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Fossil tragulids of the Siwalik Formations of southern Asia

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Abstract

Tragulids are common in the Early Miocene through Pliocene Siwalik faunas of the Indian Subcontinent where they are represented by as many as 17 species. Large collections of Siwalik fossils have recently been made by collaborative projects from Harvard University, the University of Arizona, the Geological Survey of Pakistan, and the Pakistan Museum of Natural History. The collections together comprise over 3700 specimens, including dental, cranial, and postcranial elements. Most of this fossil material is from northern and southwestern Pakistan from well-dated stratigraphic sections. The oldest definite tragulids are from the Early Miocene Vihowa Formation and are around 18.7 Ma, while the youngest are in the Pliocene Tatrot Formation and are 3.3 Ma.

The fossil tragulids of the Siwaliks differ from the extant species in a number of ways. Importantly, they have a much wider range of body sizes, ranging from 1 to nearly 76 kg. Consequently the small species overlap with the smallest species of extant *Tragulus*, while the large species approach medium size bovids and cervids. Compared to other ruminants, Siwalik tragulids are also relatively abundant and species rich. Although the status of some described species is uncertain, preliminary analysis indicates there are many as yet undescribed species. Three genera are known and typically at least four species co-exist at any one time during the Miocene.

The history of the south Asian tragulids can be correlated to documented environmental changes. The Siwalik deposits formed in a large fluvial system, with mostly forested or wooded low relief floodplains having abundant cover and fruit. Isotopic analyses of tooth enamel and soil carbonates indicate the vegetation was dominated by C3 plants until 9 Ma, after which there was a shift to a more seasonally dry monsoon climate, undoubtedly accounting for a Late Miocene change in the relative abundance of tragulids.

Key words: Tragulidae, Siwaliks, Miocene, *Dorcabune*, *Dorcatherium*, *Siamotragulus.*

1. Introduction

Tragulid species make up an important part of the Neogene Siwalik mammal faunas of the Indian Subcontinent, although the number and status of the various species is in doubt. Fossil collections that included tragulids were discovered early in the exploration of the Siwaliks, apparently being among Falconer's materials (Lydekker 1876: p. 44) recovered as early as 1842. Subsequently, there are now substantial collections in various museums including the Natural History Museum (London), the Geological Survey of India in Calcutta, Punjab University in Chandigarh, the Wadia Institute of Himalayan Geology in Dehra Dun, the American Museum of Natural History, the Yale Peabody Museum, the Bavarian State Collection of Palaeontology and Geology, and the Geological Institute, State University of Utrecht. In addition, large collections of Siwalik fossils have recently been made by collaborative projects between Harvard University and the Geological Survey of Pakistan (GSP), as well as between the University of Arizona and the Pakistan Museum of Natural History. In contrast to the earlier collections, for the most part this material is from well dated stratigraphic sections and can be placed within a reliable chronostratigraphic framework (Raza et al. 1984, 2002; Lindsay et al. 2005; Antoine et al. 2013; Barry et al. 2013; Flynn et al. 2013). This paper is then a preliminary report on these recently collected materials. It will be followed by a more comprehensive report once all the materials have been analyzed and the species delimited and revised.

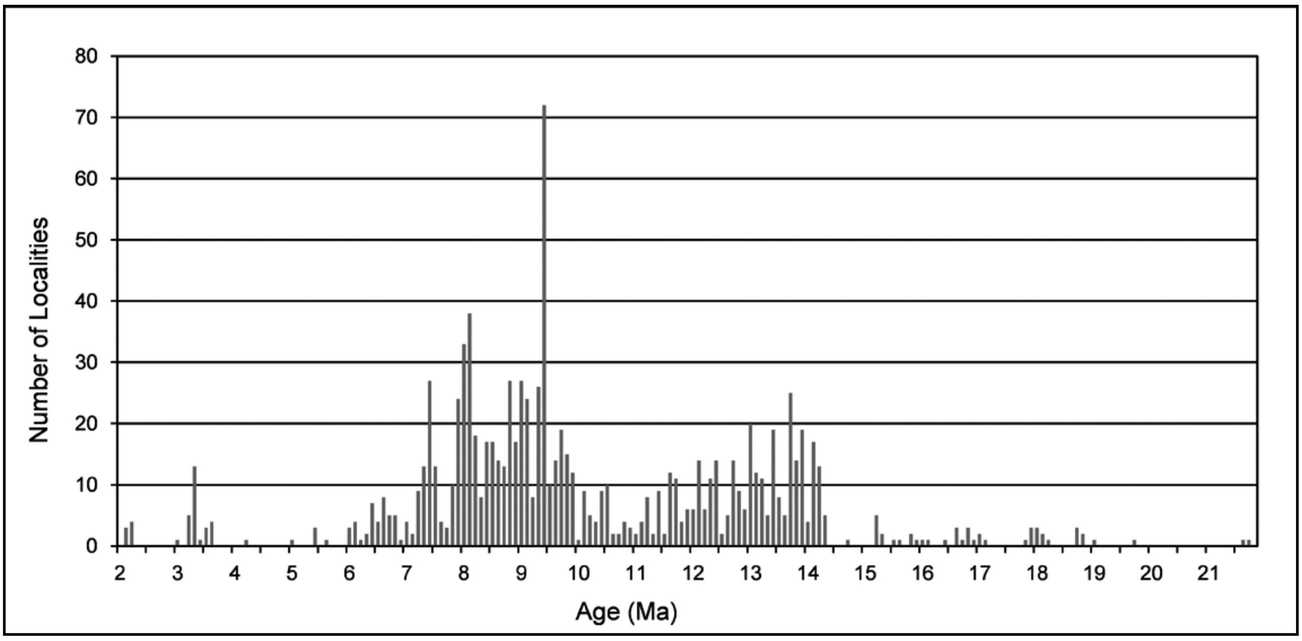
The oldest, securely dated Siwalik tragulids are from the Vihowa Formation and are 18.7 Ma (Lindsay et al. 2005), while tragulids from the upper member of the Chitarwata Formation are at least 22 and perhaps as old as 26 Ma (Lindsay et al. 2005). The family persisted in the Siwaliks until the Pliocene, being known from the Tatrot Formation with an approximate age of 3.3 Ma (Barry et al. 2002). During this time interval tragulids are species rich, with typically at least four co-occurring species within shorter time intervals. This contrasts to extant tragulids, but compares favorably to the five to seven co occurring species of bovids. Siwalik tragulids are also relatively common. They are most abundant in the Early and Middle Miocene, but subsequently their relative abundance is much diminished so that they become rare finds in the latest Miocene and Pliocene. The fossil species also differ from extant species in a number of other ways. Most importantly, they have a much wider range of body sizes. The smallest species is estimated to be just over 1 kg, while at least four species are over 25 kg, with the largest specimen estimated to be nearly 76 kg. Thus the small fossil species overlap with the smallest species of extant *Tragulus*, while the large species are very much larger than individuals of the largest living tragulid *Hyemoschus* and approach medium size bovids and cervids.

