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## Ruminant Fauna from the Tertiary Hills (Neogene) of the Siwaliks of Pakistan

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**Abstract:** The Siwalik formations of northern Pakistan consist of (fluvial) deposits of ancient rivers that were formed from the early Miocene up to the late Pliocene. The tertiary continental deposits of the Siwaliks are highly fossiliferous with a diverse array of terrestrial and freshwater vertebrates in which ruminants are fairly abundant. The rich Siwalik fossil record presents a detailed history of the prehistoric mammals of the Indian Subcontinent. In this research it was analyzed individual well-sampled sites to study the past ruminant community. The Siwalik fossil record becomes increasingly informative for diverse research questions in paleobiology as a result of its growing and robust data set. The fossils from Pakistan may also document the first appearance and subsequent radiation of giraffes and bovids, two groups that dominate the late neogene (tertiary) as well as the modern herbivore faunas. Throughout the Siwalik formations, the ruminants are by far the most abundant mammal group. The number of ruminant species, as recorded in the tertiary hills of the Siwaliks is clearly greater than that observed in most ecosystems today, which probably indicates overall greater species richness than is typically present. Today, the ruminants constitute the largest group of ungulates, with more than 190 species and its distribution is widespread in all continents except Australia and Antarctica.

**Key words:** Ruminants, siwaliks, tertiary (Neogene)

### INTRODUCTION

In the last decade, considerable work has been done on the mammalian fauna of the Siwalik deposits. The Neogene formations of Pakistan contain a diverse assemblage of fossil vertebrates that are the basis of mammalian evolution in southern Asia. Because of the continuous deposition of the Siwalik series rocks of the Potwar Plateau in Pakistan through almost all of the Neogene, Siwaliks (Potwar Plateau) are considered as a critical continent for understanding the origin and early evolutionary history of several higher-level mammalian taxa, including artiodactyls<sup>[1]</sup>. The artiodactyls have long been suspected to hold important clues for reconstructing early phases of their evolutionary history. Ruminant artiodactyls are the most geographically and ecologically successful living group of large mammals (Fig. 1). The suborder Ruminantia is traditionally defined as the artiodactyls that possess a cuboid fused with the navicular and incisiform lower canines. The former character is ambiguous because of its occurrence in the late Eocene ruminant-like genus *Amphimeryx* from Western Europe<sup>[2]</sup>, whereas the second feature is rarely preserved in fossils of primitive ruminants.

Pecora (horned ruminants) and Tragulina-Pecora are today considered as the most diversified ruminants. Fossil

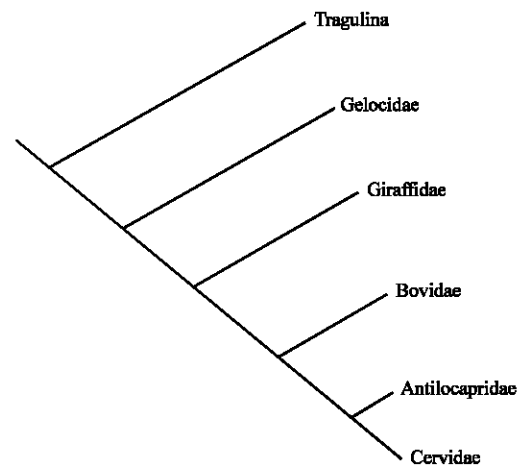


Fig. 1: Simplified Cladogram illustrating the interrelationships between different families of ruminants (modified from Janis and Scott<sup>[40]</sup>). The term Gelocidae designates a heterogeneous assemblage of extinct hornless pre-pecoran ruminants. Bovidae and Antilocapridae are described collectively in the text

remains are well known during the Neogene in Eurasia, North America and Africa. Globally, the phylogenetic relationships between early ruminants are misunderstood,

