)

Y 50051 Damaged frontlet with bases of both horn cores.

Locality Y 959 (7.2 - 6.6 Ma)

Y 52539 Right p4.

Discussion. This species, if distinct, has a chronostratigraphic range from 7.4 to ca. 6.9 Ma or perhaps slightly younger. In this interval the scarce Siwaliks reduncine teeth are only slightly larger than those of *Kobus porrecticornis* (Figure 4), while the horn cores are larger (Figure 18).

Character variation continues as in *Kobus porrecticornis*. For example the supraorbital pits of Y 50958 are smaller than in a gazelle, transverse ridges were probably present on its front surface, and the horn core was slightly divergent (Figure 22A,B). The frontlet Y 50051 has close insertions (Figure 22C) and Y 16792 (Figure 22D, E) has a spreading base of its pedicel as was seen in early *Kobus* sp.1 horn cores. Limited sinuses just above the orbit at the lowermost front of the pedicel are visible in Y 47018 and degree of divergence lessens distally (Figure 22F). As far as teeth go the upper molar Y 50817 has a localised rib on the wall of the paracone and a slight outbowing on the metacone behind it, no basal pillar, and a central fossette less pointed lingually in its centre and with more of a U-shape than a V. The first and last characters give it a decidedly reduncine

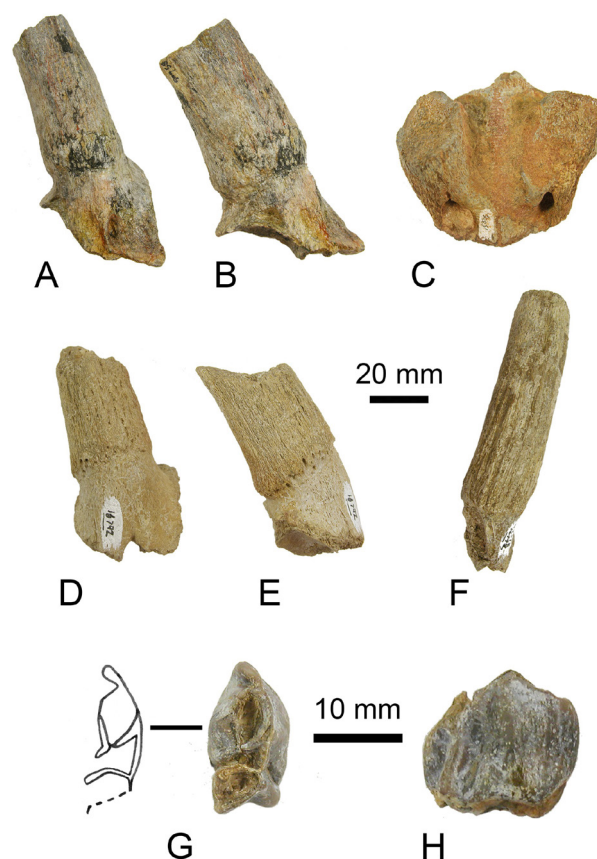


Figure 22. *Kobus* sp. 2. Y 50958, right horn core with parts of orbit and frontal in A) anterior and B) lateral views. Y 50051, frontlet with damaged bases of both horn cores in C) dorsal view. Y 16792, right horn core base in D) anterior and E) lateral views. Y 47018, left horn core in F) anterior view. Y 52539, right p4 in G) occlusal and H) labial views. An outline of is shown for the p4. Scales: 20 mm. for the horncores, 10 mm for the premolar.

appearance. The p4 of Y 52539 (Figure 22G, H) has a closed anterolingual wall like some later Reduncini in Africa, for example Hadar Formation AL156-1A (Gentry 1981, figure 1), but the closure is complete in early wear in the Siwaliks tooth. The deep valley labially in front of the hypoconid is also decidedly reduncine-like.

?Antilopinae, spp.

A number of unidentified teeth of gazelle size or smaller occur in the Late Miocene and apparently record the presence of at least one additional species of antilopine. They fail to fit the known *Gazella* or *Kobus* species or even the scarce teeth discussed under *Tethytragus* and *Caprotragoides*. All occur later than supposed examples of the boselaphine *Elachistoceras* in the Middle and earlier Late Miocene. These include the following:

Y 190a,b from Locality Y 17 (8.0 Ma) (Figure 23A-D). Right m2 and right m3. Their size appears to be a slightly better fit for *Gazella lydekkeri* than *Kobus porrecticornis*, but the m3 looks like that of an African neotragine with rather sharply pointed stylids and labial lobes. It would be interesting if this antelope had a neotragine-like feeding regime since neotragines with such teeth are smaller sized. The m2 has a goat fold, the m3 has a slender little crescentic rear lobe offset labially, and both teeth have a small-moderately sized basal pillar.

Y 51726a,b from Locality Y 889 (8.0 Ma) (Figure 23E-H). Right m2 and m3. The m2 may be a different individual from the m3. The tiny basal pillars are unlike Y 190 and there are good reduncine-like goat folds. It is not a gazelle and is too small for the contemporaneous *Kobus porrecticornis*.

Y 52501 from Locality Y 456 (7.4 - 7.0 Ma). A right mandible with m1 – broken m3 with no central fossettes on m1 or front part of m2. It has curved not flat lingual walls, moderate-large sized basal pillars, and central fossettes with some curvature. The last character may be a consequence of the dentition being in late wear. This is not a neotragine-like morphology, so it would not be conspecific with Y190 above. It is too small to fit *Gazella lydekkeri*.

Y 49797 from Locality Y 913 (6.4 Ma). A right lower molar (probably m1) in a shallow mandible fragment. Too small to be *Kobus* at such a late date and the mandible is too shallow to fit *Gazella*.

And Y 49801 also from Locality Y 913 (6.4 Ma). A right lower molar in a mandible fragment.

Tribe ANTILOPINI or CAPRINI

Genus *TETHYTRAGUS* Azanza and Morales, 1994

Type species. *Tethytragus langai* Azanza and Morales, 1994.

Diagnosis. Medium-sized bovid with horn cores inserted partly on the orbit and partly on the cranial vault, fairly vertical in lateral view and divergent in frontal view. The horn cores are long and stylized, with a very compressed oval section in the transverse direction and regularly curved towards the rear. There may be a slight torsion whose orientation varies according to the species. The ornamentation of furrows and folds is strong without development of keels. Dentition of primitive morphology very close to that of *Eotragus* but the cheek teeth are more hypsodont and on the molars the styles and stylids are less developed. (Diagnosis from Azanza and Morales, 1994, with the original in French.)

Remarks. *Tethytragus* is a Middle or Middle-Late Miocene

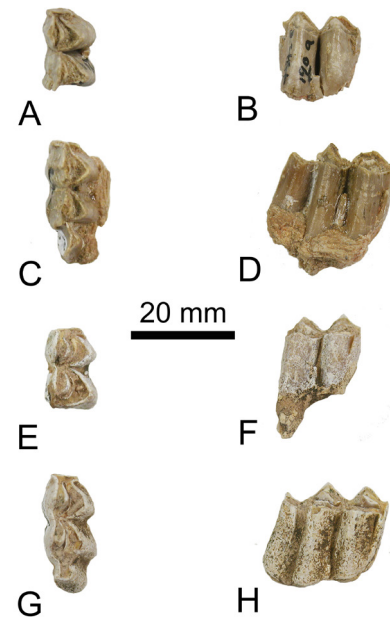


Figure 23. ?Antilopinae, spp. Y 190a,b, (A,B) right m2 and (C,D) m3 in occlusal and labial views; Y 51726a,b, (E,F) right m2 and (G,H) m3 in occlusal and labial views. Scale 20 mm.

bovid of Europe and Turkey, known from about 15.0 Ma onwards. It contains three species larger than gazelles but resembling them in its basic morphology with the horn cores somewhat compressed, curved backwards, without keels, and inserted closer together than in *Eotragus*. Sometimes there are sinuses in the frontals. Supraorbital foramina are small and placed up against the base of the horn pedicels. The teeth are little different from *Eotragus* but the molars are longer relative to the premolars (Gentry, 1990, figure 6) at least in some species. *Tethytragus* is not known to be related to any later antelopes, but could be a suitable ancestor or relative of later Caprini such as *Protoryx*. It has been confused in the past with the Late Miocene *Caprotragoides* in India and the Middle and Late Miocene *Gentrytragus* in Africa.

Tethytragus sp.

Estimated age. 13.4? - 12.4 Ma

Material.

- Locality Y 828 (13.4 Ma)
- Y 40731 Right m3, tiny basal pillar.
- Y 40733 Left lower molar.
- Y 46611 Part of left mandible with p4 and alveoli of p2 and p3.
- Locality Y 822 (13.0 Ma)
- Y 40920 Left horn core.
- Locality Y 825 (12.8 Ma)
- Y 40970 Left horn core.
- Locality Y 750 (12.7 Ma)
- Y 39223 Right p4.
- Locality Y 783 (12.7 Ma)
- Y 32887a Right piece of horn core.
- Y 32887b Left piece of horn core.
- Locality Y 634 (12.3 Ma)
- Y 20006 Right m3.

Locality Y 647 (12.4 Ma)

Y 23600 Horn core piece

Y 23601 Right horn core.

Y 23968 Right horn core piece.

Discussion. The horn cores (Figure 24) are backwardly curved, more compressed than in the *Tethyragus* species of Spain and Turkey, with a central anteroposterior level of maximum transverse thickness, the lateral surface probably flatter than the medial one, without keels or transverse ridges, inserted above the orbits, moderately inclined, insertions close together, poorly divergent, pedicel higher at the front than at the back, an extensive but shallow postcornual fossa, frontals not raised between the horn bases, sinuses in frontals anteromedially to supraorbital pits but probably not within the pedicels and certainly not reaching to top of pedicels, small supraorbital pits. The horn cores were probably not short. The more doubtfully attributed horn core Y 23600 shows possible incipient torsion or bracing at one side of its base.

A few dental remains (Figure 25) could be conspecific with the horn cores, but there is no association. If correctly identified they extend the stratigraphic range of the species slightly from 13.4 to 12.3 Ma.

The various teeth (Figure 25) look slightly divergent from the similar-sized Boselaphini of the period but it is hard to pinpoint what produces this visual impression. They are too large for *Chinjikeros kanatti* and, while their size is suitable for *Hypsodontus sokolovi*, the mandibular ramus of one of them, Y 46611, is too shallow (Figure 25J). The unworn m3 Y 40731 (Figure 25F) has a hypsodonty index of at least 84%. The p4 of Y 46611 has a primitively simple transverse ridge of the metaconid (Figure 25I). The m3 Y 20006 shows slight or moderate outbowings of its lingual ribs, long and narrowly-pointed labial lobes, a small basal pillar, an incipient goat fold, and all four lobes narrowly joined in the centre of tooth. A molar (Y 40733) (Figure 25C, D) from the same locality as Y 40731 and Y 46611 has a goat fold, moderate basal pillar, outbowed ribs on its lingual wall, and pointed labial lobes, but is large compared to the m3s.

An unworn left m3 (Y 40732) from locality Y 828 has no basal pillar. It is probably too large for this species and is certainly large for its age (13.4 Ma), being near the size of Y 40967, a mandible with teeth in late wear that might belong to *Helicoportax praecox* (Gentry *et al.*, 2026).

Tethyragus is a genus of much taxonomic and zoogeographical interest. Essentially it consists of early Eurasian antelopes larger than *Gazella* that had acquired backwardly-curved horn cores unlike *Eotragus*. The Siwaliks remains reported here have a date probably within the span of *T. langai* and *T. stehlini* in Spain and central Europe (MN7/8). The Turkish *T. koehlerae* is best known from the earlier Paşalar and Çandır (MN 5 or 6) localities (Köhler, 1987; Gentry, 1990) and, more disturbingly, from Sivas in MN11 or 12 (the *Tethyragus* cf. *T. koehlerae* of Bibi and Güleç, 2008). The Siwaliks p4s discussed here are within the size range of *T. langai* and *T. koehlerae* and the lower molars within the size range of *T. langai* which seems to have larger measurements for these teeth (Gentry, 1990, figure 6; Azanza and Morales, 1994, table 4). An advanced condition of p4 in which the metaconid approaches the paraconid on its lingual side (the “molarisation” of many authors) is seen in *T. koehlerae* from Çandır (Geraads, 2003, p. 189, figure 9) but not in *T. koehlerae* from Paşalar, nor in *T. langai*, nor in our p4 Y 46611. The teeth of *T. stehlini* are not known. It should be noted that *T. langai*

differs from *T. koehlerae* and what is known of *T. stehlini* in having a hint of clockwise (homonymous or inverse) torsion in its horn cores, lower horn pedicels especially anteriorly, and larger supraorbital pits, suggesting that *Tethyragus* may have a connection with the mainly Turolian genus *Oioceros* (Azanza *et al.*, 1998).

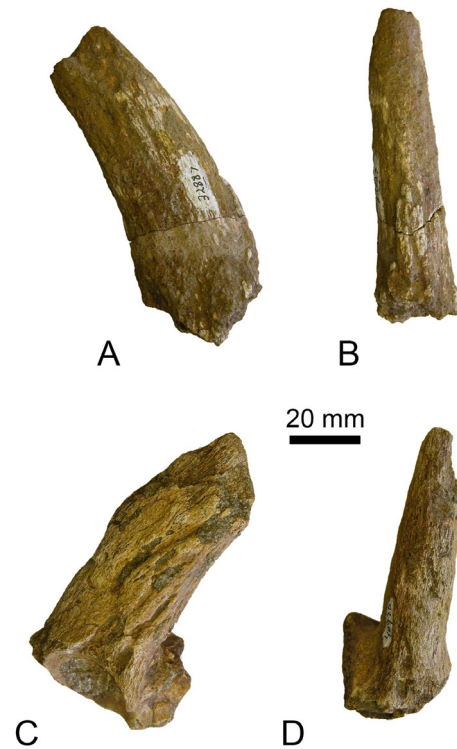


Figure 24. *Tethyragus* sp. Y 32887, right horn core in A) lateral and B) anterior views. Y 40970, left horn core in C) lateral and D) anterior views. Scale 20 mm.