2. Materials

Including material in the Yale Peabody Museum and American Museum of Natural History, the new collections together comprise over 3700 specimens. These are mostly isolated teeth, jaws, and postcranials and, typical of Siwalik fossils, most are fragmentary and disarticulated. There is very little cranial material and only a handful of associated teeth and skeletal elements that clearly belong to one individual. The fragmentary, disarticulated preservation makes it difficult to link dental and postcranial morphologies and thus to fully characterize the species. While the teeth, and in some instances postcranial elements, of the different genera exhibit morphological differences, within genera species appear to be much more uniform. There are, nevertheless, differences in size and proportions that can be used to separate likely congeneric species. In this review dimensions of the astragalus and metapodials are used to make a preliminary separation of taxa, a strategy that works well for the Late Miocene Siwalik tragulids, but one I find is more problematic for the Middle and Early Miocene taxa.

3. Stratigraphy and Age of the Fossils

The term "Siwaliks" refers to the Neogene fluvial deposits of the Indian Subcontinent, although the term is often used to include Oligocene fluviodeltaic and marginal marine deposits in Baluchistan and Sind. Siwalik sediments are found throughout the subcontinent along the southern margin of the Himalayas in Pakistan, India, and Nepal (Corvinus and Rimal 2001, Flynn et al. 2013, Patnaik 2013). They are particularly well exposed on the Potwar Plateau of Northern Pakistan, where most of the collection under study originates. Significant exposures of the Vihowa and Chitarwata Formations are also known in the Sulaiman Range in southwestern Punjab and Baluchistan, as well as of the Manchar Formation in Sind. The Sulaiman and Manchar formations are important because they contain fossils of earliest Miocene and latest Oligocene age (Raza et al. 1984, 2002; Lindsay et al., 2005; Antoine 2013), while the Potwar localities are of Early Miocene through Pleistocene age. Siwalik fossils are found in many different depositional environments, with the richest localities typically being in small abandoned chan-



Textfigure 1: Number of Siwalik fossil localities per 100,000 year long interval.

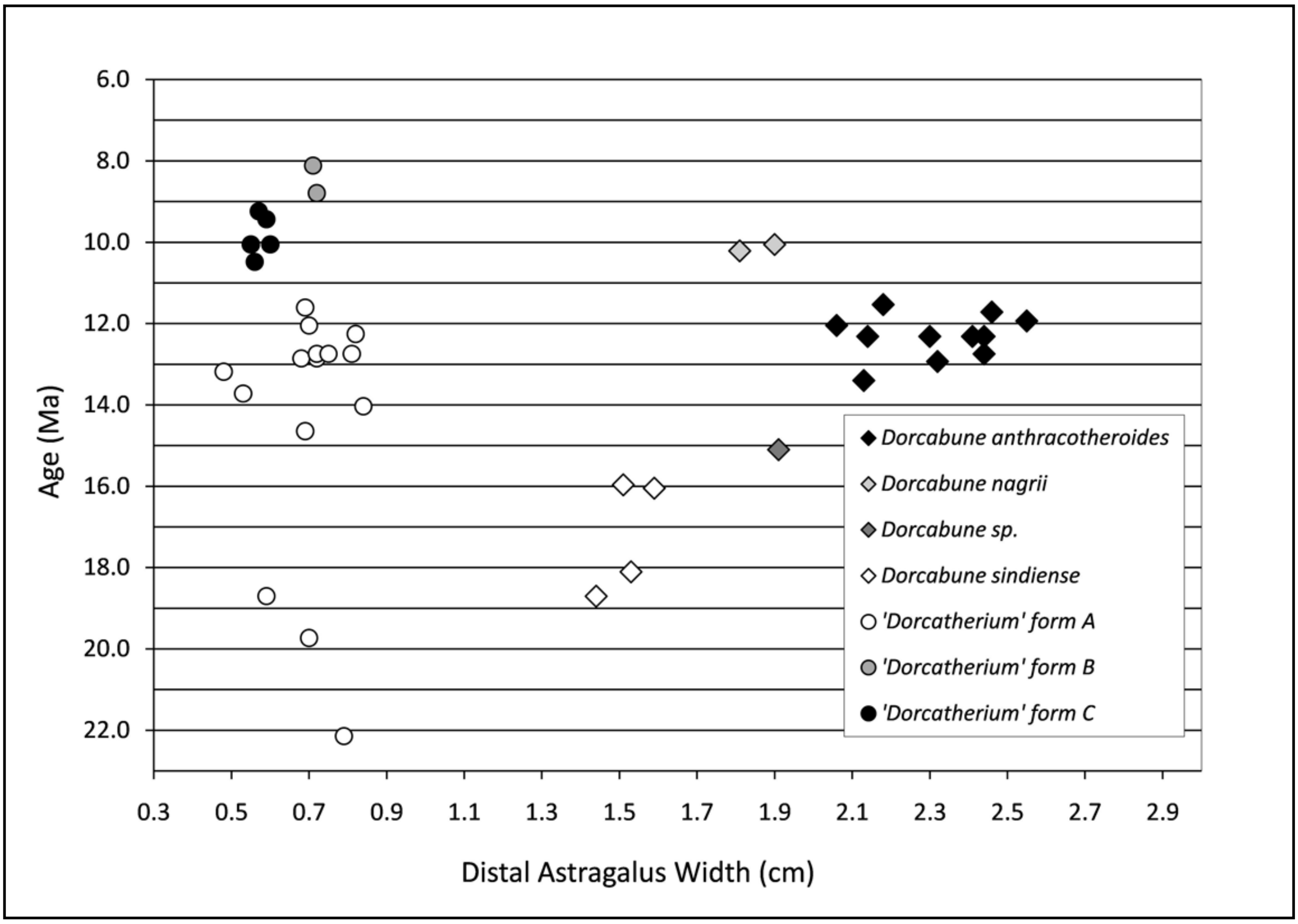
nels and channel margins of the fluvial systems (Behrensmeyer et al. 2005). On the Potwar and in the Sulaimans exposures are extensive and many years of collecting have led to the discovery of more than 1400 individual fossil sites, a large number of which can be placed on stratigraphic sections and their ages estimated using paleomagnetics (Barry et al. 2002, Lindsay et al. 2005). Textfigure 1 shows the age distribution of over 1000 sites, binned into intervals of 100,000 years duration. Most notable is the uneven distribution, with very few sites before 14 or after 6 Ma, while between 6 and 14 some intervals have very few sites and other intervals have very many. This uneven distribution is critically important when determining the stratigraphic ranges of the species (Barry et al. 2002). Finally, while most localities have only a few tragulid fossils, a few have many, making it possible to analyze variation within what can be assumed is a single species.