mainly because of the scarcity of remains of Eocene Asian ruminants. *Archaeomeryx*, the earliest known ruminant from Shara Murun (late-middle Eocene, Mongolia), is sometimes considered as the oldest of the Pecora group<sup>[3,4]</sup>. Early Miocene pecorans were not yet differentiated into the later families. At that period *Dremotherium* and various other genera were found in Europe and *Walangania* in Africa. Cervoids and giraffoids could have had predominantly vicariant origins within the Pecora, giraffoids within Africa, Arabia and/or India and cervoids further north in Eurasia. Undoubted cervids then appeared from among cervoids in the early Miocene of Europe and further east. Later again, cervids migrated to the Siwaliks and Northern Africa but this postdated the Miocene. Meanwhile, giraffids dispersed to Eurasia (beyond Siwaliks) in the middle Miocene. In the Indian Subcontinent there is virtually no Oligocene and earliest Miocene record. However, in Pakistan most of Bugti fauna extends from the Early Oligocene up to the Late/Latest Oligocene<sup>[5-8]</sup>.

#### GEOLOGY CITED

The Siwalik Group is an arrange of southern Himalayan mountains extending for about 1689 km (1050 miles), from southwest Kashmir through India into southern Nepal. The hills are noted for their extensive fossil remains. The Siwalik sediments are found in widely

separated areas all along the foothills of Himalayas (Fig. 2). The name Siwalik was introduced for the sub Himalayan rocks by Medlicott<sup>[9]</sup> and this term derived from the Siwalik Hills in Deharadun (India). It is commonly used for the molasse-type of Neogene sediments of the Himalayan foothill zone. The best record of the fossiliferous layers for the Siwalik can be found in Pakistan (Potwar Plateau).

The Potwar plateau of the Punjab Province (72°30' E, 33°00' N) is an elevated area of some 20,000 km bounded to the north by the Kala Chitta and Margala Hills, south by the Salt Range, east by the Jhelum River and west by the Indus River (Fig. 3).

The Siwalik formations have always been cryptic chronostratigraphic units and from a paleontological point of view recognition of the formations and their boundaries has been a crucial step in dating the fossils<sup>[10,13]</sup>. This practice has in the past produced much confusion and sterile debate, but it is now possible to assume that with the contribution of magnetostratigraphy as a means of dating the rocks this era of confusion is past. Boundary dates here are from Barry *et al.*<sup>[14]</sup>. (Table 1).

#### RUMINANTS FROM THE SIWALIK HILLS OF PAKISTAN

The following ruminants fauna is found in the Siwaliks of Pakistan.

