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Revision of Hipparion (Equidae, Mammalia) from the Siwalik Hills of Pakistan and India

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PREFACE

It was Professor R. G. Davies, former Chairman of the Geology Department, Panjab University, Lahore, Pakistan, who took up the idea of developing a Section of Vertebrate Fossils at Lahore. The visit of Professor G. H. R. von Koenigswald and Dr. P. Y. Sondaar from the University of Utrecht, the Netherlands in 1964 initiated the collaboration of the two departments.

In the same year they worked in the field and collected vertebrate fossils in the Siwalik Hills. Another trip was arranged in the winter of 1966 joined by Prof. and Mrs. von Koenigswald, Dr. P. Y. Sondaar, Mr. A. J. van der Meulen from Utrecht and myself. The material was then brought to Utrecht where I started working on Siwalik Equidae.

The interesting results stimulated me to study more relevant material. In September, 1967, Dr. H. de Bruijn and myself visited Professor R. Dehm in Munich, W. Germany who very kindly put all of the Siwalik Hipparion collection at my disposal. Later on I brought this collection with me to Utrecht, the study of which yielded very promising results. In June, 1968, I paid a visit to the British Museum of Natural History, London, to study the specimens stored over there. In September, 1968, I went to the United States of America for three months to study the material in the American Museum of Natural History, New York, and the Yale University Peabody Museum, New Haven, which forms a large part of the Siwalik Collection. Many individuals and organizations have helped in some way or the other to whom I wish to express my gratitude.

I am very grateful to Prof. Dr. G. H. R. von Koenigswald for allowing me to work on this project and for putting the Utrecht Siwalik collection at my disposal. His suggestions and comments at every stage were of great help to complete this work.

Dr. P. Y. Sondaar suggested the project and guided the research. The discussions with him during investigations were very stimulating and fruitful in elucidating various problems. My indebtedness to Dr. Sondaar for his support and for much more is gratefully acknowledged.

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I wish to thank Prof. Dr. R. G. Davies who instigated the study of fossil mammals in the Siwaliks and provided every facility for field work.

I am highly obliged to Prof. Dr. R. Dehm who put all of the Siwalik Hipparion material and field data at my disposal, without which this work had not been possible, I am also thankful to Dr. F. Obergfell and Dr. V. Fahlbusch for their assistance during my stay in Munich.

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I am especially thankful to Mr. Morris F. Skinner for his constructive and stimulating discussions on North American fossil Equidae. Dr. Edwin H. Colbert was also very kind in discussing the subject for which I am thankful to him.

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The credit for all the figures and plates goes to Mr. J. Luteyn for which I am highly indebted to him. Mr. P. van Heumen prepared some of the fossils for study for which I am thankful to him.

Thanks are due to Mr. P. van der Kruk who went through the manuscript with a grammatical and semantical toothcomb.

I am especially thankful to Miss Nicky M. Kroll who very efficiently converted my scrawl into a typed manuscript.

Two years of research were supported by the International Technical Assistance Department of the Ministry of Foreign Affairs, the Netherlands and an additional seven months were financed by the Education Ministry of the Netherlands. The stay in the United States of America was partially financed by the American Museum of Natural History, New York. The field trip of 1964 was financed by the Wennergren Foundation of New York and the Netherlands Organization for the Advancement of Pure Research (Z.W.O.), whereas the trip of 1966 was financed by the Werner Reimers Stiftung für anthropogenetische Forschungen, Frankfurt a/Main, W. Germany. University of the Panjab (Lahore, Pakistan) provided with a vehicle, technical staff and facilities to work in the field. Another vehicle was provided by Mr. van Haaften during the trip of 1966. The financial and technical support offered by these organizations and Mr. van Haaften is gratefully acknowledged.

Finally I wish to express my feelings of gratitude to the members of the Geological Institute, State University of Utrecht who have been very friendly and helpful during my stay in the institute.

ABSTRACT

A short account of the geology of Potwar Plateau, NW Pakistan is given. Stress is laid on the stratigraphy of the Siwalik Group of rocks which ranges from Late Miocene to Early Pleistocene in age. These continental sediments of about 20,000 feet in thickness are considered to be a continuous series of deposits without any definite break in deposition. The Lower and Middle Siwaliks are mainly composed of sandstones and clays with pseudo-conglomerates whereas the Upper Siwaliks are recognized by the presence of true conglomerates. In the Upper Siwaliks size of the pebbles increases toward the top.

Fossil mammals are represented by the following orders: Primates, Rodentia, Lagomorpha, Carnivora, Tubulidentata, Proboscidea, Perissodactyla and Artiodactyla. Forest dwelling animals form a major part of the faunal association in the Lower Siwaliks but in the Middle and Upper Siwaliks animals living in open country predominate.

Hipparion and *Equus* are the only equids (Perissodactyla) present in the Siwaliks. *Equus* is restricted to the middle and upper parts of the Upper Siwaliks. *Hipparion* is the most common mammal in the Middle Siwaliks. Representatives of the genus are described in detail from the type localities of the Nagri and the Dhok Pathan Formations and their taxonomy is revised. Two species, namely *Hipparion antilopinum* (FALCONER & CAUTLEY) 1849 and *Hipparion theobaldi* (LYDEKKER) 1877 are described from the Dhok Pathan beds. A new species *Hipparion nagriensis* from Nagri (Nagri Formation) is introduced.