4. Tragulid Species

Three genera are customarily recognized among Siwalik tragulids, *Dorcabune* with six nominal species, *Dorcatherium* with four, and *Siamotragulus* with one, to which *Tragulus sivalensis*, described by Lydekker (1882, 1884) on the basis of one upper molar, should be added. However, the status of several species is uncertain and systematic revision of them is difficult because of inadequate types that are of unknown province and age. Consequently, stratigraphic ranges of all the species are poorly known and relationships with tragulids in Eurasia and Africa are for the most part unexplored.

4.1 *Dorcabune*

At least three species of *Dorcabune* can be recognized in the new collections. These include *Dorcabune anthracotheroides*, named and cursorily described by Pilgrim (1910), and *Dorcabune nagrii* and *Dorcabune sindiense*, subsequently described by Pilgrim (1915). Because teeth and some skeletal elements of this genus are distinctive and the species differ markedly in size (Textfig. 2), most of the material can be sorted into species. *Dorcabune anthracotheroides* is the largest with, based on all the fossil material in addition to the astragali, a stratigraphic range of at least 14.1 to 10.6 Ma, while the much smaller *Dorcabune nagrii* has a stratigraphic range between 11.3 and 8.2 Ma. In Sind *Dorcabune sindiense* is present in the upper most Gaj Formation



Textfigure 2: Widths of the distal astragalus of specimens of *Dorcabune* and very small species attributed to *Dorcatherium* ? plotted against time.