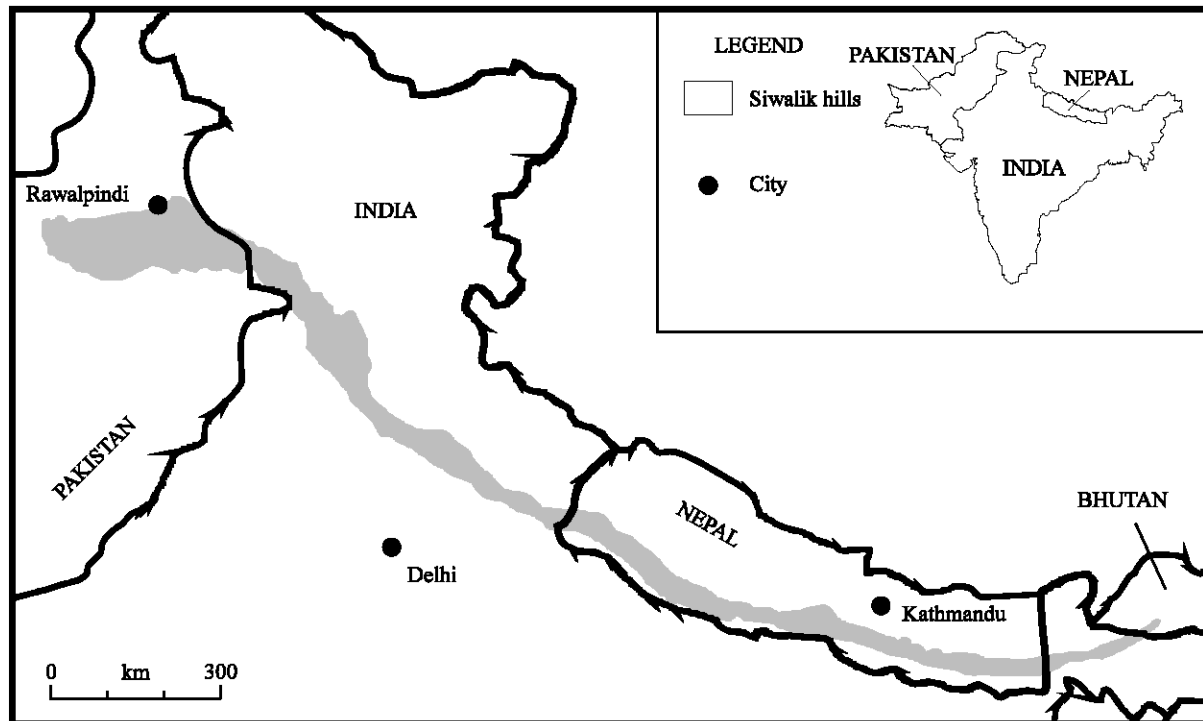


Fig. 2: Distribution of Siwalik sediments along the foothills of Himalayas

Table 1: Stratigraphic sections of siwalik group showing formations and zones

Potwar formations	The Siwali group	The Siwalik zone
Upper siwalik fms.	Upper siwalik subgroup	Boulder conglomerate zone Pinjor zone Tatrot zone
Dhok pathan Nagri Chinji Kamlial	Middle siwalik subgroup  Lower siwalik subgroup	Dhok pathan zone Nagri zone Chinji zone Kamlial zone

**Family bovidae:** The family is highly diverse, with numerous extant species and has an extensive fossil record with species in Africa, Eurasia and North America. Bovids appear to have had three major adaptive radiations at 14, 7.5 and 2 ma<sup>[15-19]</sup> but few fossils are known from sediments older than 14 ma. Its geological range is enormous-from the Kamlial formation of the Lower Siwaliks to the later Pleistocene. The Kamlial fossils are all approximately 18.3 ma old<sup>[11]</sup>, while those from the Vihowa Formation are most likely to be between 17.0 and 17.6 ma old<sup>[20-22]</sup>. The bovids present in these formations of Pakistan are considered as the oldest bovid<sup>[23]</sup>. Pilgrim<sup>[24]</sup> described 75 species of bovids from all over the Siwaliks (Appendix 1) but later on Akhtar<sup>[25]</sup> described 33 species of bovid, including the smallest bovids (*Elaschistoceras*) species from the Siwaliks of Pakistan. Solounias *et al.*<sup>[23]</sup> described the oldest bovid (*Eotragus*) from the Miocene of Pakistan (Kamlial and Vihowa formations, about 18 ma). The Siwalik Species of the family Bovidae are the following;