Hipparion nagriensis is an animal of average size with moderately large teeth which are least hypsodont among Siwalik *Hipparion* species. The foot structure is primitive and is comparable to the older European forms like *Hipparion catalaunicum* PIRLOT, 1956. *Hipparion antilopinum* has the smallest and most hypsodont teeth among the Siwalik forms. Its metapodials are the most slender among the Siwalik species. In tooth size it shows similarities to *Hipparion concudense* PIRLOT, 1956. *Hipparion theobaldi* is a large animal with heavy metapodials. The teeth are moderately hypsodont and the largest among the three species. Its foot is very much specialized and acquires great similarity to that in *Equus*. The foot structure of *Hipparion theobaldi* is comparable with that of *Hipparion crusafonti* VILLALTA, 1952 and of *Hipparion crassum* GERVAIS, 1859.

It is argued that *Hipparion* appears for the first time in the Nagri Formation *(Hipparion nagriensis)*. In the upper layers of the Nagri Formation or the lowermost parts of the Dhok Pathan Formation it gives rise to two forms: *Hipparion antilopinum* and *Hipparion theobaldi*. The latter two forms then develop independently. Increase in hypsodonty and specializations in the foot structure are seen. No conspicuous change was observed in the dental morphology. The genus becomes extinct in the topmost layers of the Dhok Pathan Formation or in the basal part of the Tatrot Formation.

ZUSAMMENFASSUNG

Eine kurze Übersicht über die Geologie des Potwar-Plateau in Nordwest-Pakistan wird gegeben. Nachdruck wird auf die Stratigraphie der Siwalik-Schichten gelegt, die vom späten Miozän bis in das frühe Pleistozän reichen. Diese festländischen Ablagerungen von etwa 20000 Fuß Mächtigkeit können als zusammenhängende Schichtfolge ohne merkliche Sedimentationsunterbrechung betrachtet werden. Die Unteren und Mittleren Siwaliks setzen sich hauptsächlich aus Sandsteinen und Tonen mit Pseudokonglomeratlagen zusammen, während die Oberen Siwaliks am Auftreten echter Konglomerate erkannt werden; die Geröllgröße nimmt in den Oberen Siwaliks nach oben zu.

Fossile Säugetiere werden durch folgende Ordnungen repräsentiert: Primates, Rodentia, Lagomorpha, Carnivora, Tubulidentata, Proboscidea, Perissodactyla und Artiodactyla. Waldbewohner bilden den Großteil der Faunengemeinschaft in den Unteren Siwaliks, in den Mittleren und Oberen Siwaliks aber herrschen Bewohner offenen Geländes vor.

Hipparion und *Equus* treten als einzige Equiden (Perissodactyla) in den Siwaliks auf. *Equus* ist auf den mittleren und oberen Teil der Oberen Siwaliks beschränkt. *Hipparion* ist das verbreitetste Säugetier in den Mittleren Siwaliks. Vertreter dieser Gattung werden im einzelnen von den Fundstellen der Nagri- und der Dhok-Pathan-Stufe beschrieben; ihre Taxonomie wird revidiert. Zwei Arten, *Hipparion antilopinum* (FALCONER & CAUTLEY) 1849 und *Hipparion theobaldi* (LYDEKKER) 1873 werden aus den Dhok-Pathan-Schichten beschrieben. Eine neue Art, *Hipparion nagriensis*, wird aus Nagri (Nagri-Stufe) aufgestellt.

Hipparion nagriensis ist ein Tier von Durchschnittsgröße mit mäßig großen Zähnen, die unter den *Hipparion*-Arten der Siwalik-Schichten am wenigsten hypsodont sind. Der Fußbau ist primitiv und mit den älteren europäischen Arten wie *Hipparion catalaunicum* PIRLOT, 1956 vergleichbar. *Hipparion antilopinum* hat unter den Siwalik-Arten die kleinsten und am stärksten hypsodonten Zähne; ebenso die schlanksten Metapodien. Die Zahngröße zeigt Ähnlichkeiten mit *Hipparion concudense* PIRLOT, 1956. *Hipparion theobaldi* ist ein großes Tier mit plumpen Metapodien. Seine Zähne sind mäßig hypsodont und unter den drei Siwalik-Arten am größten; sein Fuß ist sehr stark spezialisiert und erreicht große Ähnlichkeit mit dem von *Equus*. Der Fußbau von *Hipparion theobaldi* ist demjenigen von *Hipparion crusafonti* VILLALTA, 1952 und von *Hipparion crassum* GERVAIS, 1859 vergleichbar.

Es wird erörtert, daß *Hipparion* zuerst in der Nagri-Stufe *(Hipparion nagriensis)* erscheint. In den oberen Lagen der Nagri-Stufe oder in den tiefsten Teilen der Dhok-Pathan-Stufe entstehen aus ihm zwei Formen: *Hipparion antilopinum* und *Hipparion theobaldi*. Diese zwei Formen entwickeln sich unabhängig voneinander. Man kann Zunahme der Hypsodontie und Spezialisierungen im Fußbau erkennen. In der Zahnmorphologie ist kein auffälliger Wechsel zu bemerken. *Hipparion* stirbt zur Zeit der obersten Lagen der Dhok-Pathan-Stufe oder der basalen Teile der Tatrot-Stufe aus.

I. INTRODUCTION

The Siwalik continental deposits of over 20,000 feet in thickness ranging from Late Miocene to Early Pleistocene in age are mainly composed of sandstones and clays. The upper layers are characterized by the presence of conglomerates. MEDLICOTT (1864) divided this group of rocks into Lower, Middle and Upper parts on the basis of lithology. Later PILGRIM (1910B) showed that such a division was also possible on the basis of fauna. These three subgroups further consist of various formations. Vertical change from one formation to the other is always gradual; however, unconformities of local importance are seen. Animals typical of forest habitat, like suids and anthracotherids are very common in the Lower Siwaliks. In the Middle Siwaliks these animals are gradually replaced by those inhabiting open countries. *Hipparion* is the most abundant mammal in the Middle Siwaliks, and along with it antelopes are also common. In the Upper Siwaliks *Equus*, *Bos* and *Archidiskodon* are predominant mammals and also depict open country environment.