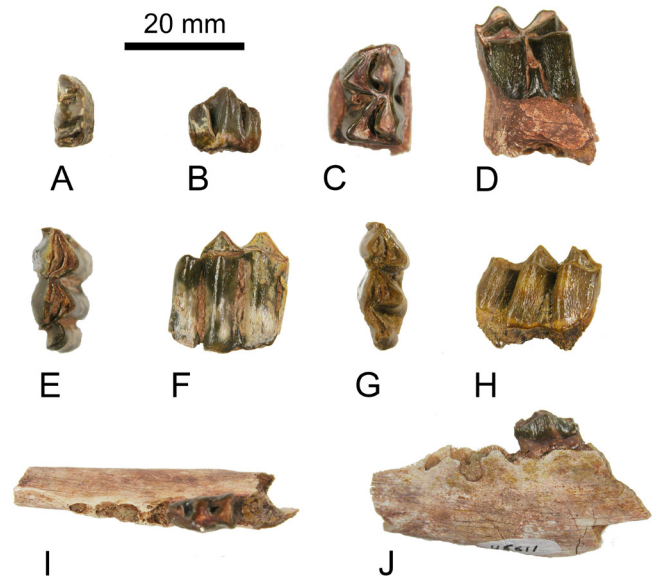


Figure 25. *Tethyragus* sp. Y 39223 right p4 in A) occlusal and B) lingual views. Y 40733 left molar in C) occlusal and D) labial views. Y 40731 right m3 in E) occlusal and F) labial views. Y 20006 right m3 in G) occlusal and H) labial views. Y 46611 left mandible with crown of p4 in I) occlusal and J) labial views. Scale 20 mm.

Protoryx enanus from the Turkish MN7/8 localities of Catakbağyaka and Sofça is a species with possible links to *Tethytragus*. It has horn cores larger than *Tethytragus* but smaller than all other *Protoryx* (Köhler, 1987, figure 50), while the absence of sinuses in the horn pedicels raises additional doubts about its generic attribution. Interestingly *Protoryx enanus* postdates the Paşalar and Çandır *T. koehlerae* in Turkey, but is contemporaneous with other *Tethytragus* in Europe. All this makes a complicated context in which the Siwaliks horn cores and teeth may play a part.

Genus *CAPROTRAGOIDES* Thenius, 1979

Type species. *Caprotragoides potwaricus* (Pilgrim, 1939)

Hippotraginae gen. indet. (cf. *Tragoreas*) *potwaricus* Pilgrim, 1939

Diagnosis. Medium to large sized antelopes. Horn cores implanted fairly vertically on the frontal plane, regularly curved backwards and presenting a moderate divergence; their insertion is close, the pedicle is elongated at the front. No torsion or keel. The section of the horn core is elliptical with variable, but generally quite marked mediolateral compression. The craniofacial angle is moderate. The preorbital fossae are very developed. Orbital rims quite developed. The small supraorbital foramina, are located at the base of the pedicle. Postcornual grooves are absent. The nuchal crests are very developed. (Modified from the emended diagnosis of Thomas [1984] with the original in French.)

Remarks. *Caprotragoides* was founded by Thenius (1979) for the species “Hippotraginae gen.indet. (cf. *Tragoreas*) *potwaricus*,” which Pilgrim (1939) based on a frontlet GSI B630. The holotype frontlet was said to have been found “on the road from Chinji to Nagri” (Pilgrim, 1939, p. 87) and therefore thought to have come from the Nagri Formation, making it between 11.3 and 10 Ma. It is quite large for its age. Thomas (1984, plate 1 figure 6) located another (?left) horn core, AMNH 96648, from Ramnagar, India. He thought that the locality might be within the time span of the Chinji Formation, but the horn core was probably collected by the joint American Museum of Natural History-Yale University-Geological Survey of India expedition of 1935 for which locality data is unreliable. Recent biostratigraphic correlations (Sehgal *et al.*, 2022) suggest the Ramnagar sediments are equivalent in age to the middle and upper part of the Chinji Formation, that is ca. 13 to 11.4 Ma.

Gentry (1970) referred material from Fort Ternan to the Indian species, including some notably hypsodont teeth, and in 1978 described a skull from the Ngorora Formation, Kenya. He rejected a hippotragine affiliation and suggested congeneric status with some Middle Miocene European horn cores named *Gazella stehlini* by Thenius (1951). Thenius’ species therefore could not be a gazelle and was eventually put into a new genus *Caprotragoides* alongside the Indian and Kenyan species by Thenius (1979). However, abundant teeth of *Caprotragoides stehlini* at Paşalar turned out to have a generalised rather primitive morphology at odds with the large and hypsodont teeth at Fort Ternan (Gentry 1990). The situation was remedied when Azanza and Morales (1994) separated a new European and Turkish genus, *Tethytragus*, from Indian *Caprotragoides* and from a new African genus, *Gentrytragus*. We may note that neither *Caprotragoides* nor *Gentrytragus* need be related to *Tethytragus*, that teeth of *Caprotragoides* are still unknown (Pilgrim records that parts of two left maxillae from two individual antelopes, both with heavily worn teeth,

were found with the holotype), and that no definite fossils of *Caprotragoides* have come to light in our material.

?*Caprotragoides*, sp. indet.

Estimated age. 10.2 - 8.6 Ma

Material.

Locality Y 450 (10.2 Ma)

Y 16900 Left horn core and pedicel.

Locality Y 258 (10.2 Ma)

Y 46515 Left upper molar.

Locality Y 325 (8.8 Ma)

Y 12367 Left m3 in mandible fragment.

Locality Y 388 (8.7 Ma)

Y 14860 Left mandible with back of m2 and most of m3.

Locality Y 156 (8.6 Ma)

Y 3411 Left mandible with m2 and partial erupting m3.

Discussion. These fossils are more than 2.0 myr later than *Tethytragus* sp. The horn core Y 16900 (Figure 26A, B) is preserved for about half of its original length and is essentially that of a large gazelle, but too large to fit the *Gazella lydekkeri* from Locality Y 450. It tapers little and in life it would have been long (ca. 200 mm). The level of maximum transverse thickness lies posteriorly, there are no keels or transverse ridges but the surface is covered with irregular longitudinal grooves and ridges. The basal compression at 73% changes to 61% at a height of 50 mm above the base, and both sides are flattened, the lateral more so than the medial. The horn core appears to have slight and constant divergence. It is inserted above the orbits, backwardly curved, without torsion or with only the slightest heteronymous torsion. There are no sinuses at the base of the pedicel, the pedicel is short with a pronounced overhanging rim of the horn core above, and the frontals between the horn bases are not higher than the dorsal

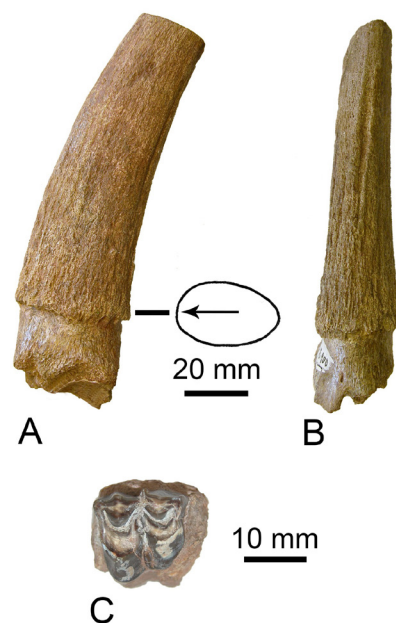


Figure 26. ?*Caprotragoides*, sp. indet. Y 16900, left horn core with cross section at base in A) lateral and B) anterior views. Arrow indicates anterior of the cross section. Scale 20 mm. Y 46515, left upper molar in C) occlusal view. Scale 10 mm.

orbital rims. None of these characters seem as if they would be unacceptable in *Caprotragoides* or *Gentrytragus*.

The upper molar Y 46515 (Figure 26C) is only very tentatively identified as this species. It appears large for a gazelle at this early date. It is brachyodont, has a small or tiny basal pillar, a well-outbowed paracone labial wall, and a poorly convex metacone one. The slightly smaller posterior part and absence of a interdental wear facet suggest it may be an M3. It could be grouped with the horn core Y 16900 to indicate a minimum number of species.

The mandibles, which are also only very tentatively included, are younger in the sequence than Y 46515 or the teeth mentioned under *Tethytragus* sp. and could be *Caprotragoides*. If so, they would extend *Caprotragoides*' range to 8.6 Ma. The m3 of Y 12367 shows broad outbowings of lingual walls, it has a tiny basal pillar, and the small third lobe is offset labialwards and has a central fossette. The measurable m2 and m3 are no longer than in the Siwaliks *Gazella* or *Kobus*.

It is not inconceivable that the horn core Y 16900 is conspecific with *Caprotragoides potwaricus*, but all four dental specimens seem rather small compared to the horn core. The basal diameters (34.2×25.0 mm) of the horn core are very close to those of AMNH 96648 at 35.1×24.8 mm and smaller than the *C. potwaricus* holotype measured by Thomas (1984) as 39.5×31.0 mm and by Pilgrim (1939) as 41×30.5 mm. The *Gazella lydekkeri* horn cores Y 18026 and Y 6563, dated at 10.2 and 10.1 Ma, were large members of that species, but smaller than Y 16900 and their identification need not be doubted for the moment. Other bovids at Locality Y450 are the first representatives in our collections of *Selenoportax*, *Miotragocerus*, and *Gazella lydekkeri*.

Genus *DORCADORYX* Teilhard de Chardin and Trassaert, 1938

Type species. *Dorcadoryx triquetricornis*, Teilhard de Chardin and Trassaert, 1938, figures 33-6, plate 1 figures 3-4.

Diagnosis. A small antelope, with skull as in *Gazella*, but with closely set triangular horn-cores, the anterior edges of which converge anteriorly. Horizontal ramus of the mandible very deep posteriorly. Molars as in *Gazella*, but premolars strongly reduced. Lower p4 of the complicated type. Fossa lachrymalis wide and deep. (From the original diagnosis of Teilhard de Chardin and Trassaert, 1938.)

To this we would add that the horn cores in frontal view diverge very slightly, the divergence being constant, while the long axis of the horn core cross-section is at an approximately 35 degree angle to the skull mid-line. In lateral view the horn cores are steeply inclined and only very slightly curved backwards. Distally there are weak anterior and posterior keels, while the pedicel is tall, at a more upright angle than the horn core itself, and slightly swollen with a small sinus that does not reach into the base of the horncore. The horn cores have barely observable clockwise torsion, and their surface is covered with irregular, faint longitudinal gooves and ridges. Lower p4 has fused paraconid and metaconid forming a closed anterolingual wall. Chen (2005) has presented a longer list of characteristics that focus on the skull and dentition.

Discussion. Several species of *Dorcadoryx* are known from China in various locations thought to date from the Late Miocene to Early Pliocene, around 8 or 7 to 4 Ma. The type species was described from the Yushe Basin and comes from the early Pliocene Nanzhuangou fauna (Qiu *et al.*, 2013, figure 1.7c; Wang *et al.*, 2013, figure 1.2f).

Some aspects of the nomenclature and morphological limits of *Dorcadoryx* are unclear. In founding the genus Teilhard de Chardin and Trassaert (1938) synonymised the first of two “*Tragoreas* sp.” of Bohlin (1935, figures 84-5) with their new type species *D. triquetricornis*. They did not mention two other already-named species which Bohlin had assigned to *Tragoreas* and which by their own implication should belong to *Dorcadoryx*, namely *Tragoreas lagrelii* Bohlin, 1935 and the larger *Gazella palaeosinensis* Schlosser, 1903. Schlosser's species was defined on teeth. Despite their larger size than the teeth of other *Dorcadoryx*, the referred horn core of this latter species (Bohlin, 1935, figure 83) is seemingly no bigger in its basal diameters than are *D. triquetricornis* or *lagrelii*. However the horn core of the second “*Tragoreas* sp.” of Bohlin (1935, figure 86) is slightly bigger than other *Dorcadoryx*. More difficulties arose in separating *Dorcadoryx* teeth from those of *Gazella altidens* Schlosser, 1903. Only the lower teeth of *G. altidens* were thought by Bohlin (1935) to belong to a gazelle. He placed the upper teeth in *D. lagrelii* and his final opinion (Bohlin, 1941, p.107) was that these upper teeth should carry the name *altidens*. He did not acknowledge or realise that this would make *Dorcadoryx altidens* a senior synonym of *D. lagrelii*; on the other hand he had not designated a single specimen as lectotype, so we are not bound to follow his proposal. Many years later a new *Dorcadoryx*, *D. orientalis*, was described from the Bahe Formation by Chen (2005), the earliest species of the genus and dated to 8.07 Ma (Zhang *et al.*, 2013). Its horn cores are longer and with stronger backward curvature than *D. triquetricornis*. Kostopoulos (2009a) has suggested sinking *Dorcadoryx* in *Tragoreas* and *lagrelii* in *triquetricornis*. We continue to place both species in *Dorcadoryx* and to ignore the complication with *G. altidens*.

Within all these constraints *Dorcadoryx* species appear to be slightly larger than most Late Miocene gazelles and some characters differ or may be more frequently present than in *Gazella*: anterior and posterior keels distally on the horn cores, a barely perceptible clockwise (homonymous) torsion, the front of the pedicel high in profile and looking more upright than the front of the base of the horn core proper, notably small supraorbital pits, and a shorter cranium with its curving roof sloping more strongly downwards posteriorly. The teeth are those of generalised non-boselaphine bovids and much like those of gazelles. However the p4s show approach or fusion of paraconid and metaconid to form a closed lingual wall in the anterior part of the teeth.