Species	Appearance in the siwalik hills of Pakistan
<i>Miotragocerus dhokpathanensis</i> Akhtar, 1992.	Middle Siwalik.
<i>Tragocerus browni</i> Pilgrim, 1937.	Middle Siwalik.
<i>Tragocerus punjabicus</i> Pilgrim, 1937.	Middle Siwalik.
<i>Pachyportax latidens</i> (Lydekker) Pilgrim, 1937.	Upper Siwalik (Tatrot Zone).
<i>Pachyportax giganteus</i> Akhtar, 1992.	Middle Siwalik.
<i>Selenoportax vexillarius</i> Pilgrim, 1937.	Lower & Middle Siwaliks.
<i>Selenoportax lydekkeri</i> Pilgrim, 1937.	Middle Siwalik.
<i>Selenoportax dhokpathanensis</i> Akhtar, 1992.	Middle Siwalik.
<i>Selenoportax tatrotensis</i> Akhtar, 1992.	Upper Siwalik (Tatrot Zone).
<i>Helicoportax praecox</i> Pilgrim, 1937.	Lower Siwalik (Chinji Zone).
<i>Tragoportax salmontanus</i> Pilgrim, 1937.	Middle Siwalik.
<i>Tragoportax islami</i> Pilgrim, 1939.	Middle Siwalik.
<i>Ruticeros pugio</i> Pilgrim, 1939.	Middle Siwalik.
<i>Elaschistoceras khawistanensis</i> Thomas, 1977.	Middle Siwalik.
<i>Proamphibos lachrymans</i> Pilgrim, 1939.	Middle & Upper Siwaliks (Tatrot Zone).
<i>Proamphibos kashmiricus</i> Pilgrim, 1939.	Upper Siwalik (Tatrot Zone).
<i>Proamphibos dhokawanensis</i> Akhtar, 1992.	Middle Siwalik.
<i>Hemibos triquetricornis</i> Rutimeyer, 1866.	Middle & Upper siwaliks.

<i>Bubalus bathygnathus</i> Akhtar, 1992.	Upper Siwalik.
<i>Bubalus jarikasensis</i> Akhtar, 1992.	Upper Siwalik.
<i>Bos Kashmiricus</i> Akhtar, 1992.	Upper Siwalik.
<i>Bison sivdensis</i> (Falconer) Lydekker, 1878.	Upper Siwalik.
<i>Bison crassicornis</i> Richardson, 1854.	Upper Siwalik.
<i>Hydaspicobus auritus</i> Pilgrim, 1939.	Upper Siwalik (Tatrot Zone).
<i>Vismucobus patulicornis</i> (Lydekker) Pilgrim, 1939.	Upper Siwalik.
<i>Indoreduca gaalensis</i> Akhtar, 1992.	Upper part of Middle Siwalik.
<i>Sivadenota sepulta</i> Pilgrim, 1939.	Upper Siwalik (Tatrot Zone).
<i>Sivacobus palaeindicus</i> (Lydekker) Pilgrim, 1939.	Upper Siwalik.
<i>Antilope subitorta</i> Pilgrim, 1937.	Upper Siwalik.
<i>Antilope planicornis</i> Pilgrim, 1939.	Middle Siwalik.
<i>Antilope intermedius</i> Akhtar, 1992.	Middle Siwalik.
<i>Gazella lydekkeri</i> Pilgrim, 1939.	Middle Siwalik.
<i>Gazella padriensis</i> Akhtar, 1992.	Middle Siwalik.
<i>Eotragus noyei</i> Solounias <i>et al.</i> , 1995.	Lower Siwalik (Kamlial Zone).

**Family cervidae:** The family Cervidae contains nearly all-living Cervoidea. They exhibit a wide variety in ruminant body size and shape from the little South American Padu to the giant Alaskan moose. The most outstanding and typifying character among cervids, except *Hydropotes*, is the possession of antlers in males<sup>[26]</sup>. Formerly used definitive cervid characters like the doubled lacrimal aperture, the lacrimal pit and the antorbital vacuity are sometimes also present in Moschidae and Palaeomerycidae. During the evolution of cervids their cranial appendages changed immensely not only in size, structure and morphology, but also in proportions, cranial position and orientation of pedicles. Early to Middle Miocene primitive cervids that appeared in Europe show great dental and skeletal similarities to their moschid ancestors. Late Miocene genera known from Europe are more obviously advanced towards later antlered deer. The tooth morphology and crown height in these Miocene species was less advanced than in Pliocene deer. Cervids entered the Siwaliks during the Plio-Pleistocene and they showed the similarity with the Pliocene fossil record of deer in Europe.

Several species of cervids have been described mainly from the Upper Siwalik rocks of the Western Sub Himalayas including the Siwalik Hills and adjoining ranges in India and the Southern Kashmir, Potwar and the trans Indus Hill ranges of Pakistan. The earlier identification was based on a few fragmentary specimens and their holotype designations including maxillary fragments and rarely skulls.