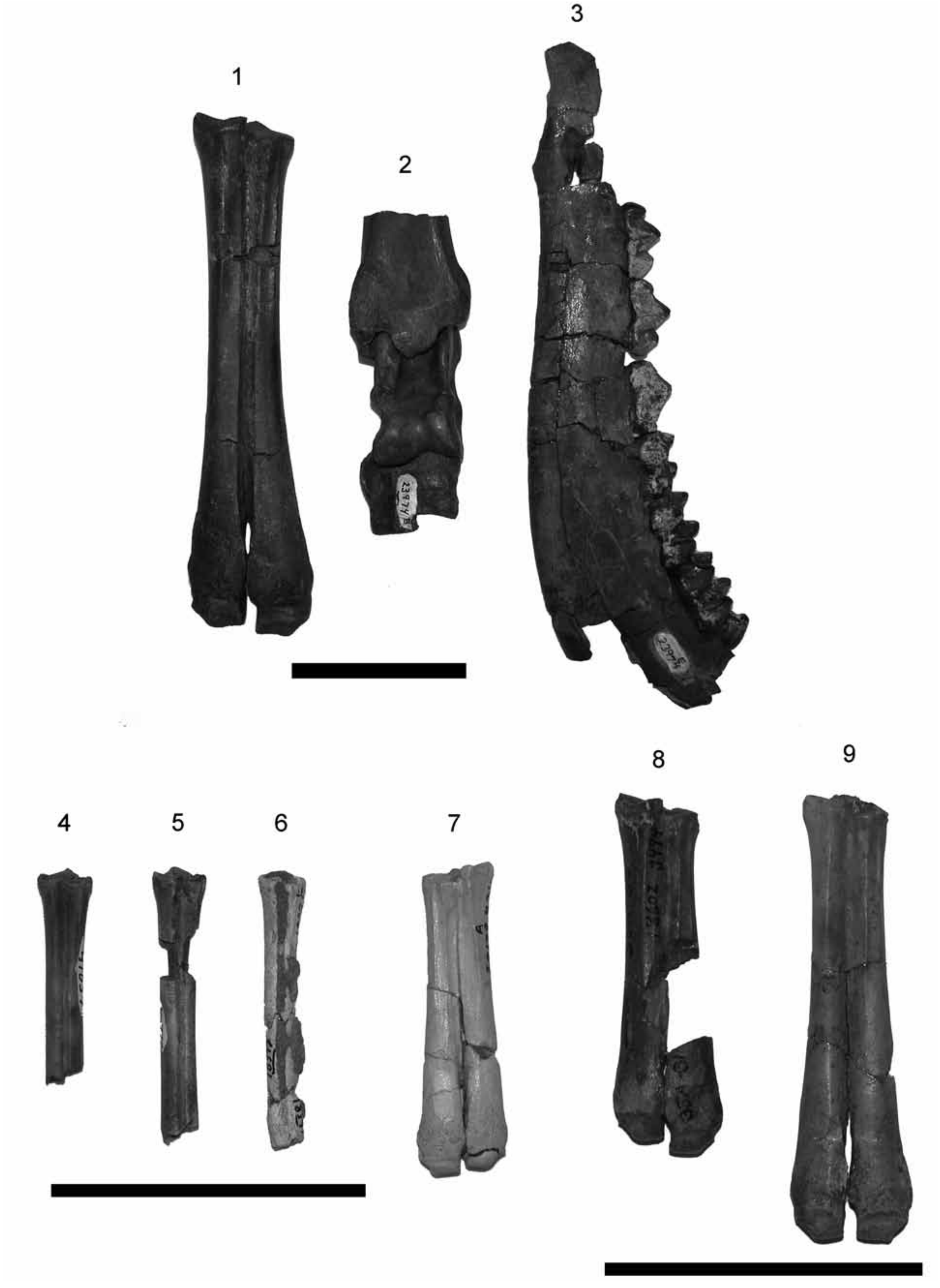


Figure 1: (1, 2, 3) Associated postcranial elements and left mandible of a single individual of *Dorcabune anthracotheroides* (GSPY 29974). Postcranial elements include a left metatarsal and a fused right distal tibia and fibula, right astragalus, and right cuboid-navicular-ecto-mesocuneiform (all in dorsal view). The mandible is in labial view with alveolus for p1 and crowns of p2 to m3. **(4, 5, 6,)** Three left incomplete metatarsals attributed to *Siamotragulus* (from left to right GSPY 41037, GSPY 40772, and GSPY 18397) compared to a metatarsal of *Dorcatherium* form 3 (GSPY 20179). The specimens are respectively 11.9, 13.4, 8.1 and 10.1 million years old. All in dorsal view. **(7, 8, 9)** A metatarsal of *Dorcatherium* form 5 on the left (GSPY 18602) compared to a metatarsal of *Dorcatherium* form 6 on the right (GSPY 23906). The proximal widths of the two specimens are very nearly equal. The age of GSPY 18602 is 12.3 Ma and that of GSPY 23906 13.4 Ma. Both in dorsal view. Scale bars are 5 cm.

and lower third of the Manchar Formation, as well as on the Potwar where specimens have been found in the Kamlial and lowest Chinji Formations. The Potwar occurrences establish a minimum range of 16.8 to 13.6 Ma, but the Manchar and Gaj localities might be considerably older. In addition to these three taxa, there is possibly a fourth species, as a few postcranials from the Kamlial Formation, including a 15.1 million year old astragalus (*Dorcabune* sp. on Textfig. 2), are too large for *Dorcabune sindiense*. However, the size dispersion among specimens of *Dorcabune anthracotheroides* (Textfig. 2) suggests strong sexual dimorphism in the genus, adding to the complexity of recognizing species. On present evidence *Dorcabune welcommi* (Ginsburg et al. 2001) is difficult to differentiate from *Dorcabune sindiense*.

An associated distal tibia, astragalus, cuboid-navicular complex, metatarsal, and mandible of *Dorcabune anthracotheroides* (Fig. 1) shows that in this adult individual the distal tibia was fused with the remnant of the fibula and the slender 3rd and 4th metatarsals were fused proximally with free distal ends. In addition, the ecto-mesocuneiform is fused to the cuboid-navicular complex, while the astragalus has a well marked facet for the medial malleolus of the tibia, a deep pit for a posterior astragalofibular ligament, a shallow lateral incurvature between the proximal and distal trochleas, and a subdued lateral prominence for the superior calcaneal articulation. The latter two features give the lateral face of the astragalus a flatter, more bovid like aspect and allow the astragalus of *Dorcabune* to be distinguished from that of *Dorcatherium*. The fused cuboid-navicular and ecto-mesocuneiform complex, fused metatarsals, and the pit for the posterior astragalofibular ligament are characteristic of tragulids. A proximal 3rd metacarpal of a different individual (GSP Y 46194) is similar to that of *Dorcatherium crassum* in lacking the interlocking mechanism described by Morales et al. (2012) for *Dorcatherium naui*.