Hipparion DE CHRISTOL, 1832, evolved from *Merychippus* LEIDY, 1857, in the Miocene in North America and afterwards the genus spread over to Asia, Europe and Africa. The presence of the genus *Hipparion* in the Siwaliks was first mentioned by OWEN (1846) who looked at some of the material in the British Museum of Natural History, London and considered it to be similar to *Hipparion 'gracile'*. From then onward various people have been collecting and studying fossil Equidae in the Siwaliks. For further details the reader is referred to the part of this paper dealing with previous work.

Hipparion remains are obtained from nearly every part of the Middle Siwaliks containing fossils. Usually a great number of isolated teeth are found, because they are the hardest part of the skeleton and withstand the effects of weathering and decay more easily than the fragile skulls and other parts of the skeleton.

The purpose of this study is to revise the taxonomy of the genus *Hipparion* from the Siwaliks, and to provide a firm basis for evolutionary studies. All the available material (skulls, jaws, teeth and postcranial skeleton) has been used, so as to give a comprehensive picture of the animal. Stress is laid on the study of the manus with special reference to phylogeny and function. A phylogenetic tree is presented to show the apparent relationships and geological distribution of the species of Siwalik *Hipparion*.

The concept of species denotes a population or group of populations within which gene exchange is possible, but which is reproductively isolated from other such groups. Since the species described in this review are extinct, they are of necessity based on morphological criteria; but it may be pointed out that morphologies are controlled by the complex of genetic compositions of the animals. In this connection the statement of RADINSKY (1963) has been found most agreeable where he explains that although most species are recognized on morphological basis, the concept of a species should be based on its most fundamental character, i.e. its genetic isolation.

1. PREVIOUS WORK ON SIWALIK HIPPARION

Studies of fossil equids from the Siwaliks were first made by OWEN (1846). He observed some of the material sent by Cautley to the British Museum of Natural History and distinguished the teeth of the extinct slender-legged horse or hippothere as identical to the European *Hippotherium 'gracile'* KAUP, 1833.

The first systematic study was made by FALCONER & CAUTLEY (1849). They differentiated two genera of the Siwalik equids, *Hippotherium* and *Equus*. Their subgenus *Hippotherium* was represented by *H. antilopinum*. It should be kept in mind that FALCONER did not publish any memoir of the fossil Equidae from the Siwaliks. The only means of identifying these species are from the mentioned specimens stored in the British Museum, and from the small scale figures in the 'Fauna Antiqua Sivalensis'.

GAUDRY (1862, p. 231) concluded that the limb bones of *Hippotherium antilopinum* FALCONER & CAUTLEY, 1849, from the Siwaliks closely resembled the slender bones of *Hipparion 'gracile'* from Pikermi.

VON MEYER (1865, p. 17) described some upper molars of a hippothere collected by Schlagintweit in the Siwaliks of Nurpur and Kushalghar. He concluded that *Hippotherium antilopinum* of FALCONER & CAUTLEY could not be distinguished from his *Equus primigenius = (Hipparion 'gracile')*.

GAUDRY (1873, p. 32) observed that certain fossil equid teeth from China, in the British Museum, looked identical with those of the Indian hippotheres. He further mentions (p. 40) that certain Siwalik foot bones, in the British Museum, figured in the 'Fauna Antiqua Sivalensis' assigned to *Hippotherium antilopinum* are monodactyl.

COPE (1888) erected a new genus for this species, considering it as monodactyl (after GAUDRY) and gave it the name *Hippodactylus antilopinum*.

Another comprehensive study of the fossil equids from the Siwaliks is LYDEKKER'S (1877–1887). He describes some upper cheek teeth of a horse from the Siwaliks under the name *Sivalhippus theobaldi* (1877, p. 31). In the same paper he notes that probably two species of *Equus* and two of *Hippotherium* existed in the Siwaliks. Later in the same year (p. 82) he shows that *Sivalhippus* was the same as the second species of *Hippotherium*, which was accordingly named *Hippotherium theobaldi*. Following GAUDRY'S conclusions he thought that the bones showing monodactyl foot belonged to *Equus*. In 1882 LYDEKKER distinguished between the milk teeth of *H. antilopinum* and *H. theobaldi:* "In *H. antilopinum* the anterior 'pillar' is subcylindrical and completely enclosed by cement in the mass of the crown: the posterior 'pillar' does not extend backward as far as the hinder border of the crown; while in the second milk molar the same 'pillar' is disconnected from the body of the tooth. The enamel is much plicated, and the cement of great thickness.

In *H. theobaldi*, on the other hand, the anterior 'pillar' is much compressed, so as to be longitudinally elongated; it also stands out distinctly from the crown, so that its posterior border forms a free sharp edge: the posterior 'pillar' extends backward as far as the hinder border of the crown; while in the second milk molar the same 'pillar' is united with the adjacent 'crescent'. The enamel is but slightly plicated, and the cement thin." In 1886 LYDEKKER re-examined the foot bones and concluded that they were in fact of *Hipparion antilopinum*, therefore the bones of slender *Hipparion* which retained lateral digits were assigned to another species, *H. punjabiense*. In 1884 he proposed a new species *Hippotherium feddeni* from Perim Island (southwestern India, in the Gulf of Cambay) on the basis that it had a subcircular protocone and a constricted hypocone, moreover he remarks upon the size of the teeth as intermediate between the two pre-existing species. In the year 1887 (p. 58) he summarized his work: "of *Hipparion* there are apparently at least three species; viz. *H. antilopinum* agreeing in size with *H. 'gracile'*, but with only one functional digit to each foot; a second form, to which the name *H. punjabiense* has been provisionally assigned, of nearly the same dimensions, but apparently having three complete digits; and a larger species with the same number of digits known as *H. theobaldi*. A fragment of an upper jaw from Perim Island could not be satisfactorily identified with either of these three froms, and if distinct the name *H. feddeni* has been suggested for it."