Arif and Shah<sup>[27]</sup> and Ghaffar<sup>[28]</sup> have been critically reviewed the Siwalik cervids and the following species are considered valid.

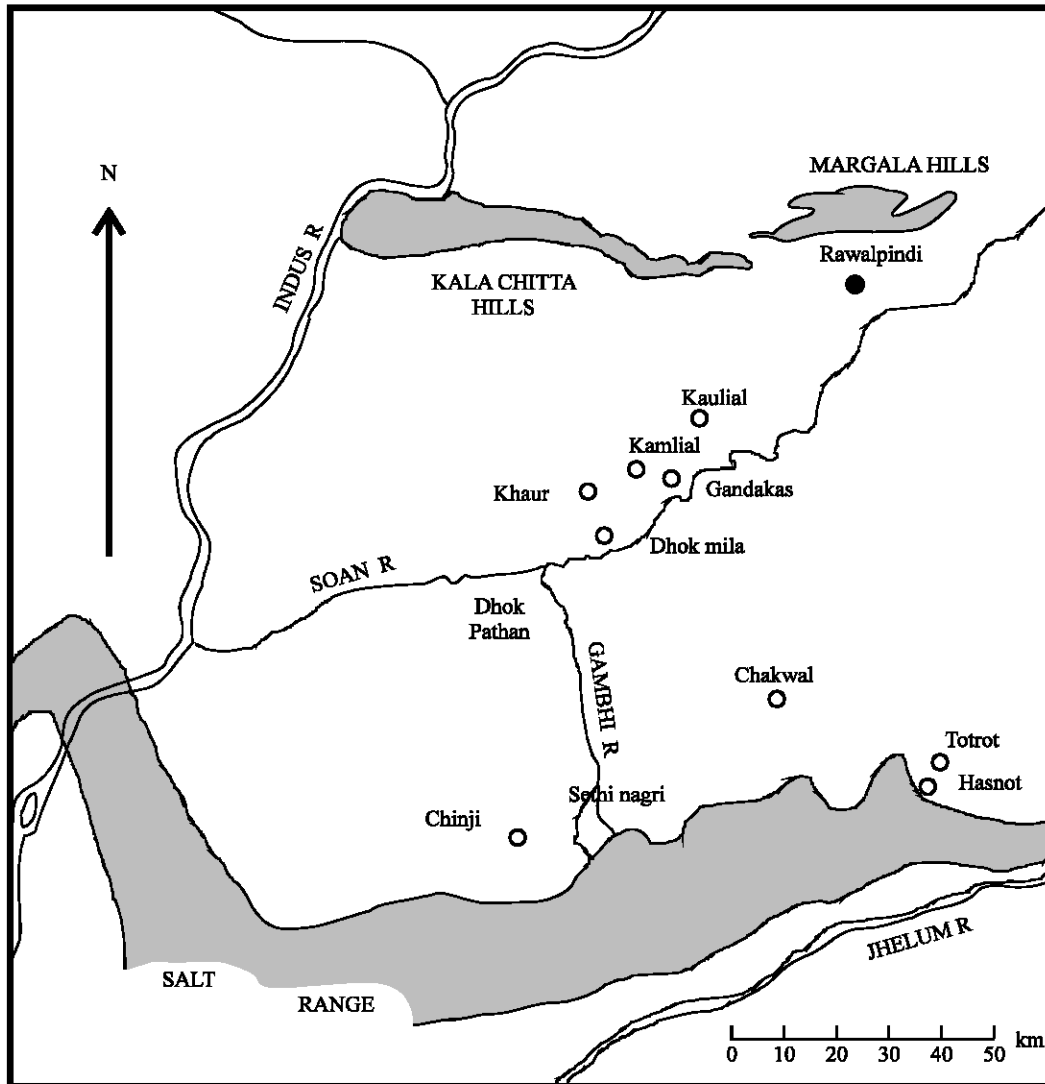


Fig. 3: Map of Potwar Plateau showing main fossil localities

Species	Appearance in the siwalik hills of Pakistan
<i>Cervus punjabiensis</i> Brown, 1926.	Upper part of Middle Siwalik-Upper Siwalik.
<i>Cervus rewati</i> Arif and Shah, 1991.	Upper part of Middle Siwalik-Upper Siwalik.
<i>Cervus sivalensis</i> Lydekker, 1884.	Upper part of Lower Siwalik-Upper Siwalik.
<i>Cervus simplicidens</i> Lydekker, 1876.	Upper part of Middle Siwalik-Upper Siwalik.
<i>Cervus triplicidense</i> Lydekker, 1876.	Upper part of Middle Siwalik-Upper Siwalik.

**Family giraffidae:** The family Giraffidae represents only two living species, the Okapi (*Okapia johnstoni*) and the Giraffe (*Giraffa camelopardalis*)<sup>[29]</sup>. Both species today are present in Africa (Ethiopian region). However, the

Giraffidae have a rich fossil history consisting of approximately thirty species throughout the Neogene of the Old World<sup>[30-33]</sup>. The giraffids started their history in the early Miocene. They appeared in the early Miocene sediments Africa of central Asia from where they dispersed to Europe most probably in the Middle Miocene. The giraffids record in South Asia begins from the early Miocene times, from where they later dispersed to Southeast Asia.

