

# Stability in higher level taxonomy of Miocene bovid faunas of the Siwaliks

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The bovid faunas of the Siwaliks (Pakistan) show little change in structure or higher level taxonomy through much of the Middle and Late Miocene. Species of Bovinae and Antilopinae are abundant and Caprinae very rare.

## Introduction

The Neogene vertebrate faunas of the Siwaliks of Pakistan and northern India are contained in a thick sequence of fluvial sediments associated with the Himalayan orogeny. They have attracted scientific attention since the first half of the 19th century and research is still ongoing. One such collaborative project in recent years was undertaken by the Geological Survey of Pakistan and the Pakistan Museum of Natural History, together with Harvard University and the University of Arizona. The crucial contribution of this study has been to establish a chronology for a great number of fossiliferous localities in the Potwar Plateau based on palaeomagnetic measurements. To create this chronological framework 36 stratigraphic sections have been measured and correlated to each other and the Geomagnetic Polarity Time Scale and then correlated locally to an additional 11 sections by using lithological marker horizons believed to be isochronous. No correlations were made on

the basis of biostratigraphy (Barry *et al.* 2002, Behrensmeyer & Tauxe 1982).

The Siwaliks succession has long been arranged in a set of time-transgressive formations. That part of the sequence covering the Miocene is given by Barry *et al.* (2002: table 1) as:

- Dhok Pathan Formation 10.1 to ~3.5 Ma
- Nagri Formation 11.2 to 9.0 Ma
- Chinji Formation 14.2 to 11.2 Ma
- Kamli/Murree Formation 18.3 to 14.2 Ma

The age estimates used in this paper are based on the magnetic timescale of Cande and Kent (1995), later refined by Ogg and Smith (2004). The Middle Miocene starts at a little over 16.0 Ma and the Late Miocene close to 11.0 Ma (Steininger 1999: figs. 1.1–1.2, Harzhauser & Piller 2007: fig. 1). The appearance of hipparionine horses in Old World terrestrial faunas is a good indication that the changeover to the Late Miocene has happened, and in the Siwa-

liks these horses are inferred to have appeared after 10.9 Ma (Barry *et al.* 2002). The end of the Miocene is dated at 5.3 Ma, but our bovid record does not extend so late as that, partly arising from uncertainties about the dating of localities.

The short statement to be made in this paper concerns the Miocene Bovidae so abundantly preserved in the Siwaliks from the Chinji Formation upward. It will not discuss their taphonomy and palaeoecology. Bovidae are a family of ruminant mammals containing the cattle, sheep, goats and antelopes, all characterised by horns in which the hollow horny sheaths are mounted on bony cores and in which neither sheath nor core is branched or seasonally shed. The English word “antelope” is used for bovids not native to Europe or not domesticated there, and does not corre-

spond with a scientific taxonomic category. In Eurasia tiny bovid-like dental remains are known from the early Oligocene of Mongolia onwards (Dmitrieva 2002), and the first definite Bovidae with horns appear in Eurasia and Africa at least two million years before the transition from the Early to the Middle Miocene. More information on fossil Bovidae and references thereon can be found in Bibi *et al.* (2009) and Gentry (2010).

## Bovidae of the Siwaliks Miocene

An outline classification of bovids is shown in Table 1. The Hypsodontinae probably originated from among the earlier bovid-like forms in eastern Asia. They were already present in our area

**Table 1.** A possible classification of the subfamilies and tribes of Bovidae. Miocene Siwaliks groups underlined and in boldface. Extinct groups marked with obelisks. Vertical lines to the left indicate four possible higher hierarchical groupings: (A) the early Hypsodontinae, (B) Boselaphini and allied tribes, (C) a cluster centred around Antilopini, (D) the caprine–alcelaphine group. Subfamily Antilopinae is usually regarded as the cladistic sister group to subfamily Bovinae, in which case all ranks in D would need downgrading. Sources: Gentry (1992), Gatesy *et al.* (1997), Vrba and Schaller (2000), Hernández-Fernández and Vrba (2005), Marcot (2007), Hassanin *et al.* (2012), Bärmann *et al.* (2013). The placings of *Criotherium*, *Oiocerini* and *Tethytragus* are speculative.