PILGRIM (1910) retained the genus *Hippodactylus* and made a new species *Hippodactylus chisholmi*. He distinguished it from *H. antilopinum* on the probability that it was monodactyl. He further distinguished *H. perimense* on a skull from Perim (previously described by LYDEKKER in 1884 as *H. antilopinum*) as a distinct species, different from *H. punjabiense* in respect of having a shallower preorbital fossa situated farther from the orbit, but in 1913 after re-examining the types he decided that the two species were identical.

In his critical observations upon the Siwalik Mammals, MATTHEW (1929, p. 528) concludes, "I do not think therefore that there is any evidence that *H. antelopinum* was monodactyl or any reason to maintain the genus *Hippodactylus*. That the smaller and more slenderly proportioned *Hipparions* of India had reduced lateral digits as compared with the exceptionally heavy laterals of *H. theobaldi* etc., is quite probable. This being granted, there appears no evidence for maintaining *H. punjabiense* as distinct, and with it goes *H. perimense* auct. PILGRIM, 1913. *H. chisholmi* has not been distinguished from *antelopinum* by any characters of specific value–the greater size of M^3 and 'squareness' of teeth are both probably due to greater wear as compared with the little worn type of *antelopinum*."

MATTHEW (1929, p. 525) has argued on the validity of the characters for distinction between *Hipparion antilopinum* and *Hipparion theobaldi* given by LYDEKKER. He thinks that the above mentioned characters are entirely dependent upon age and the stage of wear, and cannot be considered of any specific value. "None of the characters adduced by LYDEKKER to separate *theobaldi* from *antelopinum* appear to be valid distinctions. Nevertheless the *type* of *theobaldi* is too large to represent the milk dentition of the *type* of *antelopinum*, and comparison of various permanent dentitions from the Siwalik supports LYDEKKER'S view that there are a large and a small form the former decidely more robust and with heavier limb bones and larger lateral digits."

COLBERT (1935 C, p. 137) concludes that there are two species of *Hipparion* in the Siwaliks, a large and a small one. To quote:

"1 – There are two species of *Hipparion* in the Siwalik series, a large one, *Hipparion theobaldi*, and a small one, *Hipparion antelopinum*.

2 – The teeth of these two species differ only as regards size. There are no appreciable differences in the molar patterns.

3 – There is a constant gradation in the teeth between the two species.

4 – The foot bones of the two species are markedly different, being robust in *H. theobaldi* and very slender in *H. antelopinum*.

5 – Until associated teeth and feet of both species are found, it will be impossible to draw definite lines of distinction between them on the basis of teeth alone. Consequently it becomes necessary to establish an arbitrary line in dividing a series of teeth between these two species. In general, molar teeth that measure more than 24 millimeters in an anteroposterior direction and 25 millimeters transversely, may be assigned to the species, *Hipparion theobaldi*."

GROMOVA (1952) in her conclusions about the Siwalik *Hipparion* admits the existence of two species as already given by MATTHEW (1929) and COLBERT (1935). She further thinks that the structure of the preorbital fossa does not allow to split the genus into two groups, but the big difference in the skull measurements and certain teeth are in favour of the two groups. She thinks that the metatarsal no. AMNH 19667, figured by COLBERT (1935C, p. 141) is of young individual and if it is so, then she believes that the massivity is not a character to distinguish these two species by. The existence of *H. theobaldi* (LYDEKKER), 1877 from the base of the Chinji till the top of the Dhok Pathan Formation, however, seems to her to be doubtful. She is of opinion that it is very likely that one will be forced later on to distinguish more species. "Les restes de cette espèce caractérisent un énorme intervalle de temps: de la zone du Tchinji (Miocène supérieur, contemporain du Sarmatian Supérieur?) jusqu'à la zone de Dhok-Pathan (Pliocène inférieur ou moyen); cependant, l'existence d'une espèce unique durant un temps aussi long paraît douteuse. Il est très probable qu'on sera amené plus tard à distinguer plusieurs espèces" (p. 255). She further concludes that the shape of the preorbital fossa and proportion of the extremities distinguish Siwalik *Hipparion* from East European and Pavlodar. The elongated protocone in the upper cheek teeth and cabaloid type double knot in the lower cheek teeth are more marked in the Siwalik *Hipparion*. She further states that the smallest teeth of *H. antilopinum* correspond to the measurements of *H. moldavicum* and *H. elegans*. In the shape of the protocone and the frequency of the enamel folds she also finds similarities between *H. antilopinum*, *H. moldavicum* and *H. elegans*. She also finds analogy of Siwalik *Hipparion* with some of the Chinese forms and also with *H. primigenium* (VON MEYER), 1829 from Eppelsheim. Finally she concludes that of all the known species of *Hipparion* the Siwalik forms differ in preorbital fossa which is little developed especially in length, and this alone justifies their separation in one or more species.

FORSTEN (1968) considers the Siwalik species of *Hipparion* near or identical to *H. primigenium*. "*Hipparion primigenius* was probably distributed over most of the Old World during the Vallesian. Between the different local demes there are variations in size, but morphology was quite uniform. COLBERT (1935a) describes the upper cheek teeth from Chinji, Lower Siwaliks, as large with complicated fossette borders and long, flattened protocone, i.e. characters typical of *H. primigenius* in Europe and North Africa" (p. 85).

2. METHODOLOGY

The material concerning the Siwalik *Hipparion* was investigated virtually from every museum, also an attempt was made to compare these animals with the North American and European forms. The conclusions are drawn on the basis of morphology and statistical tests are applied wherever necessary.