Several species of the family giraffidae have been described from the Upper, Middle and Lower Siwaliks. The Siwalik species can be distinguished on the basis of their dentition and skull patterns. These species are as follows;

Species	Appearance in the Siwalik Hills of Pakistan
<i>Bramatherium perimense</i> Falconer, 1845.	Middle Siwalik
<i>Giraffokeryx chinjiensis</i> Sarwar, 1990.	Lower Siwalik
<i>Giraffokeryx punjabiensis</i> Pilgrim, 1910.	Lower Siwalik
<i>Giraffa sivalensis</i> Falconer and Cautley, 1843.	Upper Siwalik (Pinjor Zone)
<i>Giraffa punjabiensis</i> Pilgrim, 1910.	Middle Siwalik
<i>Giraffa priscilla</i> Matthew, 1929.	Lower Siwalik
<i>Helladotherium grande</i> Gaudry, 1860.	Middle Siwalik
<i>Hydaspiatherium birmanicum</i> Pilgrim, 1910.	Middle Siwalik
<i>Hydaspiatherium grande</i> Lydekker, 1878.	Middle Siwalik
<i>Hydaspiatherium megacephalum</i> Lydekker, 1876.	Middle Siwalik
<i>Hydaspiatherium magnum</i> Pilgrim, 1910.	Middle Siwalik
<i>Bramatherium geraadsi</i> Falconer, 1845.	Upper Siwalik (Pinjor Zone)
<i>Sivatherium giganteum</i> Falconer and Cautley, 1836.	Upper Siwalik (Pinjor Zone)
<i>Vishnutherium iravaticum</i> Lydekker, 1876.	Middle Siwalik

Table 2: The siwalik ruminant families, represented by number of species (recently collected data)