4.2 *Siamotragulus*

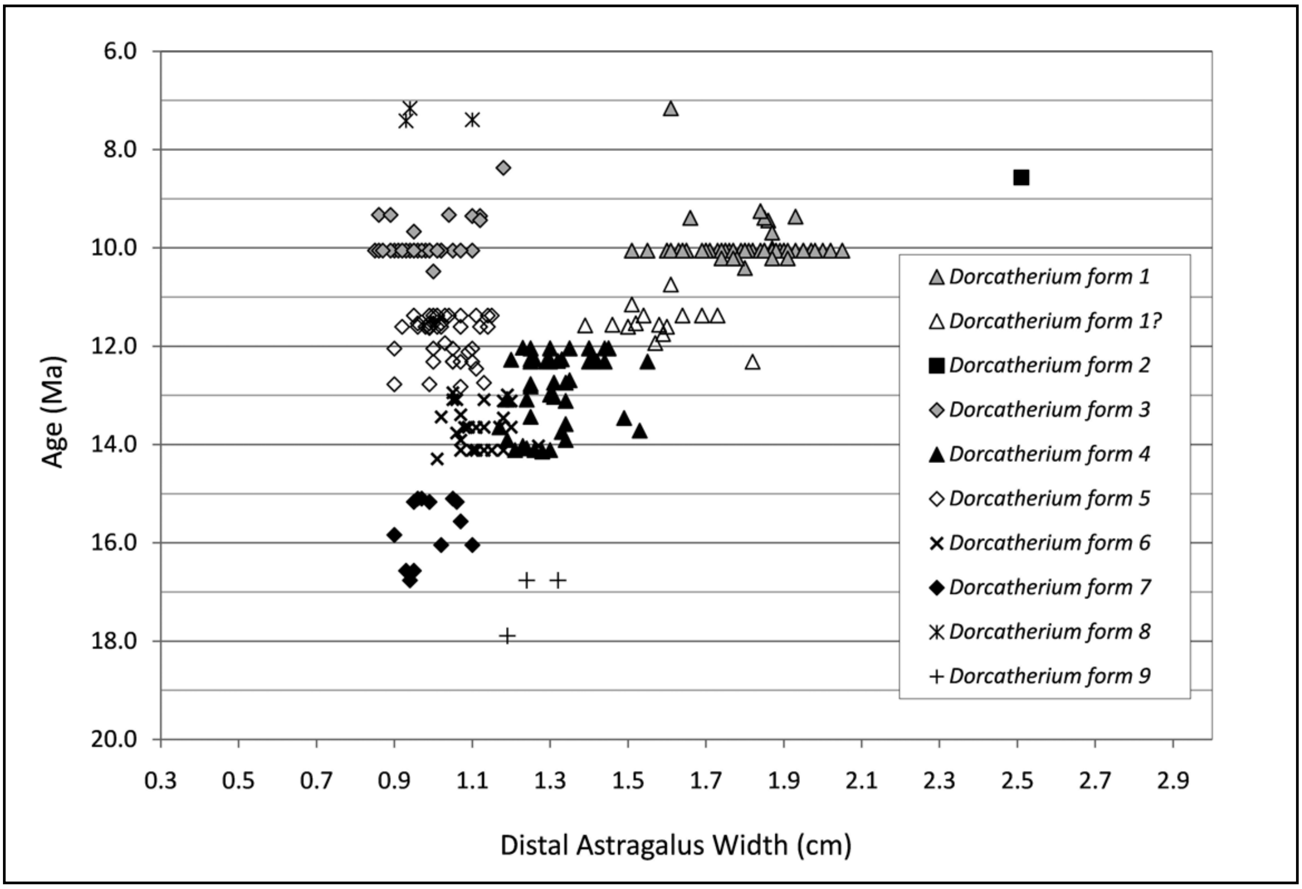
Two very small taxa are among described Siwalik species attributed to *Dorcatherium*, *Dorcatherium minimus* (West 1980) from the Middle Miocene and *Dorcatherium nagrii* (Prasad, 1968) from the Late Miocene. Both species are presumably represented in the new collections, but there is evidence that there are additional undescribed small species present as well. The two smallest specimens on Textfigure 2 (distal widths: 0.48 and 0.53 cm) are smaller than the astragalus (distal width: 0.55 cm) referred to *Dorcatherium minimus* by West (1980). However, other contemporaneous specimens are larger suggesting the presence of a second Middle Miocene small species. Morphological differences in the premolars of the Late Miocene specimens as well as slight differences in astragalus size (forms “B” and “C” on Textfig. 2) also indicate the likely presence of two small Late Miocene taxa.

Three partial metatarsals (Fig. 1) are complete enough to show the characteristic slender, elongated form of *Siamotragulus*. The specimens are 13.4 (GSPY 40772), 11.9 (GSPY 41037), and 8.1 (GSPY 18397) million years old and document the occurrence of at least two Siwalik *Siamotragulus* species in the Middle and Late Miocene. These specimens are all very much younger than *Siamotragulus bugtiensis* from the Early Miocene of Dera Bugti (Ginsburg et al. 2001). Very small tragulids are also known from the Vihowa Formation at about 18.7 to 20 Ma and possibly from the Chitarwata Formation at between 21 and 23 Ma.