The measurements were made with the metric vernier calipers to the accuracy of $^1/_{10}$th of a millimeter. In the specimens larger than 10 cm the accuracy was checked up to 1 millimeter.

The anteroposterior (length) and transverse (width) measurements of the isolated teeth were made 1 centimeter above the base so as to avoid the error arising from wear. The method was alredy applied by SONDAAR (1961) in the study of the Spanish *Hipparion*. FORSTEN (1968) in her revision of Palearctic *Hipparion* made the measurements at the neck of the tooth. This method does not seem to be reliable because in most of the cases the neck of the tooth (junction of the root and the crown) is damaged. Furthermore, the roots are fixed at a later stage. The teeth embedded in the jaws and skulls were measured on their occlusal surfaces and these measurements are treated separately. The enamel plications were counted according to the method suggested by GROMOVA (1952).

The position of different permanent cheek teeth was determined according to BODE'S (1931) method. To recheck their position in the maxillas and the mandibles they were compared with complete series.

The index of hypsodonty of unworn and little-worn teeth was considered as a ratio between the height and the length of the tooth. $HI = \frac{H}{L} \times 100$.

This ratio was calculated separately in the upper and lower molars and premolars. Height of the crown in the upper teeth was measured along the parastyle, and in the lower teeth on the metaconid.

The protocone shape index was calculated separately in medium and little-worn teeth as the ratio of the width and the length of the pillar. $PI = \frac{W}{L} \times 100$.

The massivity of the third metapodials was calculated as a ratio between the central width and the total length.

$$M = \frac{\text{Width in the centre}}{\text{Total length}} \times 100.$$

3. ABBREVIATIONS

AMNH	American Museum of Natural History, New York, U.S.A.
BM	British Museum of Natural History, London, U.K.
BSM	Bavarian State Museum for Paleontology and Historical Geology, Munich (Bayerische Staatssammlung für Paläontologie und Historische Geologie, München), W.-Germany
FAM	Frick American Mammals, the American Museum of Natural History, New York, U.S.A.
GIU	Geological Institute, State University of Utrecht, the Netherlands
IM	Indian Museum, Geological Survey of India, Calcutta
MS	Museo de Sabadell, Spain
S.P.	Survey of Pakistan
UC	University of California Paleontological Museum, U.S.A.
YPM	Yale Peabody Museum, Yale University, New Haven, U.S.A.
H	Height
HI	Hypsodonty Index
L	Length
M	Massivity
mm	millimeter
PI	Protocone Shape Index
W	Width

Note: Figures 4–17 refer to several different species, therefore they are grouped together at the end of the text.

II. GEOLOGY

1. GEOGRAPHIC DIVISION OF THE HIMALAYAS

The Himalayan mountain range is traditionally divided into three zones:

1. The Great Himalayas: the innermost line of high mountains above the limit of perpetual snow, average height 20,000 feet.
2. The Lesser Himalayas: Zone of relatively lower elevation when compared with the one mentioned above, average height 14,000 feet.
3. The Outer or Sub Himalayas: Zone of low range mountains with an average height of 3,000 feet. The Siwalik hills are classified under this division. The width of this zone is variable and may range between five and thirty miles.

The term "Sivalik Hills" (derived from Siva, the Hindu God) was originally used by FALCONER (1868) in a geographical sense. In his own words "By 'Sevalik Hills,' it is here meant to designate that range of lower elevation which stretches along the southwest foot of the Himalaya mountains, for the greatest portion of their extent from the Indus to Bramhapootra, where those rivers respectively debouch from the hills into the plains of India." The term Siwalik Hills is now frequently used in literature but it is confined to the northern part of FALCONER's 'Sevalik Hills,' covering a distance of about four hundred miles in southeast of Indus.

The Siwalik Hills are a series of parallel ridges between the flood-plain of the Ganges River and the Lesser Himalayan zone. The hills are generally low, ranging from 2,000 to 4,000 feet in height above sea level. The general strike is parallel to the Himalayas which is northwest-southeast. All the major drainage runs across the strike. These hills generally have a steep face on the south, and gentler slopes on the northern side which give them an asymmetric form.

The Siwalik rocks were considered to be flood-plain deposits by PASCOE (1920) and PILGRIM (1926), later WADIA (1949) also confirmed this theory.

According to WADIA (1949) "The formation of the long thin belt of Siwalik deposits along the foot of the Himalayas from Assam, through Kumaon and the Punjab to Sind, widening steadily in its westward extension, is now ascribed to the flood-plain deposits of a great north-west flowing river lying south of and parallel with the Himalayan chain from Assam to the furthest north-west corner of the Punjab and flowing southward to meet the gradually receding Miocene Sea of Sind and Punjab." This river was called "Siwalik River" by PILGRIM (1919) and the "Indobrahm" by PASCOE (1919). Further comments on the Siwalik deposits will be limited to the region of Potwar Plateau.

2. POTWAR PLATEAU

The Potwar Plateau is an elevated region, about 1,000 feet higher than the adjoining alluvial plains, covering an area of about 8,000 square miles. In the south it shares its boundary with the low flat hills of the Salt Range which are genetically different from the Siwalik Hills and in the north with the Kala Chitta and Margala hills. In the west it is stopped by the river Indus while in the east it gradually submerges under the alluvial plains of Gujrat.