Families	No. of species
Bovidae	34
Giraffidae	14
Cervidae	5
Tragulidae	4

**Family tragulidae:** Tragulina are believed to be of primitive grade among ruminants<sup>[26]</sup>. This group includes both North American and Eurasian forms and can be considered as a paraphyletic group of primitive non-pecoran ruminants<sup>[34]</sup>, although no consensus is established concerning the first unambiguous Pecora. During the late Palaeogene, tragulines was diversified and comprised by Eocene North American traguloids and some ambiguous Eurasian forms. Among North American Palaeogene traguloids, hypertragulids are the most primitive forms. This distinction is mainly based on their cranial and postcranial characters. Recently, however, Vislobokova<sup>[35]</sup> pointed out the presence of a new hypertragulid ruminant from the late Eocene of Khoer-Dzan (Mongolia), extending the geographical range of hypertragulids to Asia during the Palaeogene. Leptomerycids are mainly known from the late Eocene of North America onwards, but some unclear and poorly documented Asian forms are related to leptomerycids<sup>[36]</sup>. Tragulids are traditionally considered as the most primitive living ruminants<sup>[37]</sup> and they still survive as tropical relicts: the water chevrotains (*Hyemoschus*) of Africa and the mouse deer or Asiatic chevrotain (*Tragulus*) of Southeast Asia. They are characterized by their skeletal and dental features, which are primitive within ruminants and their general shape, digestive system and ethology, which are reminiscent to those of pigs<sup>[38]</sup>. The family Tragulidae is the only surviving family from the assumed paraphyletic Tragulina<sup>[37]</sup>.

Appendix 1: Bovid species described by pilgrim (1939) from the siwaliks:

Incertae sedis	
<i>Vishnumeryx daviesi</i> (Lydekker)	
Gazellinae	
<i>Gazella lydekkeri</i> Pilgrim	<i>Gazella</i> sp. cf. lydekkeri
<i>Gazella</i> (?) <i>superba</i> Pilgrim	<i>Gazella</i> sp. cf. <i>superba</i>
Gen. indet. (aff. <i>Helicotragus</i> )- <i>vinayaki</i> Pilgrim	
<i>Antelope cervicapra</i> (Linn.)	
<i>Gazella</i> sp.	Gen. indet. sp. indet.
<i>Antelope subtorta</i> Pilgrim	<i>Antelope</i> (?) <i>planicornis</i> Pilgrim
<i>Dorcadoxa porrecticornis</i> (Lydekker)	
Caprinae	
<i>Sivacpra sivalensis</i> (Lydekker)	<i>Sivacpra</i> (?) <i>crassicornis</i> Pilgrim
Gen. indet. (aff. <i>Capricornis</i> )- <i>roylei</i> - Pilgrim	<i>Pantholops hundsensis</i> Lydekker
Alcelaphinae	
Damalops palaeindicus (Falconer)	
Hippotraginae	
<i>Sivoryx cautleyi</i> Pilgrim	<i>Sivoryx sivalensis</i> (Lydekker)
<i>Sivatragus bohlini</i> Pilgrim	<i>Sivatragus</i> (?) <i>brevicornis</i> Pilgrim
Gen. indet. (cf. <i>Tragoreas</i> )- <i>potwaricus</i> Pilgrim	Gen. indet. sp. indet.
Reduncinae	
<i>Kobikeryx atavus</i> Pilgrim	<i>Cambayella watsoni</i> Pilgrim
<i>Hydaspicobus auritus</i> Pilgrim	Gen. indet. cf. <i>Hydaspicobus auritus</i>
<i>Vishmucobus patulicornis</i> (Lydekker)	<i>Indoredunca sterilis</i> Pilgrim
Gen. indet. (cf. <i>Indoredunca</i> )- <i>theobaldi</i> Pilgrim	<i>Gangicobus asinalis</i> Pilgrim
<i>Sevadnota biforis</i> Pilgrim	Gen. indet. (cf. <i>Sivadnota</i> )- <i>sepulta</i> Pilgrim
<i>Sivacobus palaeindicus</i> (Lydekker)	
Tragelaphinae	
<i>Sivoreas eremita</i> Pilgrim	
Boselaphinae	
<i>Sivaceros gradens</i> Pilgrim	<i>Sivaceros vedicus</i> Pilgrim
<i>Sivaceros</i> sp.	<i>Tragocerus punjabicus</i> Pilgrim
<i>Tragocerus browni</i> Pilgrim	<i>Tragocerus perimensis</i> (Lydekker)
<i>Tragoportax salmontanus</i> Pilgrim	<i>Tragoportax aiyengari</i> Pilgrim
<i>Tragoportax islami</i> Pilgrim	<i>Tragoportax</i> sp. cf. <i>islami</i>
Ruticerinae	
<i>Ruticeros pugio</i> Pilgrim	<i>Strepsioportax gluten</i> Pilgrim
<i>Strepsioportax chinjiensis</i> Pilgrim	<i>Pachyportax latidens</i> (Lydekker) type
<i>Pachyportax latidens</i> var.- <i>dhokpathanensis</i> Pilgrim	<i>Pachyportax nagrii</i> Pilgrim
<i>Sivaportax dolabella</i> Pilgrim	<i>Boselaphus namadicus</i> Rutimeyer
<i>Helicoportax praecox</i> Pilgrim	<i>Helicoportax tragelaphoides</i> Pilgrim
<i>Selenoportax vexillarius</i> Pilgrim	<i>Selenoportax lydekkeri</i> (Pilgrim)
<i>Perimia falconeri</i> (Lydekker)	
Bovinae	
<i>Procamphibos lachrymans</i> Pilgrim	<i>Procamphibos kashmiricus</i> Pilgrim
<i>Procamphibos</i> sp. cf. <i>lachrymans</i> .	<i>Procamphibos</i> (?) <i>hasticornis</i> Pilgrim
<i>Hemibos triquetricornis</i> Rutimeyer	<i>Hemibos acuticornis</i> (Fale. et Caut.)
<i>Hemibos antelopinus</i> Rutimeyer	<i>Bubalus platyceros</i> Lydekker
<i>Bubalus bubalis</i> (Linn) var.- <i>palaeindicus</i> (Falconer)	<i>Bucapra daviesii</i> Rutimeyer
<i>Proleptobos birmanicus</i> Pilgrim	<i>Leptobos falconeri</i> Rutimeyer
<i>Platybos aceros</i> (Rutimeyer)	Gen. indet. (cf. <i>Platybos</i> ) <i>platyrhinus</i> (Lydekker)
<i>Bison sivalensis</i> Lydekker	<i>Bos acutifrons</i> Lydekker
<i>Bos namadicus</i> Falconer	