?*Dorcadoryx* sp.

Estimated age. 9.7 - 9.4 Ma

Material.

Locality Y 337 (9.7 Ma)

Y 5983 Horn core piece.

Y 5990 Frontlet with horn cores.

Locality Y 425 (9.7 Ma)

Y 15143 Left horn core base.

Y 49607 (?Right) horn core base, perhaps the same individual as Y 15143

Locality Y 342 (9.4 Ma)

Y 5916 Right horn core base.

Discussion. The main piece is the frontlet Y 5990 (Figure 27) dating from 9.7 Ma. Its two main distinctive features are the tall front edge of the pedicel and the oblique seating of the

long axis of the cross-section of the horn cores which results in an inward tilt or strong basal convergence of the horn cores similar to extant African *Madoqua* and also seen in the *Gazella* at Langebaanweg. This frontlet is not another specimen of the *?(Sivaceros) vedicus* of a similar age in that it differs from Y 46349 in the less rapid tapering of its longer horn cores, keels present only distally, less compression (close to that of the *S. vedicus* holotype), no flattening of the medial surface, and no sinuses visible in the back of pedicels or in the frontals behind the orbits. The frontals are no higher than the dorsal part of the orbital rims, whereas *?(S.) vedicus* may have had a low intercornual ridge. The divergence of the horn cores is slight, as in *?(S.) vedicus*, but note that the two sides of the frontlet have been glued together. Compared with the horn core Y 16900 of *?Caprotragoides*, sp. indet. (Figure 26), Y 5990 is smaller, the maximum transverse thickness of the base of the horn core lies less posteriorly, and the anterior edge of the horn pedicel is high.

The height of the anterior edge of the horn pedicel resembles *Dorcadoryx triquetricornis* as do other characters, many of which are shared with other bovids and not distinctive for *Dorcadoryx*. However, the horn cores are longer, there is no anterior keel in the proximal part of the horn core, the horn cores are set at a lower inclination with only very slight backward curvature, and the supraorbital pits are long, quite deep and not especially narrow. The cranial roof is not preserved on Y 5990, so its curvature and slope are unknown.

Y 5916 is about 80 mm long and the break at its lower end appears to be across the top of the pedicel. If this were so, there would be no sinuses reaching the top of the pedicel. The maximum mediolateral width on this horn core lies slightly posterior to the centre of the anteroposterior diameter, an anterior keel was probably present distally, the lateral surface is flatter than the medial one, the divergence is nearly constant, and there is only the slightest backward curvature. There is a small sinus low in the pedicel of Y 49607.

In summary these fossils do not fit *?(Sivaceros) vedicus* which already carries more than enough uncertainty about its relationships. They share little with *Dorcadoryx* other than its size and non-boselaphine aspect.

Tribe CAPRINI Gray, 1821

The Caprini, formerly the subfamily Caprinae, contains nearly all Eurasian bovids that are neither Boselaphini or their relatives nor Antilopini or Reduncini. They are a coherent group zoogeographically and taxonomically, and their lowly hierarchical position in cladistic classifications does not mean that they are less dominant in Eurasia than are three or four bovid tribes together in Africa. They are often larger than Antilopini and living species show frontals raised between horn insertions and with extensive sinuses internally, cranial roofs angled downwards on the line of the facial axis, high-crowned cheek teeth with an uncomplicated occlusal pattern and no basal pillars, p4s often with paraconid-metacnid fusion to form a closed lingual wall anteriorly, and sometimes shortened metapodials. Many Late Miocene Eurasian bovids were acquiring characters of the various later Caprini (Gentry, 2000) and even of goats (in subtribe Caprina in Hassanin *et al.*, 2012; see Table 4). Much parallel evolution seems to have occurred and the ancestries of living species may be separate well back into the Miocene. Frequent differences from Boselaphini are more upright horn core insertions in side view, infraorbital foramen higher above the tooth row, median indentation at the back of the palate situated more anteriorly relative to the level of the paired lateral indentations, inclined cranial roofs, simple occlusal pattern of the teeth, and a tendency to shorten the premolar rows anteriorly.

The three fossil genera *Palaeoryx*, *Protoryx* and *Pachytragus* and other relatives were originally found at the classical Turolian localities of Pikermi, Samos and Maragheh and came to contain many species names. Through much of the 20th century they were taken as Hippotragini, but Gentry (1971, 2000) placed them in the Caprinae (the current Caprini). This has not always been accepted, especially for *Palaeoryx*, but few continue to regard them as Hippotragini. Gentry (1971) thought that *Protoryx* contained only the type species *P. carolinae* at Pikermi. He further thought that fossils from Samos Quarry 5 were an advanced species for which the best available name was *Pachytragus crassicornis* Schlosser, 1904, and that most of the rest of the Samos “*Protoryx*” was a second less advanced species, best named *Pachytragus laticeps* Andree, 1926. Robinson (1972) described the first-known pre-Turolian member of the group in the Beglia Formation, Tunisia, and Solounias (1981) contributed further to the ongoing discussion. Following the recovery of new Samos material from 1993 onwards, Kostopoulos (2009a) proposed another round of far-reaching and complicated name changes (Table 6). He thought that in addition to the Pikermi *Protoryx carolinae* there was another species of *Protoryx*, found only on Samos and represented only by three specimens from the old collections: (1) the lectotype frontlet of *Pachytragus crassicornis* (Schlosser, 1904, plate 11 figures 11a+b); (2) the lectotype skull of *Pseudotragus capricornis* Schlosser (1904, plate 10 figs 7-7b); (3) the holotype skull of *Pseudotragus longicornis* Andree 1926. For these three specimens he used the name *Protoryx capricornis* (Schlosser 1904). The first two are type species of their genera so the names *Pachytragus* and *Pseudotragus*, both of Schlosser (1904), become junior synonyms of *Protoryx*. Since Kostopoulos concluded that *Protoryx* could not include any other Samos species, he founded a new genus, *Skoufotragus*, to solve the problem.

At the end of March 2012 AWG was in Munich and able to see once more the type specimens of *Pseudotragus capricornis* Schlosser (1904, plate 10 figures 7-7b) and *Pachytragus crassicornis* Schlosser (1904, plate 11 figures 11a-b) and,



Figure 27. *?Dorcadoryx* sp. Y 5990. Frontlet in A) anterior and B) right lateral views. Scale 20 mm.

Table 6. *Protoryx* group species at Samos.

Kostopoulos (2009a) scheme	Former taxonomy
<i>Protoryx capricornis</i> (Schlosser, 1904) MN11, ~7.8-7.4 Ma (Kostopoulos 2009a, fig.14, but his text, p. 376, is doubtful about provenance of the three specimens.)	<i>Pseudotragus capricornis</i> Schlosser, 1904 pl.10 figs. 7-7b. <i>Pachytragus crassicornis</i> Schlosser, 1904 pl.11 figs. 11a+b. <i>Pseudotragus longicornis</i> Andree, 1926 pl.10 figs. 2-3.
<i>Skoufotragus zemalisorum</i> n.sp. Earlier MN12, ~7.4-7.2 Ma (Horn cores overlap and smaller than in <i>schlosseri</i> .)	
<i>Skoufotragus laticeps</i> (Andree, 1926) Later MN12, ~7.2-7.0 Ma	<i>Pachytragus laticeps</i>
<i>Skoufotragus schlosseri</i> (Andree, 1926) MN12 or 13, ~7.0-6.8 Ma	<i>Pachytragus crassicornis</i> excluding lectotype

contra to the opinion of Kostopoulos (2009a), thought they could not be conspecific. *Pseudotragus capricornis* differs from *Pachytragus crassicornis* by its horn cores being more compressed mediolaterally, a character clearly linked with their enlarged anteroposterior diameter basally. Its appearance is of a smaller species with relatively larger horn cores. The horn cores are also more backwardly curved and the supraorbital foramina are less close together and not in pits. In this paper we shall assign the single Siwalik fossil to the name *Protoryx*.

Genus *PROTORYX* Major, 1891

Type species. *Protoryx carolinae* Major, 1891, as argued by Pilgrim and Hopwood 1928.

Diagnosis. Moderate sized (moderate to large for their period), skull proportions high and narrow rather than low and wide, horn cores somewhat compressed mediolaterally, with a tendency to a flattened lateral surface, inserted fairly close together, with little divergence, inserted fairly uprightly, curved backwards, with no torsion, cranial roof angled appreciably downwards, and with higher frontals between the horn bases than in the smaller Middle Miocene *Tethytragus*. Teeth often mesodont or hypsodont.

This diagnosis lists some of the more obvious characters of the western Turolian species hitherto included in *Protoryx* and *Pachytragus*.

Species *Protoryx* aff. *solignaci* (Robinson, 1972)

Pachytragus solignaci Robinson, 1972, figures 1-5, 7. Beglia Formation, Bled Douarah, Tunisia. (?Middle) – Late Miocene.

Protoryx solignaci Gentry, 2000.

Holotype. T. 3657: A female skull with braincase and horn bases, from Loc. 20. It is presumably conserved in the Service Géologique Tunisien, in Tunis, Tunisia.

Diagnosis. Combines strongly compressed horn cores having a strong anterior keel with primitive teeth. The cranial roof is more inclined than in Boselaphini, the frontals and pedicels are pneumatized. Compared with *Pachytragus laticeps* there is less demarcation between pedicel and horn core; there is a

small to moderate, rather shallow and tall postcornual fossa; the midfrontals are slightly less elevated; the braincase widens posteriorly; and the occiput is flatter. Adapted from Gentry (2000).

Estimated age. 11.3 Ma

Material.

Locality Y 803 (11.3 Ma)

Y 32090 Damaged cranium with partial right horn core base.

Discussion. This is a unique and totally new find in the Siwaliks (Figure 28). It comes from a level with few fossils, but just before the inferred time of the first appearance in the Siwaliks of hipparionine equids (Barry *et al.*, 2002: date adjusted for Gradstein *et al.*, 2012 timescale). The specimen is similar in size to other *Protoryx*, and in the horn cores the level of maximum transverse thickness lies centrally rather than posteriorly, there is very strong lateromedial compression (57.0×29.0 mm = 51%), the lateral surface is flatter than the medial, divergence was probably not strong, and insertions were close together. Massive sinuses within the frontals reach into the pedicels, the frontals between the horn core insertions are slightly elevated, and the supraorbital pits are small and narrow. The braincase roof is inclined downwards, there are concave depressions in the surface of the frontals posteromedially to the horncore insertions, the frontals-parietal suture takes a transverse course across the top of the skull, the temporal lines become close as they approach the occiput, and the braincase widens posteriorly. There is damage along the right side of the braincase which results in the cranium looking longer and narrower in dorsal view than it would have been in life. The nuchal crests have a smooth upwardly-convex outline, the occipital faces backwards but does nevertheless possess a central vertical line or ridge with insignificant flanking shallow depressions at its top, the anterior tuberosities of the basioccipital are not large and probably had no longitudinal ridges behind them, and there may have been a central longitudinal groove on the basioccipital. It is unfortunate that details of the length, curvature and divergence of the horn cores remain unknown.

Abundant remains of what Robinson (1972) named *Pachytragus solignaci* came from early Late Miocene beds in

Tunisia in levels alongside and apparently below hipparionine horses. Similar remains were found later in equivalent time levels in Turkey and less certainly in the Namurungule Formation, Kenya (Nakaya *et al.*, 1984, plate 9 figure 4; Köhler, 1987). Gentry (2000) came to think that *P. solignaci* was too different from the advanced Samos *Pachytragus crassicornis* (*Skoufotragus schlosseri* of Kostopoulos's system) to be congeneric and assigned it to *Protoryx*. Kostopoulos (2009a) did not mention how *P. solignaci* should be classified. Y 32090 has several features of *P. solignaci*: strong compression of the horn cores, a weaker distinction between the top of the pedicel and the horncore base, little elevation of the midfrontals between the horn bases, the braincase widening posteriorly, and a rather flat occipital surface. The horn core compression exceeds that seen in *P. solignaci*; otherwise these characters are plausibly primitive.

The Locality Y803 cranium may be less advanced than a *Protoryx* cranium from Mahmutgazi, Turkey (MN11, Köhler, 1987, figures 55-6), in the lower inclination of its cranial roof and its anteriorly narrower basioccipital. It has more compressed horn cores and a more sloping cranial roof than a *Protoryx* cranium from Kohfidisch (Vislobokova, 2007, plate 14 figure 1), but is similar in little elevation of the frontals between the horn core bases. It is unlike Samos *Pachytragus*

(or *Skoufotragus* or *Protoryx*) *laticeps* in its slightly smaller and more strongly compressed horn cores, little elevated frontals between the horn bases and in its flatter occipital surface which doesn't face partly laterally on each side. It contrasts with a cranium of *Olonbulukia tsaidamensis* from Qaidam or Chaidamu, China (Bohlin, 1937, plate 2 figures 10-11, plate 3 figure 1) by its slightly more advanced appearance. This is manifest in the horn cores looking more massive relative to overall cranial size and less widely set apart, and in the cranial roof showing no posterior downturn in profile. (A similar downturn is also visible in the Kohfidisch cranium mentioned above.) Wang *et al.* (2011) demonstrate from archives that this particular cranium (no.356) dates, most interestingly, from the Middle Miocene, but *Olonbulukia* may extend into the early Late Miocene as in the Tuosu Mammal Fauna (Woodburne *et al.*, 2013). Perhaps *Olonbulukia* is closer taxonomically to *Tethytragus* than to *Protoryx*; certainly Chen and Zhang (2007) stressed its distance from *Protoryx*. Wang, *et al.* (2018) have suggested that the Caprini may have originated on the north of the Tibetan Plateau and subsequently dispersed in the early Late Miocene.