2.1. Structure of the Potwar Area

Potwar Plateau broadly speaking is a synclinorium between the Salt Range on the south and the front ridges of the Himalayas on the north. According to WADIA (1932): "The Potwar geosyncline is a northwest branch of the greater and wider synclinorium, submerged under the Indo-Gangetic alluvium, which separates the peninsular horst from the Himalayan orogen; that so far as its rock sequence is concerned, the Potwar basin is a small scale replica of this wide trough which extends from the Jhelum to the Bay of Bengal; that the same tectonics as is revealed in the Potwar prevails all through this area in a somewhat modified or simpler form." The length of the synclinorium is about 150 miles and its greatest width reaches approximately 75 miles. The axis of the synclinorium parallels and lies a little south of the Soan River. The rocks have undergone severe folding and faulting movements. Reverse faults are typical for this region. Wherever the Siwalik rocks are found in contact with the older formations, the plane of junction is usually a reversed fault. The general trend is eastnorthest-westsouthwest, but the strike changes abruptly to northwest-southeast direction immediately to the east of Jhelum. This change is in correspondence with that in the strike of the Himalayas.

WADIA (1932) divided the Potwar area structurally into four distinct belts or "strike zones", with an east-west lineation, which succeed each other in the following order from north to south.

1. The faulted and isoclinally folded belt, commencing from the Margala–Kala Chita hills and extending southward to the Khairi Murat hill. This belt, about 12 miles wide, shows the greatest tectonic disturbance and compression. Faults in this zone are of 'reverse' type, the most northerly one being a thrustplane, which brings the Eocene limestones above the Miocene sandstones.
2. The Soan Syncline belt, of about 23 miles width and nearly 100 miles in length. This belt extends westsouthwestward from Rawalpindi to Makhad on the Indus.
3. South of this is the belt of open anticlines and synclines, extending from Domeli, near Jhelum to Daud Khel on the Indus; and finally,
4. The Salt Range monocline, with its overthrust north limb, presenting steep escarpments, toward the south and gentle dipslopes to the north. In the scarp face Palaeozoic and Mesozoic rocks are exposed.

The Soan Syncline belt wich lies in the middle of the trough is the broadest unit and stratigraphically it is most complete. It possesses nearly the complete Tertiary sequence. The rocks exposed in this syncline range from Eocene to Early Pleistocene in age. The general eastnortheast-westsouthwest strike abruptly changes to northwest-southeast direction to the east of Jhelum producing a deep syntaxial angle. WADIA (1932) has suggested that there is evidence of a greater amount of lateral compression on the northwest because of unvaryingly vertical dip of the strata than on the opposite limb of the fold. In the southeastern limb a moderate amount of subordinate folding can be observed. The intensity of pressure would have been gradually decreasing from north to south. Usually faults are not observed in the basin proper, but along the periphery dislocations of the nature of reverse-faults, especially at the eastnortheast end are of frequent occurence.

3. SIWALIK DEPOSITS

The Siwalik deposits of approximately 20,000 feet in thickness are composed of alternating bands of sandstones and argillaceous material. The thickness of these bands varies from 70 to 120 feet and an average thickness of 100 feet is frequently observed. There are no wide-spread breaks in the deposition sequence, but small local unconformities do occur. Cross-bedding is a very common feature in the sandstones throughout the Siwalik deposits. In a vertical sense each formation gradually grades into the next one with slight change in lithological properties. KRYNINE (1937) notes that the composition of the Siwalik sandstones is usually constant and, throughout the whole thickness of some 20,000 feet, closely approaches an average content of 40% quartz, 15% feldspar, 6% mica (mostly biotite) and from 35 to 40% of metamorphic rock fragments chiefly in the form of schist and phyllites. This composition is described as very constant inspite of the variation in appearance of the rocks. The quartz grains of these rocks are generally angular. KRYNINE (1937) described the heavy mineral suite as rather poor and monotonous. Minute pieces of red sandstone and chert are present. Limestone and chert fragments are not uncommon in the Upper Siwaliks. Some of the Nagri sandstones as well as some of the red sandstones and mudstones of the Chinji Formation have been reported by KRYNINE, to show evidence of post-depositional subaerial weathering, forming small red authigenic hematite concretions surrounded by hematitic haloes. The homogeneity of the sediments and the constant northwest-southeast strike of the Siwalik deposits from Assam to Potwar make the idea of deposition of these strata in a multitude of isolated basins to be unlikely.

WADIA (1949, p. 263) briefly discusses the nature of the Siwalik deposits and the processes involved. "The composition of the Siwalik deposits shows that they are nothing else than the alluvial detritus derived from the subaerial waste of the mountains, swept down by their numerous rivers and streams and deposited at their foot. This process was very much like what the existing river systems of the Himalayas are doing at the present day on their emerging to the plains of the Punjab and Bengal."

3.1. Historical Review

The occurrence of fossil bones in India was certainly known to the people in ancient times. FERISHTA (1360) in his summary of the history of the Moghel and Pathan emperors tells that in the reign of Feroz Shah the Third they had to dig near Hirdar for irrigational purposes. "In course of the operations bones of elephants and men were discovered in the unbedded mount. Those of the human fore arm are measured three yards. Some of the bones were petrified, while others were still in the condition of bone." From then onward many people have been looking from time to time for fossil bones and teeth but no serious work was ever done before the 19th century. For a detailed historical account the reader is referred to FALCONER'S (1868) memoir.

It was in the eighteen thirtees that reliable descriptions of Siwalik fossils were given in the transactions of the Asiatic Society of Bengal, and from then onward FALCONER took keen interest in these fossils with the able assistance of Captain CAUTLEY. FALCONER (1868) placed his Siwalik beds (now mainly placed in the Upper Siwaliks) in the middle portion of the Tertiary system and considered them of Miocene Age. However, he recognized the fact that the Siwalik beds had been deposited in a considerable period of time. To quote his words "it would be, perhaps, not unphilosophical to conceive that the epoch of the

Sewalik fauna may have lasted through a period corresponding to more than one of the Tertiary periods of Europe." FALCONER (1868, p. 28).