The Siwalik species of family Tragulidae are as follows<sup>[39]</sup>,

Species	Appearance in the Siwalik Hills of Pakistan
<i>Dorcatherium majus</i> Lydekker, 1876.	Siwaliks (Lower, Middle, Upper).
<i>Dorcatherium minus</i> Lydekker, 1876.	Siwaliks (Lower, Middle, Upper).
<i>Dorcabune anthracotherioides</i> Pilgrim, 1910.	Lower Siwalik (Chinji Zone).
<i>Dorcabune nagrii</i> Pilgrim, 1915.	Middle Siwalik

**Choice of species:** we have mentioned the species of the ruminants, which have yielded significant fossil record. Geographically, widespread species of Siwaliks are also considered thoroughly. This study avoids mentioning those species having an insignificant fossil record and those that have fossil record, fragmentary in nature. In this study most emphasis is given to those species, which are collected from Pakistani Siwaliks for the last two decades by the various workers.

## CONCLUSIONS

Bovids were numerous in the Neogene of the Siwaliks. Pilgrim<sup>[24]</sup> described 75 species of bovids in which indet. species were 17 and 28 were new to science. Pilgrim described some species just on a single specimen. Later on Akhtar<sup>[25]</sup> described bovid faunas from the Siwaliks and determined 33 species. Solounias *et al.*<sup>[23]</sup> described a new species of what they considered as the oldest bovid. Four species of Tragulidae are considered as valid in Pakistani Siwaliks. *Dorcatherium nagrii* has been rejected already owing to descriptions on the basis of single isolated tooth. *Dorcabune hyaemoschiodus* and *Dorcabune latidens* were also rejected found synonym to *Dorcabune anthracotherioides* and *D. onigrii*, respectively<sup>[10]</sup>. The family Cervidae is represented by a single genus, *Cervus*, having five species. Fourteen species of giraffids have been reported from the Siwaliks, which are mostly confined to the Dhokpathan Formation and until now only one species has been reported from the Soan Formation (Table 2).

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