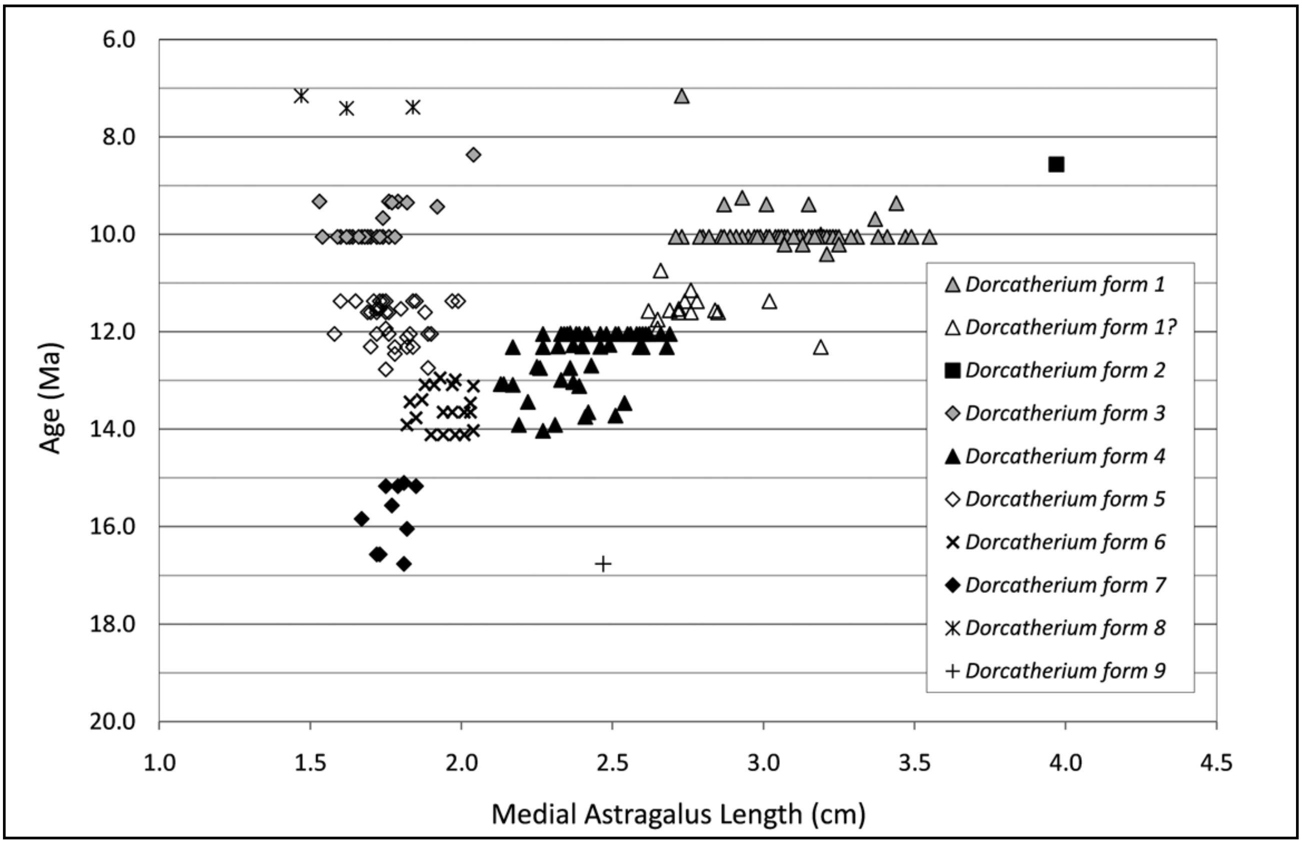
4.3 *Dorcatherium*

Other, larger Siwalik species attributed to *Dorcatherium* include *Dorcatherium majus* and *Dorcatherium minus*, both described by Lydekker (1876). These two species are part of a complex assemblage which could include as many as nine or even ten different taxa. A plot of the width of the distal astragalus against time for instance (Textfig. 3) shows separation of numerous clusters that are likely to be distinct species. Note, however, that while the astragalus width gives good separation for the Late Miocene taxa, the Middle Miocene clusters are not as distinct from one another. Between 14 and 12 Ma there were apparently multiple species of overlapping size. A plot of the medial length of the astragalus against time (Textfig. 4) improves separation of the Middle Miocene groups, indicating there were differences in limb proportions among these groups. Overall, although the most visible distinctions between these putative species reflect differences in size and proportions, examination of the dental material in some cases supports the clustering based on postcranial materials. An interesting example is the taxon labeled “form 8” in Textfigs 3 and 4, which differs from the similar sized older “form 3” in that it has molars with higher crowns. The same high crowned species apparently also occurs in the Tatrot Formation at 3.3 Ma. The consistent trend of size increase among the larger species is also noteworthy.

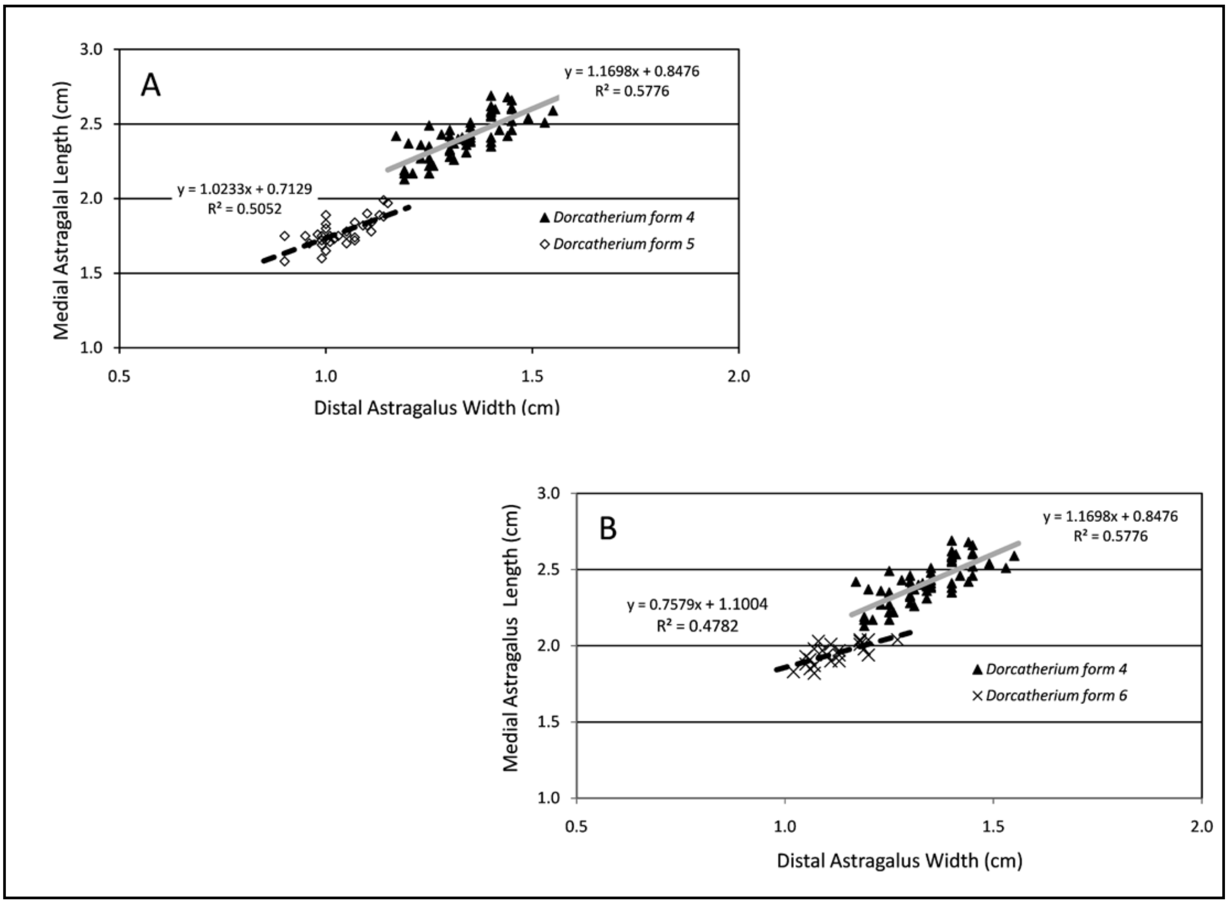
Differences in skeletal proportions suggest the taxa of the *Dorcatherium* complex fall into two subgroups. One subgroup, exemplified by form 5, has short and stouter limb elements and the other, exemplified by form 6, relatively long and slender limbs. This is seen in plots of astragalus length versus width for selected pairs of species (Textfig. 5) and in the dimensions of the very few intact metatarsals (Fig. 1 and Textfig. 6). The extant water chevrotain, *Hyemoschus aquaticus*, is allied with the short, stout taxa.