The summary of FALCONER'S (1868, pp. 28–29) ideas about the Siwaliks is given below, "Beside the mere zoological interest of the subject, the Sewalik inquiries involve these conclusions.

1. The upheavement of a narrow belt of the plains of India at the foot of the Himalayas into hills 3,500 feet high along 11° of longitude, or about 800 miles, after the long establishment on the continent of such modern forms as quadrumana, camel, giraffe, and existing species of reptiles.
2. A great upheavement of the Himalayas, extending to many thousand feet, and equal to the elevation of a tract which formerly bore a tropical fauna, up to a height which now causes a climate of nearly arctic severity. Remains of rhinoceros, antelope, hyaena, horse, large ruminants, found at 16,000 feet above the sea.
3. Conditions in India during the Tertiary period precisely the reverse of what have held in Europe. Instead of a succession of periods with successive decrease of temperature, India has now as high a temperature, if not higher, than it ever had during the Tertiary period. The upheavements have operated to increase the heat. In lat. 30°, at 7,000 feet above the sea, the mean temperature, making the compensation for the elevation, and reducing it to the level of the sea, is 81,2° Farenheit, or equal to that of the equator. The same excess of temperature holds generally over the continent, as contrasted with the eastern side of the continent of Asia.
4. Instead of numerous subdivisions of the Tertiary period with successive faunas, facts tend to the conclusion that India had one long term, and one protracted fauna, which lived through a period corresponding to several terms of the Tertiary period in Europe."

FALCONER'S work was further elaborated by R. LYDEKKER who published his work in the "Paleontologica Indica" and many short notes in the "Record of the Geological Survey of India" in the years 1876 to 1886. His studies, in addition to his own field work, were based upon the collection of the Indian Geological Survey Museum, Calcutta, and the British Museum, London. He learnt from his studies that the Siwalik fauna is not one single unit as FALCONER thought. Therefore he divided the Siwaliks into two parts, Lower and Upper, and regarded both of them to be of Pliocene Age. The Lower Siwaliks of LYDEKKER are equivalent to the present Middle Siwaliks.

Another extensive study of Siwalik fauna and deposits was then made by PILGRIM (1910B). He gave a revised classification of the Tertiary freshwater deposits of India, and preferred to adopt a threefold division of the Siwaliks, 'Lower', 'Middle' and 'Upper.' He tried to distinguish these three divisions of the Siwalik beds mainly on the basis of fauna. At this stage it may be kept in mind that MEDLICOTT (1864) had already given a threefold division of the Siwaliks on the basis of lithology, which he called Upper, Middle and Lower. PILGRIM discovered the Lower Siwalik fauna and considered it of Late Miocene (Tortonian) Age; further he thought the fauna of the Middle Siwaliks to be of Early Pliocene (Pontian) Age and the fauna of Upper Siwaliks of Latest Pliocene and Early Pleistocene Age.

This threefold division given by PILGRIM is accepted by all the later students of Siwalik stratigraphy. COLBERT (1935C) and LEWIS (1937) tried to refine it. They shifted the relative position of all the formations as fixed by PILGRIM and made them a little younger, but they fully agreed with the main threefold division of the Siwaliks as established by PILGRIM (1910B).

3.2. Problem of Nomenclature of the Siwalik Rock Units

The problem of nomenclature of the Siwalik rock units is very complicated. Colbert (1935 C, pp. 13–19) discussed this problem in the light of the decisions of the Committee on Stratigraphic Nomenclature, 1933. In his comprehensive discussion he has, unfortunately, confused the geographically named formations with the faunal zones. After considering the decisions of the International Subcommission on Stratigraphic Terminology of the International Geological Congress (1961) and the American Commission on Stratigraphic Nomenclature (1961) it seems that the scheme adopted by Lewis (1937, p. 197) though it has its disadvantages is the most workable plan, at present, and it will be followed with little modifications in this paper.

Siwalik Group	Upper Siwalik Subgroup	Tawi Formation Pinjor Formation Tatrot Formation
	Middle Siwalik Subgroup	Dhok Pathan Formation Nagri Formation
	Lower Siwalik Subgroup	Chinji Formation Kamlial Formation

According to Pakistan Stratigraphic Code the term Siwalik Series originally used by Medlicott (1864) should be replaced by the term Siwalik Group. The term Subgroup suggested by the American Commission on Stratigraphic Nomenclature (1961, p. 651) is used for the Lower, Middle and Upper Siwaliks.

4. STRATIGRAPHY

As already mentioned Falconer considered the Siwalik deposits as one unit, later Lydekker divided them into two horizons with a lower group of 10,000 feet and an upper of 4,000 feet in thickness. Pilgrim (1910 B) gave a threefold division and later he subdivided these three units into different 'stages' mainly on the basis of fauna.

The field evidence shows that there is always a gradual vertical passage from one formation to the other except between Kamlial and Chinji where a definite lithologic break exists. There are many unconformities of local importance only. For instance an unconformity has been observed at the base of the type section of Tatrot but this is not recognized at all places.

4.1. Lower Siwaliks

The average thickness of this subgroup is approximately 4,000 feet.

The Lower Siwalik Subgroup of rocks is mainly composed of dark and bright red sandstones and clays with pseudoconglomerates. The lower portion always retains its character of dark colour and ridge forming sandstones, while the upper portion can very easily be distinguished by its bright red coloured clays, with much thinner less prominent sandstone intercalations. In the words of Pilgrim (1910 B, p. 189) who first recognized this unit: "Besides the concretionary conglomerates there are calcareous nodular beds and clays, the whole deeply tinted red, and by the colouration alone, sharply marked off from the overlying Middle Siwaliks. Real pebbles are entirely absent."

The genera *Listriodon, Hemimeryx, Giraffokeryx, Dinotherium, Trilophodon* are the most common mammals of this subgroup.