Y 32090 is not so large, robustly-built, nor heavily-horned as the *Protoryx* and *Prosinotragus* skulls described by Bohlin (1935) from loc 116 of the Chinese Baode fauna late in the Late

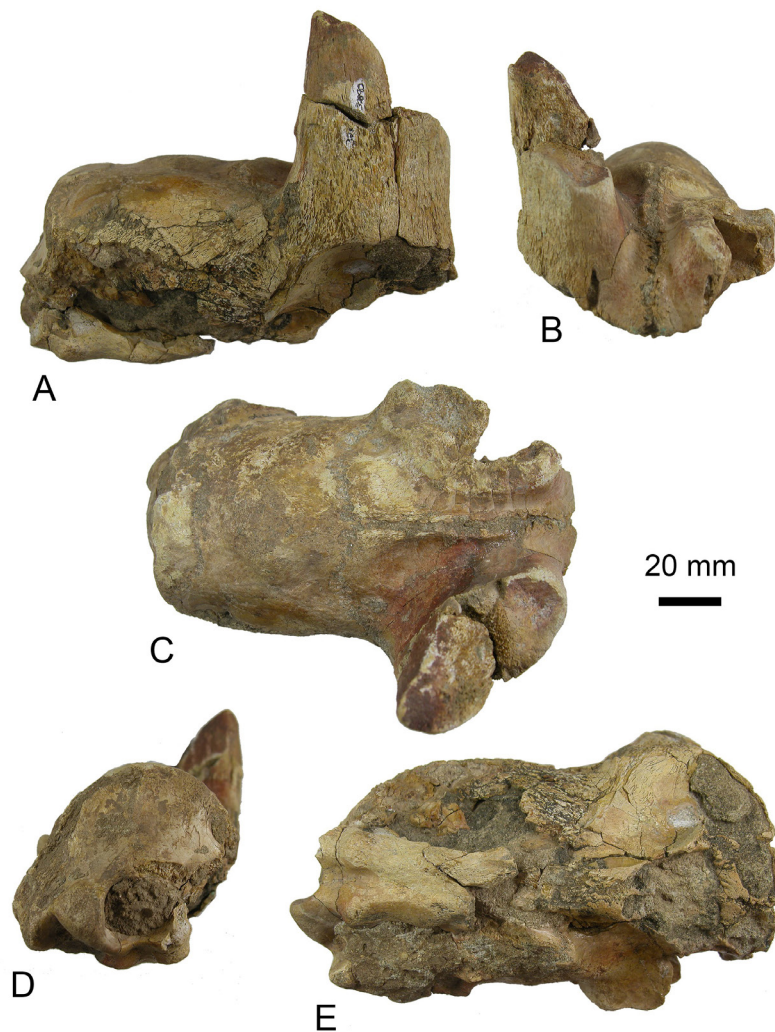


Figure 28. *Protoryx* aff. *solignaci* Y 32090. Cranium in A) right lateral, B) anterior, C) dorsal, D) posterior, and E) ventral views. Scale 20 mm.

Miocene. Two of the species of this group were placed in a new genus *Macrotragus* by Chen and Zhang (2007).

Remarks. One of the most valuable features of Y 32090 is that its age is known. At 11.3 Ma it lived during the Middle to Late Miocene transition and pre-dated the appearance of hipparionine horses in the Siwaliks. This befits its better agreement with the earlier *Protoryx solignaci* than with Turolian species. The most reasonable verdict is to see it as a more easterly representative of a group of transitional Middle-Late Miocene Caprini which had become closer to *Pachytragus/Skoufotragus* than to earlier and smaller *Tethytragus*-like forms. We can add to what Kostopoulos has called “the endless discussion” of these antelopes by speculating that if the lectotype skull of *Pseudotragus capricornis* Schlosser 1904 were a late survivor into early Samos horizons of the *Protoryx solignaci* group, then this would have contributed much to the taxonomic confusion with the later *Pachytragus/Skoufotragus* group in MN12 at Samos and Maragheh.

CONCLUSIONS

While Bovinae dominate the Miocene Siwalik bovid assemblages (Table 5 and Gentry *et al.*, 2025), other bovid groups were present as well with their number of species increasing in the Late Miocene. Here we recognize 15 antilopine species (or probable species) from the Miocene deposits of Pakistan, belonging to three tribes. Two species are new, with both belonging to new genera, while only five of the others have previously been named. The remaining ones are known from cranial material that allows us to distinguish them from other Siwalik antilopines, but in most instances we think they belong to already named taxa from other geographic regions. One (*?Protragelaphus* sp.) probably belongs to a unnamed species, but because the available material is inadequate for defining a new species, we refrain from naming it at this time.

Much of the interest in Siwalik antilopines lies in their bearing on the origins of the tribes Antilopini, Reduncini, and Caprini. *Chinjikeros kanatti* is the earliest likely member of the Antilopinae, but it is not clearly an Antilopini. By about 13.2 Ma a probable species of *Gazella* appears, a genus within the Antilopini and thus marking the definite appearance of that tribe in the Siwaliks. Then, around the start of the Late Miocene (ca. 10.2 Ma) *G. lydekkeri* appears and remains until at least 7.9 Ma as one of the most commonly fossilised Siwaliks species alongside the boselaphines. Beginning with *?Protragelaphus* sp. (10.8 Ma) a succession of somewhat larger Antilopini with heteronymously spiralling horn cores appear, overlapping and exceeding the size of contemporaneous gazelles. Five species are now known, all rare and known only from horn cores.

While too little is known of these Siwalik spiral-horned antilopines for us to judge how they relate to non-Siwalik species, they clearly establish zoogeographic links with the western faunas of Turolian age. The origin of *Antilope* probably lies within *Prostrepsiceros*, and eventually we might be able to see an early Siwalik *Prostrepsiceros* as marking the appearance of *Antilope* in the subcontinent.

Fossil Reduncini have long been known in the Siwaliks from the Dhok Pathan Formation of the Hasnot area and possibly earlier (Pilgrim, 1939). The GSP/Harvard collection now shows that a small reduncine species or succession of species occurred by at least 8.7 and possibly by around 9.4 Ma. With the appearance of *Kobus porrecticornis* at about 8.1 Ma the relative abundance of reduncine remains begins

to predominate over gazelles. *Kobus porrecticornis* then joins *Miotragocerus punjabicus* as the two commonest bovids in their time range, just as *Gazella lydekkeri* had been with *M. pilgrimi*. An ecological linkage between the species change overs for the two lineages might be investigated further with a related ongoing question concerning the taxonomic position of Reduncini relative to Antilopini (Bibi, 2014). Another question with zoogeographical implications concerns how many subgroups of “Reduncini” we might be dealing with and what are the phylogenetic connections between African reduncines (truly Reduncini since they include *Redunca*), the Siwaliks Miocene ones, and the reduncines of the Pinjor Formation with their relatively strong temporal ridges? The current information about African reduncines suggests a first appearance of around 7.0 Ma and possibly earlier (Bibi *et al.*, 2009; Gentry, 2010).

Neither Hippotragini nor Alcelaphini have been found in the Miocene of the Siwaliks although very full information is available on African Hippotragini at ca. 7.0 Ma (Geraads *et al.*, 2008) and African alcelaphine teeth of a similar date have been identified (Thomas, 1980). It also remains to be seen how the Pinjor hippotragines, again with relatively strong temporal ridges, have evolved from other hippotragines.

Fossils of Caprini are extremely rare in the Siwaliks Miocene. Three temporally well-spaced species (*Tethytragus* sp. spanning 13.4 to 12.4 Ma, *?Caprotragoides*, sp. indet. at 10.2 to possibly 8.6 Ma, and *?Dorcadoryx* sp. spanning 9.7 to 9.4 Ma) could belong to either Antilopini or Caprini, but their more precise affinities remain unknown. The unique *Protoryx* cranium dates from 11.3 Ma, just before the appearance of hipparionine horses in the Siwaliks, and agrees best with *P. solignaci* found in transitional Middle to Late Miocene beds of Tunisia and Turkey. The relationships of this species with Turolian *Protoryx*, *Pachytragus*, or *Skoufotragus* in the west, and the relationships of Caprini with Alcelaphini, have yet to be decided.

Table 5 lists all the bovid species we have recognized in the Miocene Siwaliks. In addition to the antilopines, these include: 4 hypsodontines, an indetermined bovid, 17 boselaphines, and 3 possible stem-Bovini (not counting the nominal *Pachyportax latidens*) (Gentry *et al.*, 2026). The oldest of these, *Paleohypodontus zinensis*, is Oligocene in its first occurrence and several species date from the Early Miocene. It is not, however, until just before 14 Ma that bovids become both abundant and diverse in the Siwaliks of the Subcontinent, which is in large part the result of changes in the depositional settings (Barry *et al.*, 2002; Behrensmeyer *et al.*, 2005).

The bovid faunas of the Siwaliks have long lasting stability with occasional substitution of species. The changes that occur are not closely coordinated across the six lineages (Table 5), or at least, if the changes were coordinated, they are not reflected in coinciding morphological changes in separate lineages. Starting at 14.1 Ma there are three well-differentiated boselaphines and one antelopine, a pattern that persists and is reflected in the relative abundance of the species, with boselaphines predominating well into the Late Miocene. In addition, throughout the sequence there are species with very short durations and species with longer durations (Table 5), so that there is a mix of both boselaphines and antilopines having both long and short durations from the Middle through the Late Miocene.

In the Middle Miocene the taxonomic affinities of the species are not decipherable with any confidence, but with the appearance in the Late Miocene of spiral-horned antilopines and species of the *Miotragocerus/Tragoportax* complex there

are then interesting similarities and differences from species in western Eurasia.

The distal width of the astragalus provides a measure of size that allows comparison of multiple, morphologically different species. Figure 29 shows the width of the distal astragalus plotted against age for 26 antelopines and 531 presumed boselaphines. The 26 antelopines belong to *Gazella lydekkeri*, species of *Kobus*, and what is labelled “Small spp. complex,” namely individuals that could be either *Chinjikeros kanatti* or *Gazella* sp. Astragali of the larger spiral-horned antelopines and Caprini have yet to be recognized, although some of the specimens listed as boselaphines may belong to these species instead.

Apart from the poorly fossiliferous intervals, a notable feature on Figure 29 is the size gap between the smallest boselaphine, *Elachistoceras khauristanensis*, and the larger boselaphines; a gap that forms as early as 13 Ma and widens in the Late Miocene. Initially it is filled by antelopines of the “small spp. complex” and eventually by *Gazella* and *Kobus* and possibly some of the larger species for which we have no size data (principally *Prostrepsiceros vinayaki*, *?Prostrepsiceros* large sp., *Nisidorcus planicornis*, and *?Dorcadoryx* sp.).

A second notable feature is the pattern of size among Antelopines on Figure 29. Just as with the boselaphines (Gentry *et al.*, 2026), there is a steady increase over time in size of the larger species, first seen with the appearance of *Kobus* at the beginning of the Late Miocene and continuing with the subsequent appearance of larger *Kobus* species. Since the species of *Gazella* remain much the same size this eventually produces an increase in the range of sizes that is asymmetrical with expansion to the right. The interaction between the antelopines and boselaphines, assuming there was an interaction, should be of future research interest.

Finally, the most conspicuous feature of Figure 29 is the size increase over time, with ever larger species appearing. This is in accord with “Cope’s Rule,” the general observation that body size tends to increase in lineages over time (Stanley, 1973). The question is of course why and the answer in the case of the bovids is undoubtedly related to environmental and vegetative changes and shifting diet and predation (Badgley *et*

al., 2008; Bibi, 2007a,b; Cerling *et al.*, 2025; Gentry *et al.*, 2025). It is noteworthy, however, that the same data show size increases among Siwalik giraffoids, tragulids, and although the data is more sparse, suids and anthracotheres. The specifics of this should be of future research interest.

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REFERENCES

- Abbas, S. G., Babar, M. A., Khan, M. A., Aftab, K., Riaz, A., Ghaffar, A., and Akhtar, M., 2018. Fossil Bovidae from Late Miocene Dhok Pathan Formation of Siwaliks, Northern Pakistan. *Pakistan Journal of Zoology* 50, 217–218. <http://dx.doi.org/10.17582/journal.pjz/2018.50.1.217.228>
- Agusti, J., Cabrera, L., Garcés, M., Krijgsman, W., Oms, O., and Parés,

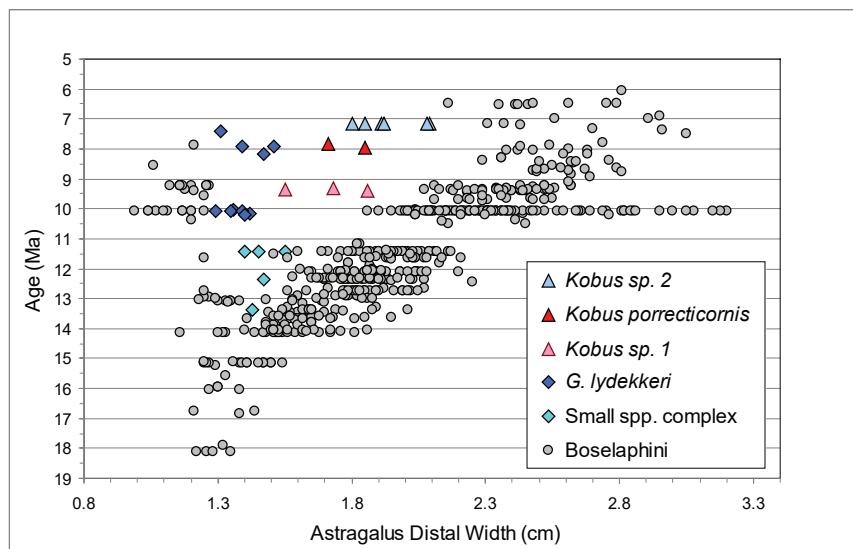


Figure 29. Measurements of the distal width (cm) of the astragalus (data in Appendix 3) plotted against geologic age. Data include 26 antelopines and 531 presumed boselaphines.