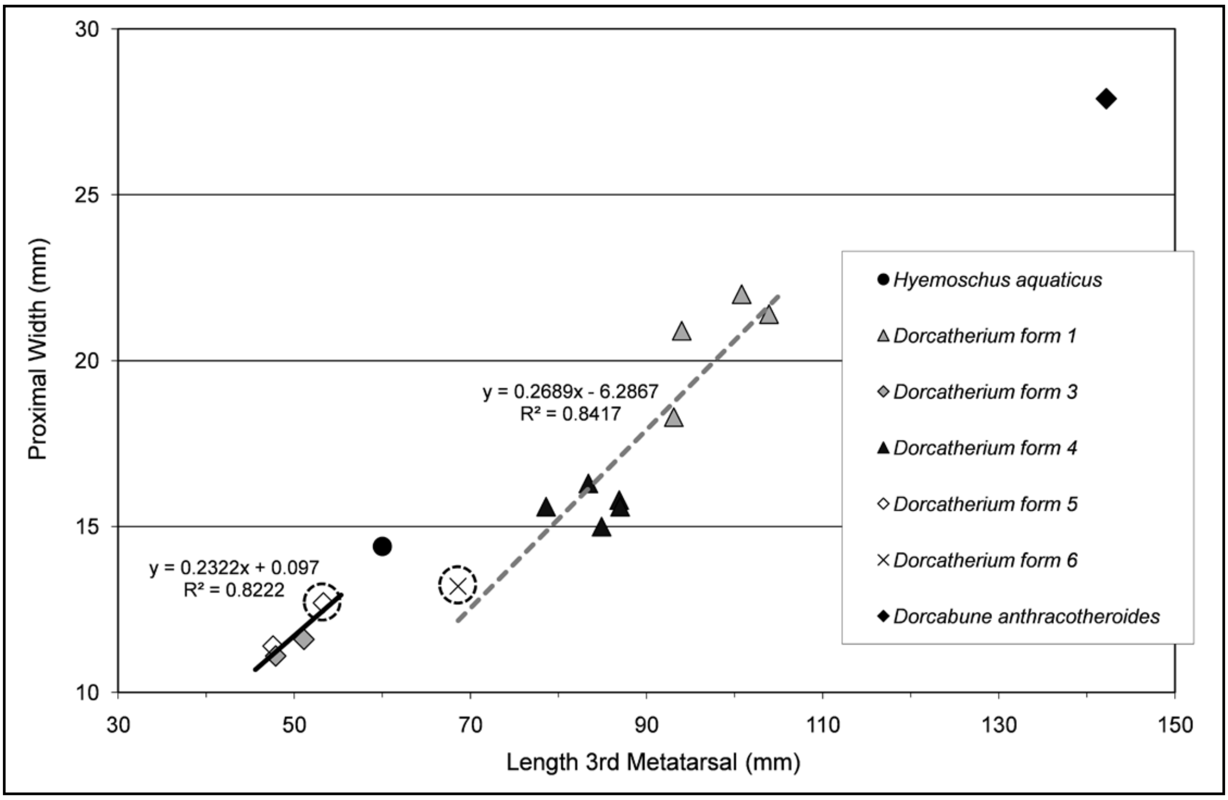
Textfigure 3: Widths of the distal astragalus of specimens of the *Dorcatherium* complex plotted against time.