<b>A</b>	Subfamily †HYPSODONTINAE † <b>HYPSODONTINI</b>	— Middle Miocene, perhaps diphyletic to other bovids.
<b>B</b>	Subfamily BOVINAE: <b>BOSELAPHINI</b> TRAGELAPHINI <b>BOVINI</b>	— nilgai and four-horned antelope. — kudu, bushbuck group. African. — cattle, buffalo.
<b>C</b>	Subfamily ANTILOPINAE: CEPHALOPHINI NEOTRAGINI <b>ANTILOPINI</b> † <i>Criotherium</i> PELEINI <b>REDUNCINI</b>  †OIOCERINI	— duikers. African. — dik dik, steinbok and other small antelopes. African. — impala, blackbuck, saiga antelope, gazelles. — Late Miocene, plus † <i>Palaeoreas</i> , coming from Antilopini. — Vaal rhebok, <i>Pelea capreolus</i> . African — waterbuck and reedbuck group, perhaps originating from near the ancestry of <i>Pelea</i> . — Late Miocene, includes † <i>Urmiatherium</i> .
<b>D</b>	Subfamily HIPPOTRAGINAE: HIPPOTRAGINI ALCELAPHINI  ?Subfamily of its own: † <b>Tethytragus</b>  ?Subfamily of its own: <i>Pantholops</i>  Subfamily <b>CAPRINAE</b> : RUPICAPRINI or NAEMORHEDINI <i>Budorcas</i> OVIBOVINI CAPRINI	— roan, sable antelope, oryx, addax. — hartebeest and wildebeest group. This and the preceding tribe arose near the base of the Caprinae.  — Middle Miocene. Relationship with <i>Oiocerini</i> , <i>Hippotragini</i> , <i>Pantholops</i> or Caprinae still to be decided.  — chiru, one Asian genus near the origin of Caprinae.  — chamois, serow, goral. — takin, not in the Ovibovini. — muskox. — goats, but tribe for sheep still to be decided.

of southern Asia before the end of the Oligocene and perhaps penetrated as far as Saudi Arabia by the Early Miocene. They acquired horn cores in the Middle Miocene perhaps in parallel to other bovids, and spread widely before disappearing later in the Middle Miocene. The suggestion that they could be an Old World branch from the same stem as Antilocapridae, and diphyletic from other (true) bovids, needs further investigation.

Within the Bovinae, the two species of Boscaphini today are relicts but boselaphines were prominent in Siwalik Middle and Late Miocene faunas and also present in Africa, Europe and eastern Asia. Bovini descended from Boscaphini and the earliest known bovine comes from the Late Miocene of the Siwaliks, judged by the appearance there of large, high-crowned (hypsodont) teeth with complicated occlusal surfaces (Bibi 2007). Tragelaphini, despite their phyletic links to Boscaphini, are an African group and have not been found in the Siwaliks.

In the Antilopinae, the Neotragini look like a paraphyletic assemblage of small African antelopes (Hassanin *et al.* 2012, Bärmann *et al.* 2013), from among whose early relatives sprang the Antilopini. The latter contains the Indian blackbuck and its many spiral-horned relatives in the Eurasian Late Miocene, as well as the widespread *Gazella* and some other genera. A Middle Miocene appearance of *Gazella* seems to be demonstrated in the Siwaliks and east Africa, but it is possible that these supposed early gazelles could be the ancestors or close relatives of other genera as well as of later *Gazella* species.

Reduncini evolved from Antilopini, or both did from undifferentiated early Antilopinae which would have been little different at that stage of their history from primitive Boscaphini. Today Reduncini are found only in Africa but in the Miocene and (for a second time?) in the late Pliocene they were in the Siwaliks and bore a limited resemblance to modern kobs. The teeth of reduncines gradually became more occlusally complex but remained or became smaller in relation to skull size than in other antelope tribes, perhaps because grasses and other vegetation in habitats near water are more nutritious.