- J.M., 2001. A Calibrated Mammal Scale for the Neogene of Western Europe; State of the Art. *Earth-Science Reviews* 52, 247–260. [http://dx.doi.org/10.1016/S0012-8252\(00\)00025-8](http://dx.doi.org/10.1016/S0012-8252(00)00025-8).
- Akhtar, M., 1995. *Pachyporax giganteus*, New Species (Mammalia: Artiodactyla: Bovidae) from the Dhok Pathan, District Chakwal, Punjab, Pakistan. *Pakistan Journal of Zoology* 27, 337–340. <http://dx.doi.org/10.1002/gj.3971/v2/review1>.
- Andree, J., 1926. Neue Cavicornier aus dem Pliocän von Samos. *Palaeontographica* 67, 135–175.
- Arambourg, C., 1941. Antilopes nouvelles du Pléistocène ancien de l'Omo (Abyssinie). *Bulletin du Muséum National d'Histoire Naturelle série 2* 13, 339–347.
- Azanza, B. and Morales, J., 1994. *Tethytragus* nov. gen. et *Gentrytragus* nov. gen. Deux nouveaux Bovidés (Artiodactyla, Mammalia) du Miocène moyen. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen Amsterdam* 97, 249–282.
- Azanza, B., Nieto, M. and Morales, J., 1998. *Samotragus pilgrimi* n. sp., a new species of Oiocerini (Bovidae, Mammalia) from the Middle Miocene of Spain. *Comptes Rendus de l'Académie des Sciences, Sciences de la terre et des planètes Paris* 2, 326, 377–382. [http://dx.doi.org/10.1016/S1251-8050\(98\)80309-1](http://dx.doi.org/10.1016/S1251-8050(98)80309-1).
- Badgley, C., Barry, J.C., Morgan, M.E., Nelson, S.V., Behrensmeyer, A.K., Cerling, T.E., and Pilbeam, D., 2008. Ecological changes in Miocene mammalian record show impact of prolonged climatic forcing. *Proceedings of the National Academy of Science* 105 12145–12149. <https://doi.org/10.1073/pnas.0805592105>.
- Badgley, C., Barry, J., Behrensmeyer, A.K., Cerling, T., Flynn, L.J., Morgan, M.E., and Pilbeam, D., 2025a. Fifty Years in the Foothills: Ecosystem Evolution in the Neogene Siwalik Record of Pakistan. *Annual Review of Earth and Planetary Sciences* 53, 479–509. <https://doi.org/10.1146/annurev-earth-080723-082338>.
- Badgley, C., Morgan, M.E., and Pilbeam, D. 2025b. Preamble to Framing Chapters. In: Badgley, C., Morgan, M.E., and Pilbeam, D. (Eds.), *At the Foot of the Himalayas: Paleontology and Ecosystem Dynamics of the Siwalik Record of Pakistan*. Johns Hopkins University Press, Baltimore, pp. 1–2.
- Bärmann, E.V. and Rössner, G.E., 2011. Dental nomenclature in Ruminantia: Towards a standard terminological framework. *Mammalian Biology* 76, 762–768. <http://dx.doi.org/10.1016/j.mambio.2011.07.002>.
- Bärmann, E.V., Rössner, G.E., and Wörheide, G., 2013. A revised phylogeny of Antilopini (Bovidae, Artiodactyla) using combined mitochondrial and nuclear genes. *Molecular Phylogenetics and Evolution* 67, 484–93. <http://dx.doi.org/10.1016/j.ympev.2013.02.015>.
- Barry, J.C. and Behrensmeyer, A.K., 2025. Documenting the Siwalik fossil record. In: Badgley, C., Morgan, M.E., and Pilbeam, D. (Eds.), *At the Foot of the Himalayas: Paleontology and Ecosystem Dynamics of the Siwalik Record of Pakistan*. Johns Hopkins University Press, Baltimore, pp. 34–53.
- Barry, J.C., Morgan, M.E., Flynn, L.J., Pilbeam, D., Behrensmeyer, A.K., Raza, S.M., Khan, I.A., Badgley, C., Hicks, J., and Kelley, J., 2002. Faunal and environmental change in the late Miocene Siwaliks of northern Pakistan. *Paleobiology Memoirs* 3, 1–71. [Supplement to *Paleobiology* vol.28, No.2] [http://dx.doi.org/10.1666/0094-8373\(2002\)28\[1:faecit\]2.0.co;2](http://dx.doi.org/10.1666/0094-8373(2002)28[1:faecit]2.0.co;2).
- Behrensmeyer, A.K., Badgley, C.E., Barry, J.C., Morgan, M.E., and Raza, S.M., 2005. The paleoenvironmental context of Siwalik Miocene vertebrate localities. In: Lieberman, D.E., Smith, R.J. and Kelley, J. (Eds.), *Interpreting the Past: Essays on Human, Primate, and Mammal Evolution in Honor of David Pilbeam*. Brill, Boston, pp. 47–61. http://dx.doi.org/10.1163/9789047416616_010.
- Behrensmeyer, A.K., Badgley, and Morgan, M.E., 2025. Siwalik Taphonomy: Fossil Assemblage Preservation. In: Badgley, C., Morgan, M.E., and Pilbeam, D. (Eds.), *At the Foot of the Himalayas: Paleontology and Ecosystem Dynamics of the Siwalik Record*. Johns Hopkins University Press, Baltimore, pp. 54–85.
- Behrensmeyer, A.K. and Barry, J.C., 2025. Rocks, Rivers, and Time. In: Badgley, C., Morgan, M.E., and Pilbeam, D. (Eds.), *At the Foot of the Himalayas: Paleontology and Ecosystem Dynamics of the Siwalik Record*. Johns Hopkins University Press, Baltimore, pp. 12–33.
- Bibi, F., 2007a. Origin, paleoecology and paleobiogeography of early Bovini. *Palaeobiogeography, Palaeoclimatology, Palaeoecology* 248, 60–72. <http://dx.doi.org/10.1016/j.palaeo.2006.11.009>.
- Bibi, F., 2007b. Dietary niche partitioning among fossil bovids in late Miocene C3 habitats: Consilience of functional morphology and stable isotope analysis. *Palaeogeography, Palaeoclimatology, Palaeoecology* 253, 529–538. <http://dx.doi.org/10.1016/j.palaeo.2007.06.014>.
- Bibi, F., 2013. A multi-calibrated mitochondrial phylogeny of extant Bovidae (Artiodactyla, Ruminantia) and the importance of the fossil record to systematics. *BMC Evolutionary Biology* 13, 166. <http://dx.doi.org/10.1186/1471-2148-13-166>.
- Bibi, F., 2014. Assembling the ruminant tree: combining morphology, molecules, extant taxa, and fossils. *Zitteliana B* 32, 197–211. <http://dx.doi.org/10.5282/ubm/epub.22396>.
- Bibi, F. and Güleş, E.S., 2008. Bovidae (Mammalia: Artiodactyla) from the Late Miocene of Sivas, Turkey. *Journal of Vertebrate Paleontology* 28, 501–519. [http://dx.doi.org/10.1671/0272-4634\(2008\)28\[501:bmafit\]2.0.co;2](http://dx.doi.org/10.1671/0272-4634(2008)28[501:bmafit]2.0.co;2).
- Bibi, F., Bukhsianidze, M., Gentry, A.W., Geraads, D., Kostopoulos, D.S., and Vrba, E.S., 2009. The fossil record and evolution of Bovidae: state of the field. *Palaeontologia Electronica* 12.3.10A, 1–11. http://palaeo-electronica.org/2009_3/169/index.html.
- Blainville, H.M.D. de 1816. *Prodrome d'une nouvelle distribution systématique du règne animal*. *Bulletin des Sciences, par la Société Philomathique de Paris* 3, 105–124.
- Bohlin, B., 1935. Cavicornier der *Hipparion*-Fauna Nord Chinas. *Palaeontologia Sinica C* 9, 4, 1–166.
- Bohlin, B., 1937. Eine tertiäre Säugetier-Fauna aus Tsaidam. *Palaeontologia Sinica C* 14, 1, 1–111.
- Bohlin, B., 1941. *Gazella (Proteraceros) gaudryi* (Schlosser) and *Gazella dorcadoides* Schlosser. *Bulletin of the Geological Institution of Upsala* 28, 79–122. [Cover of A.W. Gentry's reprint is dated 1939]
- Bohme, M., Spassov, N., Ebner, M., Geraads, D., Hristova, L., Kirscher, U., Kötter, S., Linnemann, U., Prieto, J., Roussiakis, S., Theodorou, G., Uhlig, G., and Winklhofer, M., 2017. Messinian Age and Savannah Environment of the Possible Hominin *Graecopithecus* from Europe. *PLoS ONE*, 12(5). <http://dx.doi.org/10.1371/journal.pone.0177347>.
- Bouvrain G., 1978. *Protragelaphus theodori* n. sp. (Mammalia, Artiodactyla, Bovidae) du Miocène de Macédoine (Grèce). *Géologie Méditerranéenne* 5, 229–236. <http://dx.doi.org/10.3406/geolm.1978.1045>.
- Bouvrain, G., 1979. Au nouveau genre de Bovidé de la fin du Miocène. *Bulletin de la Société Géologique de France ser.7* 21, 507–511. <http://dx.doi.org/10.2113/gssgfbull.s7-xxi.4.507>.
- Bouvrain, G., 1980. Le genre *Palaeoreas* (Mammalia, Artiodactyla, Bovidae), systématique et extension géographique. *Paläontologische Zeitschrift* 54, 55–65. <http://dx.doi.org/10.1007/bf02985883>.
- Bouvrain, G., 1982. Révision du genre *Prostrepsiceros* Major 1891 (Mammalia, Bovidae). *Paläontologische Zeitschrift* 56, 113–124. <http://dx.doi.org/10.1007/bf02988790>.
- Bouvrain, G., 1992. Antilopes à chevilles spiralées du Miocène supérieur de la province gréco-iranienne : nouvelles diagnoses. *Annales de Paléontologie* 78, 49–65.
- Bouvrain G., 1996. Les gazelles du Miocène supérieur de Macédoine, Grèce. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 199, 111–132. <http://dx.doi.org/10.1127/njgpa/199/1996/111>.
- Bouvrain, G., 1997. Les bovidés du Miocène supérieur de Pentalophos (Macédoine, Grèce). *Münchner Geowissenschaftliche Abhandlungen A* 34, 5–22.