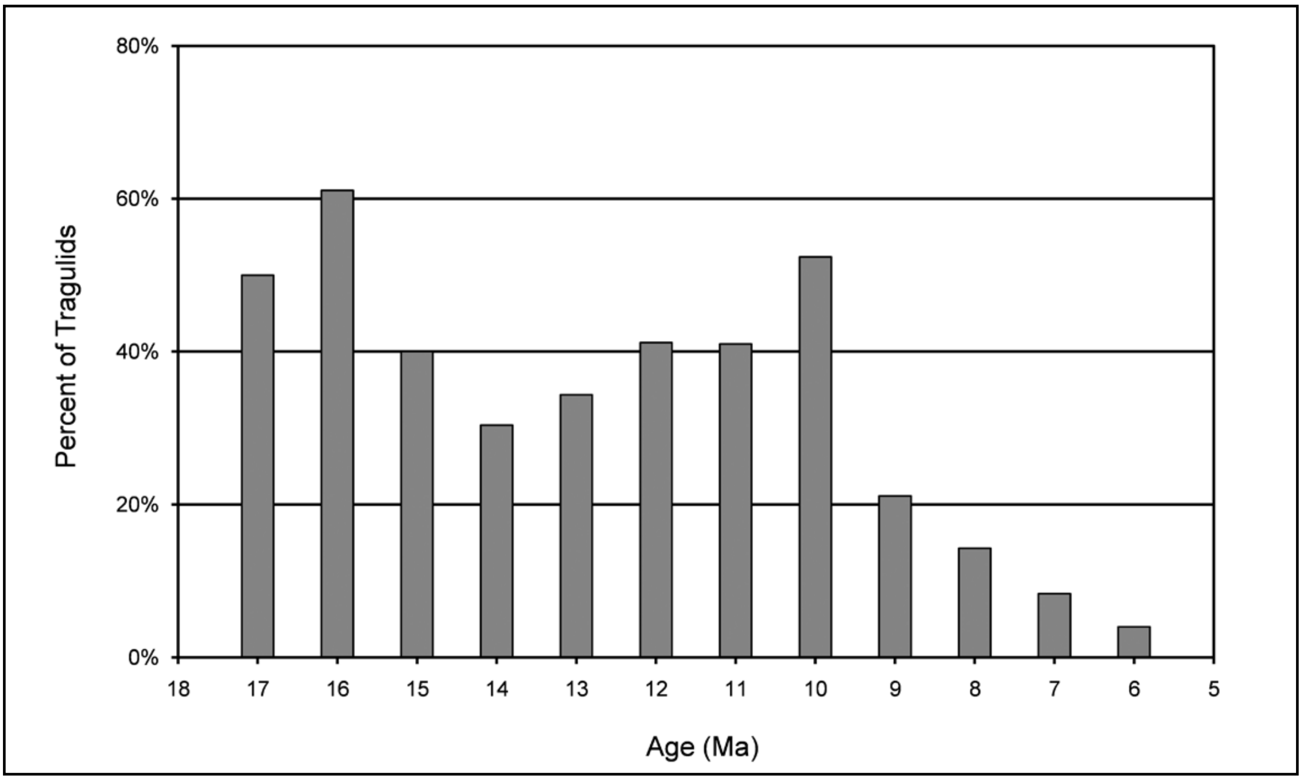
Textfigure 4: Lengths of the medial astragalus of specimens of the *Dorcatherium* complex plotted against time.



Textfigure 5: Widths of the distal astragalus for species of the *Dorcatherium* complex plotted against their medial lengths. **(A)** *Dorcatherium* form 4 v. *Dorcatherium* form 5, **(B)** *Dorcatherium* form 4 v. *Dorcatherium* form 6.



Textfigure 6: Length versus proximal width of 3rd metatarsals of specimens of the *Dorcatherium* complex and *Dorcabune anthracotheroides*. The filled circle is *Hyemoschus aquaticus* (Harvard Museum of Comparative Zoology 6011). The two points circled are the specimens 8 and 9 illustrated on Fig. 1.



Textfigure 7: Percentage of tragulids in small ruminant fauna (bovids + tragulids) over time. Based on counts of the number of astragali and cuboid-naviculars. Data combined into bins of one million years duration.

5. Tragulid Abundance and Environmental Change

Prior to 9.5 Ma tragulids are nearly as common as bovids in the collections. Based on counts of the astragali and cuboid-naviculars, between 17 and 10 Ma 30% to over 60% of the smaller ruminants were tragulids (Textfig. 7). After 10 Ma the numbers steadily decline to just 4% at the end of the Miocene. Although the taphonomical effects of size need to be considered, these numbers presumably reflect relative abundance in the living communities and mark changes in the ecological structure of the ancient communities.

The change in abundance roughly corresponds to significant climate related environmental change (Badgley et al. 2008). The Siwaliks formed in a large fluvial system, with the depositional settings most productive of fossils being the lithologically mixed fills of the smaller floodplain channels. Many paleosols are present and, although some may have formed under waterlogged, grassy vegetation, the low relief floodplains were mostly forested or wooded with abundant cover and fruit (Retallack 1991). Isotopic analyses of tooth enamel and soil carbonates indicate that the vegetation was dominated by C3 plants until ca. 10 - 9 Ma, after which there were significant changes in precipitation with a shift to a more seasonally dry monsoon climate (Quade et al. 1989, Morgan et al. 2009). The carbon isotope record shows that by 8 Ma there was considerable C4 grass on the floodplains and by 7 Ma extensive C4 grasslands (Barry et al. 2002). At the same time predominantly C3 communities became less common, which undoubtedly accounts for the change in the relative abundance of tragulids and the progressive Late Miocene appearance of larger species with higher crowned teeth.

6. Conclusions

In summary three main points emerge from this preliminary study. First, Siwalik tragulids are species rich, with potentially as many as sixteen species belonging to three genera and typically four or five species present at any one time. This pattern is similar to that of contemporary Miocene bovids, although Siwalik bovids are represented by many more genera. Second, the relative abundance of the Early and Middle Miocene species is only slightly less than that of bovids, but tragulids became progressively rarer in the Late Miocene and comprise only about 4% of the smaller ruminants at 6 Ma. The shift in relative abundance is not related to changes in species richness, although it is correlated to environmental change and may reflect change in species composition. And third, within genera the tragulids are morphologically uniform, but putative species differ in size and in some instances skeletal proportions.

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