*Tethyragus*, a Middle or Middle-Late Miocene bovid of Europe and Turkey (Bibi & Güleç 2008), known perhaps from about 15.0 Ma

onwards, may be present in the Siwaliks but with rather few fossils. Its subfamily or tribal affiliation has not been decided other than that it is not a boselaphine. Other extinct genera in Miocene faunas are similarly unplaced taxonomically. Finally Caprinae are a mainly Eurasian group but with only one certain occurrence in the Siwaliks.

Table 2 lists the species of Miocene Siwaliks bovids as we have identified them from horn cores and, when possible, from teeth. At first sight the list looks like an incredibly rich fauna, but this is misleading. A few entries are for early species predating the Chinji Formation, for which numbers of fossils are low and identifications still uncertain. Some entries are for single occurrences or for a few specimens with a very short time range. The bracketed entries are time successive and may be ancestor-descendant pairs or sequences. Six species or possible lineages of Middle Miocene bovids from 14.0 Ma onwards and five Late Miocene ones are commoner and better substantiated (more than ten specimens distributed over a time span) and they are the ones shown in Fig. 1. The tiny *Elachistoceras khauristanensis* has been excluded because although the originally described material (Thomas 1977) dating from around 9.0 Ma can be accepted as a boselaphine, the conspecificity of some of the rest remains doubtful.