- Bouvrain, G. and Bonis, L. de, 1986. *Ouzocerus gracilis* n.g., n.sp., Bovidae (Artiodactyla, Mammalia) du Vallésien (Miocène Supérieur) de Macédoine (Grèce). *Geobios* 19, 661–667. [http://dx.doi.org/10.1016/s0016-6995\(86\)80063-8](http://dx.doi.org/10.1016/s0016-6995(86)80063-8)
- Bouvrain, G. and Bonis, L. de., 2007. Ruminants (Mammalia, Artiodactyla : Tragulidae, Cervidae, Bovidae) des gisements du Miocène supérieur (Turolien) de Dytiko (Grèce). *Annales de Paléontologie* 93, 121–147. <http://dx.doi.org/10.1016/j.annpal.2007.03.001>
- Cerling, T.E., Behrensmeyer, A.K., Barry, J., Nelson, S.V., Morgan, M., and Quade, J., 2025. Stable isotopes as record of ecological change in the Siwalik Group of Pakistan. In: Badgley, C., Morgan, M.E., and Pilbeam, D. (Eds.), *At the Foot of the Himalayas: Paleontology and Ecosystem Dynamics of the Siwalik Record*. Johns Hopkins University Press, Baltimore, pp. 86–96.
- Chen, G., 2005. *Dorcadoryx* Teilhard et Trassaert, 1938 (Bovidae, Artiodactyla) from the Bahe Formation of Lantian, Shaanxi Province, China. *Vertebrata Palasiatica*, 43, 272–282.
- Chen, G. and Zhang, Z., 2007. Restudy of Chinese fossil bovids referred to *Protoryx* (Bovidae, Artiodactyla). *Vertebrata Palasiatica* 45, 2, 98–109.
- Colbert, E.H., 1935a. Distributional and Phylogenetic Studies on Indian Fossil Mammals. I American Museum Collecting Localities in Northern India. *American Museum Novitates* No. 796, 1–20.
- Colbert, E.H., 1935b. Siwalik mammals in the American Museum of Natural History. *Transactions American Philosophical Society* NS 26, 1–401. <http://dx.doi.org/10.2307/1005467>
- Dames, W.B., 1883. Eine neue Antilope aus dem Pliocän von Pikermi in Attika. *Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin* No. 6, 95–97.
- Deino, A., Tauxe, L., Monaghan, M., and Drake, R., 1990. 40^{ar}/39^{ar} Age Calibration of the Litho- and Paleomagnetic Stratigraphies of the Ngorora Formation, Kenya. *The Journal of Geology* 98, 567–587. <http://dx.doi.org/10.1086/629425>
- Draz, O., Ni, X., Samiullah, K., Yasin, R., Fazal, R.M., Naz, S., Akhtar, S., Gillani, M., and Ejaz, M., 2020. New Fossil Remains of Artiodactyla from Dhok Pathan Formation, Middle Siwaliks of Punjab, Pakistan. *Pakistan Journal of Zoology* 52, 1–13. <https://doi.org/10.17582/journal.pjz/20181028131031>
- Draz, O., Samiullah, K., Asrar, M., Rasul, A., Yasin, R. and Khan, L., 2021. Fossils remains of even-toed ungulates from the Middle Siwaliks, Punjab, Pakistan. *Historical Biology* 33, 1888–1897. <https://doi.org/10.1080/08912963.2020.1751836>
- Erdbrink, D.P.B., 1982. A fossil reduncine antelope from the locality K2 east of Maragheh, N. W. Iran. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie* 22 103–112.
- Fortelius, M. and Zhang, Z. (2006). An oasis in the desert? History of endemism and climate in the Late Neogene of North China. *Palaeontographica A* 277, 131–141. <http://dx.doi.org/10.1127/pala/277/2006/131>
- Gabunia L.K., 1973. Fossil vertebrate fauna of Belometscheskaya. *Tibilisi: Metsniereba*, pp.1–136.
- Gatesy, J., Amato, G., Vrba, E., Schaller, G. and DeSalle, R., 1997. A cladistic analysis of mitochondrial ribosomal DNA from the Bovidae. *Molecular Phylogenetics and Evolution* 7, 303–319. <http://dx.doi.org/10.1006/mpev.1997.0402>
- Gaudry, A., 1861. Notes sur les Antilopes trouvées à Pikermi (Grèce). *Bulletin de la Société Géologique de France* 2 18, 388–400.
- Gaudry, A., 1865. *Animaux Fossiles et géologie de l'Attique*. Paris; Librairie de la Société Géologique de France. [The whole work was issued from 1862-1867. According to Pilgrim and Hopwood (1928: 97), pp.241–323 covering ruminants, were published in 1865.]
- Gentry, A.W., 1970. The Bovidae (Mammalia) of the Fort Ternan fossil fauna. In: Leakey, L.S.B. and Savage, R.J.G. (Eds.), *Fossil Vertebrates of Africa*. Academic Press, London, pp. 243–324.
- Gentry, A.W., 1971. The earliest goats and other antelopes from the Samos *Hipparion* fauna. *Bulletin of the British Museum (Natural History) Geology* 20, 229–296.
- Gentry, A.W., 1980. Fossil Bovidae (Mammalia) from Langebaanweg, South Africa. *Annals South African Museum Cape Town* 79, 213–337.
- Gentry, A.W., 1981. Notes on Bovidae (Mammalia) from the Hadar Formation, and from Amado and Geraru, Ethiopia. *Kirtlandia* 33, 1–30.
- Gentry, A.W., 1990. Ruminant artiodactyls of Paşalar, Turkey. *Journal of Human Evolution* 19, 529–550. [http://dx.doi.org/10.1016/0047-2484\(90\)90063-h](http://dx.doi.org/10.1016/0047-2484(90)90063-h)
- Gentry, A.W., 1992. The subfamilies and tribes of the family Bovidae. *Mammal Review* 22, 1–32. <http://dx.doi.org/10.1111/j.1365-2907.1992.tb00116.x>
- Gentry, A.W., 1997. Fossil ruminants (Mammalia) from the Manonga Valley, Tanzania. In: Harrison, T. (Ed.), *Neogene Paleontology of the Manonga valley, Tanzania*. Plenum Press, New York, pp. 107–135. http://dx.doi.org/10.1007/978-1-4757-2683-1_5
- Gentry, A.W., 1999. Fossil pecorans from the Baynunah Formation, Emirate of Abu Dhabi, United Arab Emirates. In: Whybrow, P.J. and Hill, A. (Eds.), *Fossil Vertebrates of Arabia*. Yale University Press, New Haven, pp. 290–316.
- Gentry, A.W., 2000. Caprinae and Hippotragini (Bovidae, Mammalia) in the Upper Miocene. In: Vrba, E.S. and Schaller, G.B. (Eds.), *Antelopes, Deer and Relatives: Fossil Record, Behavioral Ecology, Systematics and Conservation*, Yale University Press, New Haven, pp. 65–83.
- Gentry, A.W., 2003. Ruminantia (Artiodactyla). In: Fortelius, M., Kappelman, J., Sen, S. and Bernor, R.L. (Eds.), *Geology and Paleontology of the Miocene Sinap Formation, Turkey*. Columbia University Press, New York, pp. 332–379.
- Gentry, A.W., 2004. Ruminants of Rudabánya. In: Bernor, R.L., Kordos, L., and Rook, L. (Eds.), *Multidisciplinary Research at Rudabánya, Late Miocene (MN9), Hungary: a Compendium*. *Palaeontographica Italica* 90, pp. 283–302.
- Gentry, A.W., 2008. New records of Bovidae from the Sahabi Formation. *Garyounis Scientific Bulletin, Special Issue No.5* 205–217.
- Gentry, A.W., 2010. Bovidae. In: Werdelin, L. and Sanders, W.J. (Eds.), *Cenozoic Mammals of Africa*. University of California Press, Berkeley, pp. 741–796. <http://dx.doi.org/10.1525/california/9780520257214.003.0038>
- Gentry, A.W. and Gentry, A., 1978. Fossil Bovidae (Mammalia) of Olduvai Gorge, Tanzania, parts I and II. *Bulletin British Museum (Natural History) Geology* 29, 289–446; 30, 1–83.
- Gentry, A.W., Rossner, G.E., and Heizmann, E.P.J., 1999. Suborder Ruminantia. In: Rossner, G.E. and Heissig, K. (Eds.), *The Miocene Land Mammals of Europe*. Verlag Friedrich Pfeil, Munich, pp. 225–258.
- Gentry, A.W., Solounias, N., Barry, J.C., and Raza, S.M., 2025. Siwalik Bovidae. In: Badgley, C., Morgan, M.E., and Pilbeam, D. (Eds.), *At the Foot of the Himalayas: Paleontology and Ecosystem Dynamics of the Siwalik Record of Pakistan*. Johns Hopkins University Press, Baltimore, pp. 368–388.
- Gentry, A.W., Solounias, N., Barry, J.C., and Raza, S.M. 2026. Miocene Bovidae (Mammalia) of the Siwaliks, Part 1: Hypsodontinae and Bovinae. *Palaeovertebrata* 49.1.e1. <http://dx.doi.org/10.18563/pv.49.1.e1>
- Geraads, D., 2003. Ruminants, other than Giraffidae from the middle Miocene hominoid locality of Çandır (Turkey). *Courier Forschungsinstitut Senckenberg Frankfurt-am-Main* 240, 181–199.
- Geraads, D., 2017. A reassessment of the Bovidae (Mammalia) from the Nawata Formation of Lothagam, Kenya, and the Late Miocene Diversification of the Family in Africa. *Journal of Systematic Palaeontology* 17, 2, 169–182. <http://dx.doi.org/10.1080/14772019.2017.1403493>
- Geraads, D., Blondel, C., Likies, A., Mackaye, H.T., Vignaud, P., and Brunet, M., 2008. New Hippotragini (Bovidae, Mammalia) from the Late Miocene of Toros-Menalla (Chad). *Journal of Vertebrate Paleontology* 28, 231–242. <http://dx.doi.org/10.1080/14772019.2017.1403493>

- [org/10.1671/0272-4634\(2008\)28\[231:nhbmft\]2.0.co;2](https://doi.org/10.1671/0272-4634(2008)28[231:nhbmft]2.0.co;2)
- Geraads, D., Blondel, C., Mackaye, H.T., Likius, A., Vignaud, P., and Brunet, M., 2009. Bovidae (Mammalia) from the lower Pliocene of Chad. *Journal of Vertebrate Paleontology* 29, 923–933. [http://dx.doi.org/10.1671/039.029.0311](https://doi.org/10.1671/039.029.0311)
- Geraads, D. and Güleş, E. 1999. On some spiral-horned antelopes (Mammalia: Artiodactyla: Bovidae) from the Late Miocene of Turkey, with remarks on their distribution. *Paläontologische Zeitschrift* 73, 403–409. [http://dx.doi.org/10.1007/bf02988051](https://doi.org/10.1007/bf02988051)
- Gervais, F.L.P., 1848-52. *Zoologie et Paléontologie Françaises*, vol. I. Bertrand, Paris, 271 pp. [That part of this work containing the names *Antelope clavata* and *Gazella deperdita* was published in 1850. The year of publication for the successive parts of this work can be verified from Wagner 1849:3; 1850:9; 1851:9. Wagner, A., 1849, 1850, 1851. Bericht über die Leistungen in der Naturgeschichte der Säugethiere während des Jahres 1848 (1849, 1850). *Archiv für Naturgeschichte*, 15(2), 1-30 (1849); 16(2), 1–42 (1850); 17(2), 1-32 (1851).]
- Gervais, F.L.P. and Serres, M. de., 1847. Sur les Mammifères fossiles des sables marins tertiaires de Montpellier. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences Paris* 24, 799–801.
- Gradstein, F.M., Ogg, J.G., Schmitz, M.D., and Ogg, G.M., 2012. *The Geological Time Scale 2012*. Elsevier, Amsterdam and Oxford. [http://dx.doi.org/10.1016/b978-0-444-59425-9.05001-0](https://doi.org/10.1016/b978-0-444-59425-9.05001-0)
- Gray, J.E., 1821. On the natural arrangement of vertebrate animals. *London Medical Repository* 15, 296-310.
- Groves, C. and Grubb, P., 2011. *Ungulate Taxonomy*. Johns Hopkins University Press, Baltimore, pp. 317. [http://dx.doi.org/10.1644/12-mamm-r-103](https://doi.org/10.1644/12-mamm-r-103)
- Haile-Selassie, Y., Vrba, E.S., and Bibi, F., 2009. Bovidae. In: Haile-Selassie, Y. and Woldegabriel, G. (Eds.), *Ardipithecus kaddaba*: Late Miocene Evidence from the Middle Awash, Ethiopia. University of California Press, Berkeley, pp. 277–330. [http://dx.doi.org/10.1525/9780520942509-013](https://doi.org/10.1525/9780520942509-013)
- Harris, J.M., 1991. Family Bovidae. In: Harris, J.M. (Ed.), *Koobi Fora Research Project, Volume 3, The Fossil Ungulates: Geology, Fossil Artiodactyles, and Palaeoenvironments*. Clarendon Press, Oxford, pp. 139–320. <https://doi.org/10.1093/oso/9780198573999.003.0005>
- Harris, J.M., 2003. Bovidae from the Lothagam succession. In: Leakey, M.G. and Harris, J.M. (Eds.), *Lothagam: the Dawn of Humanity in Eastern Africa*. Columbia University Press, New York, pp. 531–579. [http://dx.doi.org/10.7312/leak11870-022](https://doi.org/10.7312/leak11870-022)
- Hassanin, A., Delsuc, F., Ropiquet, A., Hammer, C., Jansen van Vuuren, B., Matthee, C., Ruiz-Garcia, M., Catzefflis, F., Areskoug, V., Nguyen, T.T. and Couloux, A., 2012. Pattern and timing of diversification of Cetartiodactyla (Mammalia, Laurasiatheria), as revealed by a comprehensive analysis of mitochondrial genomes. *Comptes Rendus Biologies, Paris* 335, 32–50. [http://dx.doi.org/10.1016/j.crv.2011.11.002](https://doi.org/10.1016/j.crv.2011.11.002)
- Heintz, E., 1971. *Gazella deperdita* (Gervais) 1847 (Bovidae, Artiodactyla, Mammalia) du Pontien du Mont Lubéron Vaucluse, France. *Annales de Paléontologie (Vertébrés)* 57, 209–229. [http://dx.doi.org/10.1515/mamm.1969.33.4.626](https://doi.org/10.1515/mamm.1969.33.4.626)
- Hernández Fernández, M. and Vrba, E.S., 2005. A complete estimate of the phylogenetic relationships in Ruminantia: a dated species-level supertree of the extant ruminants. *Biological Reviews* 80, 269–302. [http://dx.doi.org/10.1017/s1464793104006670](https://doi.org/10.1017/s1464793104006670)
- Hill, A., Drake, R., Tauxe, L., Monaghan, M., Barry, J.C., Behrensmeyer, A.K., Curtis, G., Fine-Jacobs, B., Jacobs, L., Johnson, N., and Pilbeam, D., 1985. Neogene Palaeontology and Geochronology of the Baringo Basin, Kenya. *Journal of Human Evolution* 14, 759–773. [https://doi.org/10.1016/s0047-2484\(85\)80058-0](https://doi.org/10.1016/s0047-2484(85)80058-0)
- Hooijer, D.A., 1946. Notes on some Pontian mammals from Sicily, figured by Seguenza. *Archives Néerlandaises de Zoologie* 7, 301–333. [http://dx.doi.org/10.1163/187530146x00113](https://doi.org/10.1163/187530146x00113)
- Hussain, S.T., van den Bergh, G.D., Steensma, K.J., de Visser, J.A., de Vos, J., Arif, M., van Dam, J., Sondaar, P.Y., and Malik, S.B., 1992. Biostratigraphy of the Plio-Pleistocene Continental Sediments (Upper Siwaliks) of the Mangla-Samwal Anticline, Azad Kashmir, Pakistan. *Koninklijke Nederlandse Akademie van Wetenschappen (1)* 95, 65–80.
- Kaakinen, A., Passey, B.H., Zhang, Z., Liu, L., Pesonen, L.J., and Fortelius, M., 2013. Stratigraphy and Paleoeology of the Classical Dragon Bone Localities of Baode County, Shanxi Province. In: Wang, X.-m., Flynn, L.J. and Fortelius, M. (Eds.), *Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology of Asia*. Columbia University Press, New York, pp. 203–217. [http://dx.doi.org/10.7312/columbia/9780231150125.003.0007](https://doi.org/10.7312/columbia/9780231150125.003.0007)
- Kappelman, J., Kelley, J., Pilbeam, D., Sheikh, K.A., Ward, S., Anwar, M., Barry, J., Brown, C., Hake, B.P., Johnson, N.M., Raza, S.M., and Shah, S.M.I., 1991. The earliest occurrence of *Sivapithecus* from the Middle Miocene Chinji Formation of Pakistan. *Journal of Human Evolution* 21, 61–73. [http://dx.doi.org/10.1016/0047-2484\(91\)90036-u](https://doi.org/10.1016/0047-2484(91)90036-u)
- Khan, M.A., Abbas, S.G., Aftab, K., Babar, M.A., Ali, M., Malik, M.F., and Zaman, R., 2024. New fossils of *Tragoportax* and *Gazella* from Padhri, Pakistan, and comments on these genera in the Siwaliks. *Historical Biology* 36, 1180–1187. <https://doi.org/10.1080/08912963.2022.2117041>
- Khan, M.A., Akhtar, M., Babar, M.A., Abbas, S.G., Siddiq, M.K., Nawaz, M.K., Mubashar, M., Yaqoob, H., Nazir, S., Farheen, S., and Draz, O., 2013. Some new remains of Middle Miocene mammals from the Chinji Formation, northern Pakistan. *Pakistan Journal of Zoology Supplementary Series* 12, 1–55. [http://dx.doi.org/10.17582/journal.pjz/2019.51.4.1343.1353](https://doi.org/10.17582/journal.pjz/2019.51.4.1343.1353)
- Khan, M.A., Asim, M., Babar, M.A., Abbas, S.G., Nawaz, M.K., and Ahmad, Q., 2021. New remains of *Gazella* (Bovidae) from Middle Miocene, Pakistan. *Arabian Journal of Geosciences* 14, 1703 (1–8). <https://doi.org/10.1007/s12517-021-07885-8>
- Kingston, J.D., Jacobs, B.F., Hill, A. and Deino, A., 2002. Stratigraphy, age and environments of the late Miocene Mpesida Beds, Tugen Hills, Kenya. *Journal of Human Evolution* 42, 95–116.
- Khomenko J., 1913. La faune méotique du village Taraklia du district de Bendery. *Annuaire géologique et minéralogique de la Russie* 15, 107–143
- Knotnerus-Meyer, T., 1907. Über das Tränenbein der Huftiere. *Archiv für Naturgeschichte* 73, 1, 1–152.
- Köhler, M., 1987. Bovidens des türkischen Miozäns (Känozoikum und Braunkohlen der Türkei 28). *Paleontologia i Evolucio* 21, 133–246.
- Korotkevich, E.L. and Krakhmalnaya, T.V., 1983. Неогеновый Прокобус Западного Причерноморья [Neogene *Procobus* from the Western Black Sea Area.] *Vestnik Zoologii Kiev*, 1983 (5), 27–31. (In Ukrainian with English summary.)
- Kostopoulos, D.S., 2004. Revision of some late Miocene spiral horned antelopes (Bovidae, Mammalia). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 231, 167–190. [http://dx.doi.org/10.1127/njgpa/231/2004/167](https://doi.org/10.1127/njgpa/231/2004/167)
- Kostopoulos, D.S., 2006. The late Miocene vertebrate locality of Perivolaki, Thessaly, Greece. 9. Cervidae and Bovidae. *Palaeontographica A* 276, 151–183. [http://dx.doi.org/10.1127/pala/276/2006/151](https://doi.org/10.1127/pala/276/2006/151)
- Kostopoulos, D.S., 2009a. The Late Miocene mammal faunas of the Mytilinii Basin, Samos Island, Greece: New Collection. 14. Bovidae. *Beiträge zur Paläontologie Wien* 31, 345–389.
- Kostopoulos, D.S., 2009b. Contribution to the systematics and phylogeny of *Prostrepsiceros valesiensis* Bouvain, 1982 (Mammalia, Bovidae). *Geodiversitas* 31 4, 879–891. [http://dx.doi.org/10.5252/g2009n4a879](https://doi.org/10.5252/g2009n4a879)
- Kostopoulos, D.S., 2014. Taxonomic re-assessment and phylogenetic relationships of Miocene homonymously spiral-horned antelopes. *Acta Palaeontologica Polonica* 59, 9–29. [http://dx.doi.org/10.4202/app.2011.0013](https://doi.org/10.4202/app.2011.0013)
- Kostopoulos, D.S., 2016. Palaeontology of the upper Miocene vertebrate localities of Nikiti (Chalkidiki Peninsula, Macedonia, Greece). *Artiodactyla. Geobios* 49 119–134.

- <http://dx.doi.org/10.1016/j.geobios.2016.01.011>
- Kostopoulos, D.S., 2022. The Fossil Record of Bovids (Mammalia: Artiodactyla: Ruminantia: Pecora: Bovidae) in Greece. In: Vlachos, E. (Ed.), Fossil Vertebrates of Greece Vol. 2: Laurasiatherians, Artiodactyles, Perissodactyles, Carnivorans, and Island Endemics. Springer International Publishing AG., Cham, pp. 113–204. http://dx.doi.org/10.1007/978-3-030-68442-6_5
- Kostopoulos, D.S. and Bernor, R.L., 2011. The Maragheh bovids (Mammalia, Artiodactyla): systematic revision and biostratigraphic-zoogeographic interpretation. *Geodiversitas* 33 649–708. <http://dx.doi.org/10.5252/g2011n4a6>
- Kostopoulos, D.S. and Koufos, G.D., 1999. The Bovidae (Mammalia, Artiodactyla) of the «Nikiti-2» [NIK] faunal assemblage (Chalkidiki peninsula, N. Greece). *Annales de Paléontologie* 85, 193–218. [http://dx.doi.org/10.1016/s0753-3969\(99\)80014-7](http://dx.doi.org/10.1016/s0753-3969(99)80014-7)
- Kostopoulos, D.S. and Merceron, G. 2024. On *Procobus* Khomenko, 1913 (Mammalia: Artiodactyla: Bovidae), with new evidence from the Late Miocene of Greece. *Palaeoworld* 33, 1128–1138. <https://doi.org/10.1016/j.palwor.2023.06.008>
- Kostopoulos, D.S., Sevim Erol, A., and Mayda, S., 2023. Late Miocene ‘ovibovin’ bovids (Mammalia, Bovidae) from Çorakyerler, Turkey. *Journal of Vertebrate Paleontology* 43, 1–16. <http://dx.doi.org/10.1080/02724634.2023.2232850>
- Kostopoulos, D.S. and Soubise, J., 2018. *Palaeoreas, Majorea*, and *Stryfnotherium* gen. nov. (Mammalia: Artiodactyla: Bovidae) from the Late Miocene of Greece. *Annales de Paléontologie* 104, 231–247. <http://dx.doi.org/10.1016/j.annpal.2018.04.002>
- Koufos, G.D., Kostopoulos, D.S., and Vlachou, T.D., 2009. The Late Miocene mammal faunas of the Mytilinii Basin, Samos Island, Greece: New Collection, 16 Biochronology. *Beiträge zur Paläontologie Wien* 31, 397–408. <http://dx.doi.org/10.1016/j.geobios.2010.08.004>
- Krakhmalnaya, T.V., 1996. Gipparionovaya fauna drevnego meotisa Severnogo Prichernomor'ya [*Hipparion* fauna of the ancient Meotiss of the northern Black Sea territory]. *Naukova Dumka, Kiev*, 225 pp. (In Russian).
- Kretzoi, M., 1941. Neue Antilopen-Form aus dem Soproner Sarmat. *Földtani Közlöny Budapest* 71, 336–343.
- Kurtén, B., 1952. The Chinese *Hipparion* fauna. *Commentationes Biologicae* 13, 4, 1–82.
- Lehmann, U. and Thomas, H., 1987. Fossil Bovidae from the Miocene of Sahabi, (Libya). In: Boaz, N.T., El-Arnauti, A., Gaziry, A.W., de Heinzelin, J., and Boaz, D.D. (Eds.), *Neogene Paleontology and Geology of Sahabi*. Alan Liss, New York, pp. 323–335. <http://dx.doi.org/10.1038/280137a0>
- Li, C.K. and Chi, T., 1964. Pontian mammals of Wenquan, Sinkiang. *Vertebrata Palasiatica* 8, 288–300.
- Lindsay, E. H., Flynn, L. J., Cheema, I. U., Barry, J. C., Downing, K., Rajpar, A. R., and Raza, S.M., 2005. Will Downs and the Zinda Pir Dome. *Palaeontologia Electronica* 8.1.19A, 1–18. http://palaeo-electronica.org/2005_1/lindsay19/issue1_05.htm
- Lindsay, E.H. and Flynn, L.J., 2016 Late Oligocene and Early Miocene Muroidea of the Zinda Pir Dome. *Historical Biology* 28, 1–2, 215–236. <http://dx.doi.org/10.1080/08912963.2015.1027888>
- Linnaeus, C., 1758. *Systema naturae per regna naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Editio decima reformata*, Laurentii Salvii, Stockholm, 824 pp. <http://dx.doi.org/10.5962/bhl.title.156772>
- Lungu, A.N., 1979. Antelopes of the Hipparion fauna from the middle Sarmatian of Moldavia. In: Lungu, A.N. (Ed.), *Biostratigraphical Study of the Mesozoic and Cenozoic Deposits of the Southern Borders of the Russian Platform*. Shtiintsa, Kiev, Ukraine. (In Russian), pp. 50–80.
- Lydekker, R., 1878. Crania of ruminants from the Indian Tertiaries. *Memoirs of the Geological Survey of India, Palaeontologia Indica* (10), 1, 3, 88–171.
- Lydekker, R., 1885. Catalogue of the fossil Mammalia in the British Museum (Natural History), part II. London: British Museum (Natural History), 324 pp. <http://dx.doi.org/10.5962/bhl.title.30728>
- Lydekker, R., 1886. Siwalik Mammalia – supplement I. *Memoirs of the Geological Survey of India, Palaeontologia Indica* (10), 4, 1, 1–21.
- Major, C.I.F., 1891. Considérations nouvelles sur la Faune des Vertébrés du Miocène supérieur dans l'Île de Samos. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences Paris* 113, 608–610.
- Marcot, J.D., 2007. Molecular phylogeny of terrestrial artiodactyls. In: Prothero, D.R. and Foss, S.E. (Eds.), *The Evolution of Artiodactyls*. Johns Hopkins Press, Baltimore, pp. 4–18.
- Matthee, C.A. and Davis, S.K., 2001. Molecular insights into the evolution of the family Bovidae: a nuclear DNA perspective. *Molecular Biology and Evolution* 18, 1220–1230. <http://dx.doi.org/10.1093/oxfordjournals.molbev.a003908>
- Mein, P., 1999. European Miocene Mammal Biochronology. In: Rössner, G.E. and Heissig, K. (Eds.), *The Miocene Land Mammals of Europe*. Verlag Friedrich Pfeil, Munich, pp. 25–38.
- Mein, P. and Ginsburg, L., 1997. Les mammifères du gisement miocène inférieur de Li Mae Long, Thaïlande : systématique, biostratigraphie et paléoenvironnement. *Geodiversitas* 18, 783–844.
- Métais, G., Antoine, P.-O., Marivaux, L., Welcomme, J.-L. and Ducrocq, S., 2003. New artiodactyl ruminant mammal from the late Oligocene of Pakistan. *Acta Palaeontologica Polonica*, 48, 375–382.
- Morales, J., Soria, D., Pickford, M. and Nieto, M., 2003. A new genus and species of Bovidae (Artiodactyla, Mammalia) from the early Middle Miocene of Arrisdrift, Namibia, and the origins of the family Bovidae. *Memoirs Geological Survey of Namibia* 19, 371–384.
- Nakaya, H., M. Pickford, Y. Nakano and H. Ishida., 1984. The late Miocene large mammal fauna from the Namurungule Formation, Samburu Hills, northern Kenya. *African Study Monographs Kyoto Supplementary Issue* 2, 87–131. <https://doi.org/10.14989/68313>
- Naz, S., Sultana, T., Sultana, S., Yasin, R., and Samiullah, K., 2024. New fossil remains of Bovids from the Middle Siwaliks of Punjab, Pakistan. *Historical Biology* 37, 264–281. <https://doi.org/10.1080/08912963.2023.2300639>
- Ogilby, W.E., 1833. Characters of a new species of antelope (*Antelope ellipsiprymnus*), from the collection of Mr. Steedman. *Proceedings of the Zoological Society of London Part 1*, 47–48.
- Pallas, P.S., 1766. *Miscellanea zoologica, quibus novae imprimis atque obscurae animalium species describuntur et observationibus iconibusque illustrantur* (The Hague).
- Pilgrim, G.E., 1910. Notices of new mammalian genera and species from the Tertiaries of India. *Records Geological Survey of India* 40, 63–71.
- Pilgrim, G.E., 1926. On the names and types of certain Pontian antelopes. *Annals and Magazine of Natural History London* (9) 18, 464. [Note that the plate and figure citations in Andree 1926 for *Gazella mytilinii* are given correctly in this publication but wrongly in the more widely used Pilgrim and Hopwood 1928.] <http://dx.doi.org/10.1080/00222932608633542>
- Pilgrim, G.E., 1937. Siwalik antelopes and oxen in the American Museum of Natural History. *Bulletin American Museum of Natural History* 72, 729–874.
- Pilgrim, G.E., 1939. The fossil Bovidae of India. *Memoirs of the Geological Survey of India, Palaeontologia Indica* NS 26, 1–356.
- Pilgrim, G.E. and Hopwood, A.T., 1928. Catalogue of the Pontian Bovidae of Europe. *British Museum (Natural History)*, London, 106 pp. <http://dx.doi.org/10.5962/bhl.title.118786>
- Rafeh, A., Ahmad, R.M., Iqbal, A., and Khan, M.A., 2018. Description of *Gazella* sp. from the Middle Miocene Siwaliks of Punjab, Pakistan. *Punjab University Journal of Zoology* 33, 127–131. <http://dx.doi.org/10.17582/journal.pujz/2018.33.2.127.131>