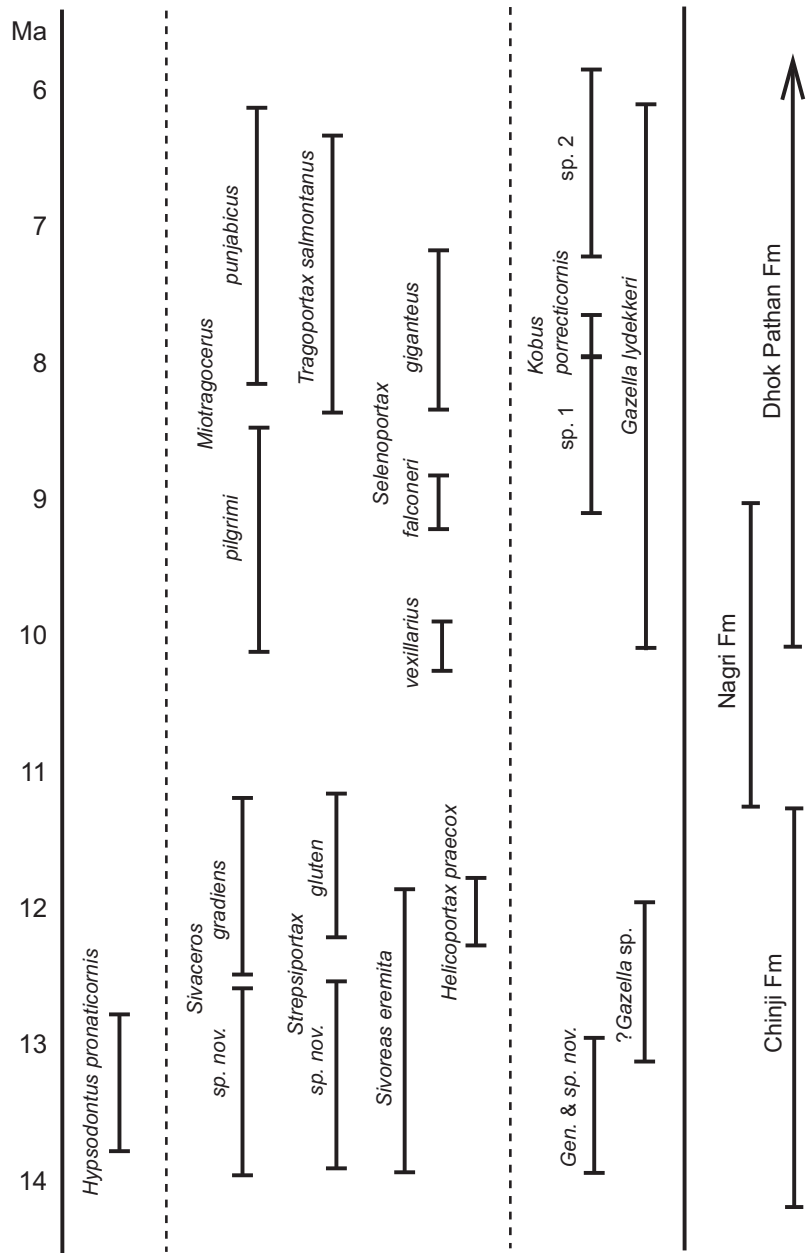
## The commoner Siwaliks bovid species

The commoner bovids as we find them in the Siwaliks had a long lasting taxonomic stability at subfamily/tribal level with occasional alterations of the species occupying what seem to be ongoing niches (Fig. 1). Appearing low in the Chinji Formation at just after 14.0 Ma *Hypsodontus pronaticornis* is represented by only four specimens but it is the last Siwaliks representative of the once widespread Hypsodontinae and endures another million years before disappearing. Next come three well-differentiated boselaphines: *Strepsiptorax*, *Sivaceros* and *Sivoreas*. The first two of these change enough of their horn core morphologies around 12.5 Ma, either by immigration or anagenesis, to justify a change in their specific names. We have not been able to

**Table 2.** Bovid species in the Siwaliks Miocene with numbers of identified specimens and time spans based on the earliest and latest fossils we can assign to each species. **I to VI** = six common Middle Miocene species; **A to E** = five common Late Miocene ones. Left brackets = likely lineages.

<b>?Family Bovidae,</b>			
Subfamily Hypsodontinae			
	<i>Palaeohypsodontus zinensis</i> Métais et al., 2003	2	25.0 to 18.5 Ma
	?Hypsodontinae sp.	1	18.3 Ma
	<i>Hypsodontus sokolovi</i> Gabunia, 1973	11	14.0 Ma
<b>I</b>	<i>Hypsodontus pronaticornis</i> Köhler, 1987	4	13.8 to ~12.8 Ma
<b>Family Bovidae</b>			
Subfamily <i>indet.</i>			
	?Bovidae sp. 1	7	18.3 Ma
Subfamily Bovinae, Tribe Boselaphini			
	<i>Eotragus noyei</i> Solounias et al., 1995	9	18.1 to 17.9 Ma
	Genus et species <i>indet.</i>	30	19.5 to 15.0 Ma
	<i>Elachistoceras khauristanensis</i> Thomas, 1977	27	14.0 to 8.5 Ma
<b>II</b>	[ <i>Strepsiptax</i> sp. nov.	28	14.0 to 12.6 Ma
	– <i>Strepsiptax gluten</i> Pilgrim, 1937	26	12.3 to 11.2 Ma
<b>III</b>	[ <i>Sivaceros</i> sp. nov.	14	14.0 to 12.6 Ma
	– <i>Sivaceros gradiens</i> Pilgrim, 1937	16	12.5 to 11.2 Ma
<b>IV</b>	<i>Sivoreas eremita</i> Pilgrim, 1939	29	14.0 to 12.0 Ma
	<i>Helicoportax praecox</i> Pilgrim, 1937	19	(?13.3)12.3 to 11.8(?11.2) Ma
<b>A</b>	[ <i>Selenoportax</i> aff. <i>vexillarius</i> Pilgrim, 1937	20	10.2 to 9.8 Ma
	– <i>Selenoportax falconeri</i> (Lydekker, 1886)	15	9.3 to 8.9 Ma
	– <i>Selenoportax giganteus</i> (Akhtar, 1995)	83	8.5 to 7.3 Ma
	? <i>Pachyportax</i> sp.	4	7.2 Ma
	Gen. <i>indet.</i> , aff. <i>Selenoportax?</i> sp.	3	9.5 to 8.9 Ma
<b>B</b>	[ <i>Miotragocerus pilgrimi</i> (Kretzoi, 1941)	100	10.2 to 8.5 Ma
	– <i>Miotragocerus punjabicus</i> (Pilgrim, 1910)	78	8.0 to 6.2 Ma
	<i>Miotragocerus</i> , ?sp. nov.	4	8.7 to 7.2 Ma
<b>C</b>	<i>Tragoportax salmontanus</i> Pilgrim, 1937	18	8.4 to 6.4 Ma
	?( <i>Sivaceros</i> ) <i>vedicus</i> Pilgrim, 1939	2	9.8 Ma
Subfamily Antilopinae, tribe undifferentiated			
<b>V</b>	Gen. et sp. nov.	12	14.0 to 13.0 Ma
Subfamily Antilopinae, Tribe Antilopini			
<b>VI</b>	[? <i>Gazella</i> sp.	18	13.2 to 12.0 Ma
<b>D</b>	– <i>Gazella lydekkeri</i> Pilgrim, 1937	61	10.1 to ?6.2 Ma
	<i>Prostrepsiceros vinayaki</i> (Pilgrim, 1939)	2	8.3 to 7.9 Ma
	? <i>Prostrepsiceros</i> , large sp.	1	8.1 Ma
	<i>Nisidorcas planicornis</i> (Pilgrim, 1939)	1	9.0 Ma
	? <i>Protragelaphus</i> sp.	1	10.7 Ma
	Large sp. <i>indet.</i>	3	9.3 to 8.7 Ma
	?Antilopinae, small sp.	6	8.5 to 6.2 Ma
Subfamily Antilopinae, Tribe Reduncini			
<b>E</b>	[ <i>Kobus</i> sp. 1	28	9.3 to 7.9 Ma
	– <i>Kobus porrecticornis</i> (Lydekker, 1878)	40	8.1 to 7.7 Ma
	– <i>Kobus</i> sp.2	30	7.3 to 5.9 Ma
Subfamily Antilopinae or Caprinae			
	<i>Tethytragus</i> sp.	7	13.0 to 12.3 Ma
	? <i>Caprotragoides</i> , sp. <i>indet.</i>	2	10.2 to 10.1 Ma
	? <i>Dorcadoryx</i> sp.	4	9.7 to 9.6 Ma
Subfamily Caprinae			
	<i>Protoryx</i> aff. <i>solignaci</i> (Robinson, 1972)	1	11.2 Ma

**Fig. 1.** Time ranges for the commoner bovids of the Siwaliks Middle and Late Miocene. The bovid record becomes deficient between 11.2 and 10.2 Ma. Horses of the *Hipparion* group appear shortly after 11.0 Ma. The three columns, from left to right, are for Hypsodontinae, Boselaphini and Antilopinae.



identify their numerous tooth remains to genus level. Around 12.0 Ma, *Sivoreas* with definite torsion in its horn cores gives rise to, or is overlapped by *Helicoportax praecox*, a fourth species which also became larger-sized than *Strepsiptortax* or *Sivaceros* species. It has been shown in Fig. 1 although its time range is problematical, the problem being that the earliest and latest putative specimens do not show unequivocally typical morphologies. Finally the early and as

yet unnamed antilopine starting at 14.0 Ma is smaller than the boselaphines and gives way to a species more like a gazelle, at around 13.0 Ma.

The most obvious faunal change in bovids occurs around or not long after the ~11.0 Ma onset of the Late Miocene, presumably linked with the arrival of hipparionine horses, changes among the Proboscidea, the dramatic decline in tragulids around 10.0 Ma, or other changes induced by climatic, geomorphological or ecological events.

The change does not become visible in the bovid record until after 10.2 Ma because of a scarcity of identifiable or provenanced bovid fossils between 11.2 and 10.2 Ma (see Fig. 1). The only boselaphine fossils in our collections within this span are a mandibular piece of *Strepsiptortax* or *Sivaceros* at 11.1 Ma, a horn core perhaps of *Helicoportax* at 11.0 Ma, and two *Elachistoceras* fossils at 10.4 and 10.3 Ma. Older and poorly provenanced collections such as that of Brown in 1923, now in the American Museum of Natural History, do contain bovids from somewhere in the gap, for example the holotype of *Selenoportax vexillarius*, and suggest an abrupt, rather than a more gradual, faunal turnover.