- Roussiakis, S.J., 2009. *Prostrepsiceros* and *Protragelaphus* (Artiodactyla, Mammalia) from the Late Miocene locality of Chomateri (Attica, Greece). *Annales de Paléontologie* 95, 181–195. <http://dx.doi.org/10.1016/j.annpal.2009.09.002>
- Qiu, Z.-x., Qiu, Z.-d., Deng, T., Li, C.-k., Zhang, Z.-q., Wang, B.-y. and Wang, X., 2013. Neogene Land Mammal Stages/Ages of China. In: Wang, X.-m., Flynn, L.J. and Fortelius, M. (Eds.), *Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology of Asia*. Columbia University Press, New York, pp. 29–90. <http://dx.doi.org/10.7312/columbia/9780231150125.003.0001>
- Raza, S.M., Cheema, I.U., Downs, W.R., Rajpar, A.R. and Ward, S.C., 2002. Miocene stratigraphy and mammal fauna from the Sulaiman Range, Southwestern Himalayas, Pakistan. *Palaeobiogeography, Palaeoclimatology, Palaeoecology* 186, 185–197. [http://dx.doi.org/10.1016/S0031-0182\(02\)00443-1](http://dx.doi.org/10.1016/S0031-0182(02)00443-1)
- Roberts, T.J., 1977. *The Mammals of Pakistan*. Ernest Benn Limited, London and Tonbridge. 361 pp.
- Robinson, P., 1972. *Pachytragus solignaci*, a new species of caprine bovid from the late Miocene Beglia Formation of Tunisia. *Notes du Service Géologique de Tunisie* 37, 73–94.
- Rodler, A. and Weithofer, K.A., 1890. Die Wiederkäuer der Fauna von Maragha. *Denkschriften der Kaiserlichen Akademie der Wissenschaften Wien* 57, 753–772.
- Saeed, Z., Khan, A.M., Iqbal, A., and Amin, M., 2018. Some New Remains of *Gazella* (Bovidae) Discovered from the Dhok Pathan Formation of the Siwaliks, Northern Pakistan. *Punjab University Journal of Zoology* 33, 113–119. <https://doi.org/10.17582/pujz/2018.33.2.113.119>
- Samiullah, K., Yasin, R., Bano, N., Rasool, B., Mubarak, M.S., Fazal, R.M., Mahboob, S., Draz, O., Al-Ghanim, K.A., Raza, T., Javed, Z., Al-Misned, F., Nazish, M., and Sarfraz, H., 2020. New artiodactyla fossils from Middle Miocene deposits of Chakwal, Punjab, Pakistan. *Geological Journal* 56, 1109–1129. <https://doi.org/10.1002/gj.39712>
- Schlosser, M., 1903. Die fossilen Säugethiere Chinas nebst einer Odontographie der recenten Antilopen. *Abhandlungen der mathematisch-physikalischen Classe der königlich bayerischen Akademie der Wissenschaften* 22, 1–221.
- Schlosser, M., 1904. Die fossilen Cavicornier von Samos. *Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients* 17, 28–118.
- Sehgal, R.K., Singh, A.P., Gilbert, C.C., Patel, B.A., Campisano, C.J., Selig, K.R., Patnaik, R., and Singh, N.P., 2022. A new genus of treeshrew and other micromammals from the middle Miocene hominoid locality of Ramnagar, Udhampur District, Jammu and Kashmir, India. *Journal of Paleontology* 96, 1318–1335. <https://doi.org/10.1017/jpa.2022.41>
- Smith, A., 1840. *Antelope ellipsiprymnus* Ogilby. *Illustrations of the Zoology of South Africa*, 12' Smith, Elder, and Co., London, pp. 28–29.
- Solounias, N., 1981. The Turolian fauna from the island of Samos, Greece. *Contributions to Vertebrate Evolution* 6, 1–232.
- Solounias, N., Barry, J.C., Bernor, R.L., Lindsay, E.H. and Raza, S.M., 1995. The oldest bovid from the Siwaliks, Pakistan. *Journal of Vertebrate Paleontology* 15, 806–814. <http://dx.doi.org/10.1080/02724634.1995.10011263>
- Stanley, S., 1973. An explanation for Cope's Rule. *Evolution* 27, 1–26. <https://doi.org/10.2307/2407115>
- Steininger, F.F., 1999. Chronostratigraphy, Geochronology and Biochronology of the Miocene "European Land Mammal Mega-Zones" (ELMMZ) and the Miocene "Mammal-Zones (MN-Zones)." In: Rössner, G.E. and Heissig, K. (Eds.) *Miocene Land Mammals of Europe*. F. Pfeil, Munich, pp. 9–24.
- Tauxe, L. and Opdyke, N.D., 1982. A time framework based on magnetostratigraphy for the Siwalik sediments of the Kaur area, northern Pakistan. *Palaeogeography, Palaeoclimatology, Palaeoecology* 37, 43–61. [http://dx.doi.org/10.1016/0031-0182\(82\)90057-8](http://dx.doi.org/10.1016/0031-0182(82)90057-8)
- Tchernov, E., Ginsburg, L., Tassy, P. and Goldsmith, N.F., 1987. Miocene mammals of the Negev (Israel). *Journal of Vertebrate Paleontology* 7, 284–310. <http://dx.doi.org/10.1080/02724634.1987.10011661>
- Teilhard de Chardin, P. and Trassaert, M., 1938. Cavicornia of south-eastern Shansi. *Palaeontologia Sinica* ns C No.6, 1–98.
- Teilhard de Chardin, P. and Young, C.C., 1931. Fossil mammals from the late Cenozoic of northern China. *Palaeontologia Sinica* C 9, 1, 1–66.
- Tekkaya, I., 1969. Kayadibi (Konya) *Bovidae* faunası hakkında ön rapor. *Maden Tetkik Araştırma Enstitüsü Dergisi*, Ankara 73, 155–159. (An English version can be found as: Preliminary Report on the Bovidae Fauna from Kayadibi, Konya. *Bulletin of the Mineral Research and Exploration (MTA Dergisi)* 73, 155–159.)
- Thenius, E., 1951. *Gazella* cf. *deperdita* aus dem mitteleuropäischen Vindobonien und das Auftreten der Hipparionfauna. *Eclogae Geologicae Helvetiae* 44, 381–394.
- Thenius, E., 1979. Zur systematischen Stellung und Verbreitung von «*Gazella*» *stehlini* (Bovidae, Mammalia) aus dem Miozän Europas. *Anzeiger der Oesterreichischen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Klasse Wien* 1, 1–6.
- Theodorou, G.E., Roussiakis, S.J., Athanassiou, A., and Filippidi, A., 2010. Mammalian remains from a new site near the classical locality of Pikermi (Attica, Greece). *Scientific Annals, School of Geology, Aristotle University of Thessaloniki, Proceedings of the XIX CBGA Congress, Thessaloniki, Greece Special Volume* 99, 109–119.
- Thomas, H., 1977. Un nouveau bovid, du Nagri, plateau du Potwar, Pakistan. *Bulletin de la Société Géologique de France* 7, 19(2), 375–383. <http://dx.doi.org/10.2113/gssgfbull.s7-xix.2.375>
- Thomas, H., 1980. Les bovidés miocènes du Miocène supérieur des couches de Mpesida et de la formation de Lukeino (district de Baringo, Kenya). In: Leakey, R.E.F. and Ogot, B.A. (Eds.), *Proceedings of the 8th Pan-African Congress of Prehistory, Nairobi, 1977*. International Louis Leakey Memorial Institute for African Prehistory, Nairobi, pp. 82–91.
- Thomas, H., 1981. Les Bovidés miocènes de la formation de Ngorora du Bassin de Baringo (Kenya). *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen B* 84, 335–409.
- Thomas, H., 1983. Les Bovidae (Artiodactyla, Mammalia) du Miocène moyen de la formation Hofuf (Province du Hasa, Arabie Saoudite). *Palaeovertebrata* 13, 157–206. [https://doi.org/10.1016/S0016-6995\(87\)80080-3](https://doi.org/10.1016/S0016-6995(87)80080-3)
- Thomas, H., 1984. Les Bovidés anté-hipparions des Siwaliks inférieurs (plateau du Potwar, Pakistan). *Mémoires de la Société Géologique de France Paris NS* 145, 1–68. <https://doi.org/10.2113/gssgfbull.s7-xix.2.375>
- Thomas, H., Sen, S., Khan, M., Battail, B., and Ligabue, G., 1982. The lower Miocene fauna of Al-Sarrar (Eastern province, Saudi Arabia). *ATLAL, Journal Saudi Arabian Archaeology Jeddah* 5, 109–136.
- Van Couvering, J.A. and Delson, E. 2020. African Land Mammal Ages. *Journal of Vertebrate Paleontology* 40, 5. <http://dx.doi.org/10.1080/02724634.2020.1803340>
- Van der Made, J. 2012. *Eotragus clavatus* (Artiodactyla, Bovidae, Boselaphini) from Sansan. In: Peigné, S. and Sen, S. (Eds.) *Mammifères de Sansan, Mémoires du Muséum National d'Histoire Naturelle* 203, 145–199.
- Vislobokova, I.A. 2007. New data on Late Miocene mammals of Kohfidisch, Austria. *Paleontological Journal* 41, 451–460. <http://dx.doi.org/10.1134/S0031030107040119>
- Vrba, E.S. and Schaller, G.B., 2000. Phylogeny of Bovidae based on behavior, glands, skulls, and postcrania. In: Vrba, E.S. and Schaller, G.B. (Eds.), *Antelopes, Deer and Relatives: Fossil Record, Behavioral Ecology, Systematics and Conservation*, Yale University Press, New Haven, pp. 203–222.
- Vrba, E.S. and Haile-Selassie, Y., 2006. A new antelope fossil, *Zephyreduncinus oundagaisus* (Reduncini, Artiodactyla, Bovidae), from the Late Miocene of the Middle Awash, Afar Rift, Ethiopia. *Journal of Vertebrate Paleontology* 26, 213–

218. [http://dx.doi.org/10.1671/0272-4634\(2006\)26\[213:anazor\]2.0.co;2](http://dx.doi.org/10.1671/0272-4634(2006)26[213:anazor]2.0.co;2)
- Wagner, A., 1848. Urweltliche Säugethier-Ueberreste aus Griechenland. Abhandlungen der Mathem-physikalischen Classe der Königlich Bayerischen Akademie der Wissenschaften München 5, 333–378.
- Wagner, A., 1857. Neue Beiträge zur Kenntnis der fossilen Säugethier-Ueberreste von Pikermi. Abhandlungen der Königlich Bayerischen Akademie der Wissenschaften 8, 111–158.
- Wang, S.-Q., Yang, Q., Zhao, Y., Li, C.-X., Shi, Q.-Q., Zong, L.-Y., and Ye, J., 2018. New Olonbulukia material and its related assemblage reveal an early radiation of stem Caprini along the north of the Tibetan Plateau. *Journal of Paleontology* 93, 385–397. <http://dx.doi.org/10.1017/jpa.2018.65>
- Wang, X.-M., Xie, G.-P., Li, Q., Qiu, Z.-D., Tseng, Z.J., Takeuchi, G.T., Wang, B.-Y., Fortelius, M., Rosenström-Fortelius, A., Wahlqvist, H., Downs, W.R., Zhang, C.F. and Wang, Y., 2011. Early explorations of Qaidam Basin (Tibetan plateau) by Birger Bohlin – reconciling classic vertebrate fossil localities with modern biostratigraphy. *Vertebrata Palasiatica* 49, 287–310. <http://dx.doi.org/10.7312/wang15012-010>
- Wang, X.-M., Flynn, L.J. and Fortelius, M., 2013. Introduction, Towards a continental Asian biostratigraphic and geochronologic framework. In: Wang, X.-m., Flynn, L.J. and Fortelius, M. (Eds.), *Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology of Asia*. Columbia University Press, New York, pp. 1–25. <http://dx.doi.org/10.7312/wang15012-intro>
- Werdelin, L., 2010. Chronology of Neogene Mammal Localities. In: Werdelin, L. and Sanders, W.J. (Eds.), *Cenozoic Mammals of Africa*. University of California Press, Berkeley, pp. 27–43. <http://dx.doi.org/10.1525/california/9780520257214.003.0003>
- Woodburne, M.O., Tedford, R.H. and Lindsay, E.H., 2013. North China Neogene Biochronology, A Chinese Standard. In: Wang, X.-m., Flynn, L.J. and Fortelius, M. (Eds.), *Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology of Asia*. Columbia University Press, New York, pp. 91–123. <http://dx.doi.org/10.7312/wang15012-002>
- Zhang, Z.-Q., Gentry, A.W., Kaakinen, A., Liu, L.-P., Lunkka, J.P., Qiu, Z.-D., Sen, S., Scott, R.S., Werdelin, L., Zheng, S.-H., and Fortelius, M., 2002. Land mammal faunal sequence of the Late Miocene of China: new evidence from Lantian, Shaanxi Province. *Vertebrata Palasiatica* 40, 3, 166–176.
- Zhang, Z.-Q., Kaakinen, A., Liu, L.-P., Lunkka, J.P., Sen, S., Gose, W.A., Qiu, Z.-D., Zheng, S.-H. and Fortelius, M., 2013. Mammalian chronology of the Late Miocene Bahe Formation. In: Wang, X.-m., Flynn, L.J. and Fortelius, M. (Eds.), *Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology of Asia*. Columbia University Press, New York, pp. 187–202. <http://dx.doi.org/10.7312/columbia/9780231150125.003.0006>