Once into the early part of the Late Miocene, we see that two boselaphine stocks are now in place: *Miotragocerus*, the standard or typical boselaphine of the Old World Late Miocene, and *Selenoportax* with torsion of its horn cores like *Sivoreas* and *Helicoportax*. *Selenoportax* rapidly became a larger animal than *Miotragocerus*, which in its turn was larger than the Middle Miocene *Sivaceros*. Around 8.5–8.0 Ma a larger *Miotragocerus* species comes in alongside a new smaller species, *Tragoportax salmontanus*, to which we have assigned 17 specimens so that it cannot be taken as rare in the Siwaliks. From this time on there are again three boselaphine lineages as was the case back in the Middle Miocene, although the signs cannot be ignored that *Selenoportax* is falling within acceptable morphological limits for defining the Bovini as noted above (Bibi 2007).

The new antilopine sharing the Late Miocene stage with the boselaphines is *Gazella lydekkeri*. And then after 8.0 Ma Reduncini which had already been present for just over a million years become much commoner than gazelles (Table 3).

Throughout the sequence there are other, more rarely fossilised, bovids in the background.

**Table 3.** Numbers of gazelle and reduncine fossils in the Siwaliks Late Miocene.

	<i>Gazella</i>	<i>Kobus</i>	Total
10.2–8.1 Ma	54	18	72
From 8.0 Ma	7	70	77
Total	61	88	149

Two species left out of Fig. 1 are *gen. indet.*, aff. *Selenoportax?*, sp. and *Miotragocerus ?sp. nov.* The first is definitely a distinctive species and probably deserves a new generic name; it lasts for 0.6 myr from 9.5 Ma but is based on only three specimens and is therefore far from common. The *Miotragocerus ?sp. nov.* has a longer span but is based on only four specimens and its relationship to the main *Miotragocerus* line is not clear. Six Late Miocene Antilopini in addition to *Gazella lydekkeri* are listed in Table 2 but all are rare fossils. Five of them are spiral-horned with interesting similarities and differences as compared with species in western Eurasia, and one of them, the *?Protragelaphus* horn core at 10.7 Ma, comes from within the period of scarce fossils discussed above and apparent in Fig. 1. The last antilopine in the list, *?Antilopinae small sp.*, looks like an artificial assemblage of teeth too small to fit *Gazella* that are scattered through part of the Late Miocene. *Tethytragus* of uncertain tribal affiliation has been wrongly associated in the past with the Late Miocene *Caprotragoides* in India and with the Middle and Late Miocene *Gentrytragus* in Africa (Gentry 2010: 772). It is represented by six or more specimens over a time span of 0.7 myr but there is a good chance of misidentifications among the fossils. A single cranium of a *Protoryx* with one partial horn core base is the only undoubted member of the Caprinae in the Siwaliks. Rather uncomfortably for present views of the *Protoryx* group it pre-dates the arrival of hipparionine horses and is close to the Middle-Late Miocene boundary. In contrast to the situation in Europe and eastern Asia, no other members of the *Protoryx*–*Pachytragus* group occur in the Siwaliks through the rest of the Late Miocene.

## Conclusion

The Miocene bovids in the Siwaliks had a long lasting structural or taxonomic stability at sub-family or tribal level (Fig. 1). Through a period of more than 7.0 myr we always find a numerical predominance of several boselaphine species and one or two small antilopines, giving a total between three and six common species at any one time. The component species change over

**Table 4.** Identified bovid species in the Siwaliks Miocene at 13.0 and 8.0 Ma and cervid and bovid species in Pakistan a century ago.

**Common species at 13.0 Ma:** *Hypsodontus pronaticornis*, *Strepsiptorax* sp. nov., *Sivaceros* sp. nov., *Sivoreas eremita*, gen. et sp. nov., ?*Gazella* sp.

Other species common at 14.0 Ma or 12.0 Ma: *Helicoportax praecox*.

Other species present between 14.0 Ma and 12.0 Ma: *Hypsodontus sokolovi*, *Elachistoceras khauristanensis*, *Tethytragus* sp.

**Common species at 8.0 Ma:** *Miotragocerus punjabicus*, *Tragoportax salmontanus*, *Kobus* sp. 1 or *porrecticornis*, *Gazella lydekkeri*.

Other species common at 9.0 Ma or 7.0 Ma: *Selenoportax falconeri* or *giganteus*.

Other species present between 9.0 Ma and 7.0 Ma: *Elachistoceras khauristanensis*, *Prostrepsiceros vinayaki*, ?*Prostrepsiceros* large sp., *Nisidorcas planicornis*, large sp. indet. (listed within Antilopini).

**Living species likely to have been in northern Pakistan in the recent past:**

*Muntiacus muntjak*, *Axis porcinus*, *Rucervus duvauceli*, *Boselaphus tragocamelus*, *Gazella bennetti*, *Antilope cervicapra*, *Capra falconeri*, *Ovis orientalis*, *Naemorhedus goral*.

time either by evolution *in situ* or by immigration, the latter coming into question especially at the start of the Late Miocene, but the dominance of the Boselaphini and Antilopinae was not broken. Other species in other sub-families or tribes did not penetrate the region or become common enough to be fossilised, and certainly they did not become dominant in the fossil record. Nor for that matter did the number of common boselaphine and antilopine species increase. The composition of the Siwaliks fauna must be taphonomic at base in so far as we only become aware of it from the fossils retrieved, but it must also be linked with other factors such as the somewhat zoogeographically isolated position of the faunas, or non-availability as source areas for fossils of habitats favourable to, say, spiral-horned antilopines and *Protoryx*.

If one takes the two Middle and Late Miocene time levels of 13.0 Ma and 8.0 Ma as examples and adds the rarer species present within a million years on either side of those dates, the total number of bovids would be eight at 13.0 Ma and ten at 8.0 Ma (Table 4). These are not outstandingly rich arrays of bovids, especially as potentially competing cervids did not appear in the region until after the Miocene had ended (contra Ghaffar *et al.* 2006, 2010). They do not contrast with the cervid + bovid fauna 200 to 100 years ago when about nine cervid and bovid species might have lived in the Siwaliks area of northern Pakistan, with more Caprinae in the mountains to the northeast and more deer in peninsular

India to the southeast (Roberts 1977, Wilson & Mittermeier 2011).

The species richness found in extant faunas and the factors controlling it need painstaking analysis (Eronen *et al.* 2011). We have not discussed here the relation between Miocene species richness, palaeoecology and taphonomy. We simply state that much palaeontological research aims at detecting differences and breaks in past faunas and so it is useful to be aware that conditions in the Siwaliks allowed an element of stability to be maintained through a long period which happened to encompass the change from Middle to Late Miocene faunas.

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## References

- Bärmann, E. V., Rössner, G. E. & Wörheide, G. 2013: A revised phylogeny of Antilopini (Bovidae, Artiodactyla) using combined mitochondrial and nuclear genes. — *Molecular Phylogenetics and Evolution* 67: 484–493.
- Barry, J. C., Morgan, M. E., Flynn, L. J., Pilbeam, D., Behrensmeyer, A. K., Raza, S. M., Khan, I. A., Badgley, C., Hicks, J. & Kelley, J. 2002: Faunal and environmental

- change in the late Miocene Siwaliks of northern Pakistan. — *Paleobiology Memoirs* no. 3: 1–71.
- Behrensmeyer, A. K. & Tauxe, L. 1982: Isochronous fluvial systems in Miocene deposits of northern Pakistan. — *Sedimentology* 29: 331–352.
- Bibi, F. 2007: Origin, paleoecology and paleobiogeography of early Bovini. — *Palaeobiogeography, Palaeoclimatology, Palaeoecology* 248: 60–72.
- Bibi, F., Bukhsianidze, M., Gentry, A. W., Geraads, D., Kostopoulos, D. S. & Vrba, E. S. 2009: The fossil record and evolution of Bovidae: state of the field. — *Palaeontology Electronica* 12(3), 10A: [http://palaeo-electronica.org/2009\\_3/169/index.html](http://palaeo-electronica.org/2009_3/169/index.html).
- Bibi, F. & Güleç, E. S. 2008: Bovidae (Mammalia: Artiodactyla) from the Late Miocene of Sivas, Turkey. — *Journal of Vertebrate Paleontology* 28: 501–519.
- Cande, S. C. & Kent, D. V. 1995: Revised calibration of the geomagnetic polarity timescale for the Late Cretaceous and Cenozoic. — *Journal of Geophysical Research* 100B: 6093–6095.
- Dmitrieva, E. L. 2002: On the early evolution of bovids. — *Paleontological Journal* 36: 204–206. [Translation from *Paleontologicheskii Zhurnal* 2002, 2: 86–88].
- Eronen, J. T., Puolamäki, K., Heikinheimo, H., Lokki, H., Venäläinen, A., Mannila, H. & Fortelius, M. 2011: The effect of scale, climate and environment on species richness and spatial distribution of Finnish birds. — *Annales Zoologici Fennici* 48: 257–274.
- Gatesy, J., Amato, G., Vrba, E. S., Schaller, G. B. & DeSalle, R. 1997: A cladistic analysis of mitochondrial ribosomal DNA from the Bovidae. — *Molecular Phylogenetics and Evolution* 7: 303–319.
- Gentry, A. W. 1992: The subfamilies and tribes of the family Bovidae. — *Mammal Review* 22: 1–32.
- Gentry, A. W. 2010: Bovidae. — In: Werdelin, L. & Sanders, W. J. (eds.), *Cenozoic mammals of Africa*: 741–796. University of California Press, Berkeley.
- Ghaffar, A., Khan, M. A., Akhtar, M., Farooq, U. & Nazir, M. 2006: The oldest Cervid from the Siwalik Hills of Pakistan. — *Journal of Applied Sciences* 6: 127–130.
- Ghaffar, A., Khan, M. A. & Akhtar, M. 2010: Early Pliocene Cervids (Artiodactyla-Mammalia) from the Siwaliks of Pakistan. — *Yerbilimleri* 31: 217–231.
- Harzhauser, M. & Piller, W. E. 2007: Benchmark data of a changing sea — palaeogeography, palaeobiogeography and events in the Central Paratethys during the Miocene. — *Palaeobiogeography, Palaeoclimatology, Palaeoecology* 253: 8–31.
- Hassanin, A., Delsuc, F., Ropiquet, A., Hammer, C., Jansen van Vuuren, B., Matthee, C., Ruiz-Garcia, M., Catzeflis, F., Areskoug, V., Nguyen, T. T. & 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.
- Hernández-Fernández, M. & 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.
- Marcot, J. D. 2007: Molecular phylogeny of terrestrial artiodactyls. — In: Prothero, D. R. & Foss, S. E. (eds.), *The evolution of artiodactyls*: 4–18. Johns Hopkins University Press, Baltimore.
- Ogg, J. G. & Smith, A. G. 2004: The geomagnetic polarity time scale. — In: Gradstein, F. M., Ogg, J. G. & Smith, A. G. (eds.), *A geological time scale 2004*: 63–86. Cambridge University Press, Cambridge.
- Roberts, T. J. 1977: *The mammals of Pakistan*. — Benn, London.
- 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. & Heissig, K. (eds.), *The Miocene land mammals of Europe*: 9–24. Pfeil, Munich.
- Thomas, H. 1977: Un nouveau bovid, du Nagri, plateau du Potwar, Pakistan. — *Bulletin de la Société Géologique de France* 7, 19: 375–383.
- Vrba, E. S. & Schaller, G. B. 2000: Phylogeny of Bovidae based on behavior, glands, skulls, and postcrania. — In: Vrba, E. S. & Schaller, G. B. (eds.), *Antelopes, deer and relatives: fossil record, behavioral ecology, systematics and conservation*: 203–222. Yale University Press, New Haven.
- Wilson, D. E. & Mittermeier, R. A. (eds.) 2011: *Handbook of mammals of the world*, vol. 2. — Lynx Ediciones, Barcelona, in association with IUCN and Conservation International.