4.1.1. Kamlial Formation

The name was derived by Pinfold (1918) from the nearby village Kamlial, but the village itself is situated on the next younger Chinji Formation and the type locality (72°30'30" E, 30°15'30" N) of the older Kamlial Formation is 5/8 mile westsouthwest of Kamlial village. "This is situated on the Khaur dome, east of Pindigheb. The thickness here is about 1,000 feet. The Kamlial rocks appear in a zone of outcrops to the north of Khaur and Pindigheb, stretching from the Indus west of Jand and thence across the re-entrant of the Jhelum into Jammu, their thickness here ranging from 1,000 to 2,000 feet and increasing from west to east," Pinfold (1918). Lithologically the formation consists of dark coloured sandstones and clays with many pseudoconglomerates. The passage from the older Murree Formation is very gradual. In Khaur and some other localities the Kamlial Formation can be separated from the Murrees by the presence of vertebrate fossils, but where there are no fossils it is very easy to confuse the two formations. Pilgrim (1913) distinguished two types of pseudoconglomerates in this formation, consisting of:

1. More or less hard, compact and very calcareous type of pebbles.
2. Much softer and less calcareous types.

The average thickness of this formation is about 1,700 feet. Wadia (1932, p. 79), "the Kamlial stage indicated the advent of clear (fresh and running) water conditions in the Punjab for the first time after the retreat of the sea of Eocene and Oligocene times and the filling up of the lagoons in which the greater part of the Murrees were laid down. Fluviatile conditions, after a few minor oscillations, were now definitely established in North West Punjab". Anderson (1927) recognized the Kamlial as the oldest member of the Siwalik Series. Of the Kamlial-Murree sequence along the Salt Range, Anderson (1927, pp. 685–686) allots 900 feet and upward to the Kamlial Formation. This formation does not yield much fossils, but those present are surely more primitive than the Chinji forms.

4.1.2. Chinji Formation

A problem similar to that observed for the Kamlial Formation exists in the case of the Chinji Formation, the village of Chinji (17 miles South of Talagang) after which the formation is named, is situated on the crest of the Nagri sandstones (next younger formation). The type locality (72°22' E, 32°41' N) is a little further to the South between the village and the Chinji forest Rest House. This formation is separated from the Kamlial by an unconformity. Lewis (1937, p. 201), however, does not recognize such a break.

Lithologically the Chinji Formation is characterized by its more argillaceous content. The Chinji is one of the most easily recognizable formations owing to its prevailing brick-red or orange-brown clays. Intercalations of grey sandstones are very frequent. The usual thickness of each clay band is 200 feet, while the sandstone bands very rarely attain a thickness of 50 feet. Dark layers of ferruginous sands are occasionally seen and lenses of pseudoconglomerates are not uncommon in the lower part. Pilgrim (1926) gives a total thickness of 2,300 feet, in the type area, assigning 1,500 feet to the lower part and 800 feet to the upper part of the Chinji.

The Chinji Formation is very rich in vertebrate remains throughout. The most common mammals are: primitive trilophodonts, dinotheres, suidae, *Giraffokeryx*, many crocodiles, turtles, lizards and aquatic birds. This type of assemblage indicates a tropical humid climate with heavy rainfall.

4.2. Middle Siwaliks

As we go north away from Salt Range, the Lower Siwaliks gradually pass into the Middle Siwaliks which are richly fossiliferous. These beds appear to be thinning east of Jhelum. Lithologically they are very easily distinguishable from the Lower Siwaliks; dominant rocks are gray soft sandstones with intercalations of pale yellow clay. Pebble beds occur here and there. The maximum thickness of 6,000 feet is found in the north of Khaur, but there is a considerable lateral variation.

Hipparion is the most abundant genus. In addition mastodons, *Stegodon*, *Giraffa* and large Antelopes are also commonly found.

4.2.1. Nagri Formation

The type locality (72°30′ E, 32°46′ N) is situated in the area of Nagri village. The formation, exposed on the northern flank of the Salt Range, is for some 80 to 85% composed of sandstones. The sandstone bands are usually 250 to 300 feet in thickness and separated by reddish clays. These clays are not as bright in colour as those in the Chinji Formation and can very easily be distinguished from the typical crimson coloured clays of the older formation. True conglomerates are rare at the base, but, pseudoconglomerates are common. The lower 1,000 to 1,500 feet are almost unfossiliferous, at least at the type locality and surrounding regions. The change from the red clays of the Chinji Formation to the grey massive sandstones appears to be rapid, as only about 80 to 120 feet of passage beds are seen. Lewis (1937) "It seems advisable to locate the base of the Nagri at the horizon where the bright red siltstones, so typical of the Chinji, die out and the thick sandstones of the Nagri begin." The total thickness is about 3,500 feet.

The Nagri fauna has been considered by all the authorities as intermediate between that of the Chinji and the Dhok Pathan Formations. However, its exact relative position is determined differently by various authors. This formation is characterized by frequent *Hipparion*. It does not yield so many fossils as the Chinji below and the Dhok Pathan above.

4.2.2. Dhok Pathan Formation

These rocks are well exposed near Dhok Pathan village along the Soan River (72°21′ E, 33°8′ N). There is a very gradual passage between the Nagri and the Dhok Pathan Formations. Light grey sandstones parted by red or deep orange clays are characteristic of the latter formation. They cover a wide region between the Salt Range and the two domes of Khaur and Dhulian and form the thickest formation in the Soan syncline. The sandstones contain a considerable amount of weathered igneous minerals. Near Dhok Pathan the thickness of these beds is a little more than 1000 feet. Most of the higher layers are removed by erosion.

There is a contrast in colour between the Dhok Pathan sediments and those of the Nagri. The sandstones are of very light grey or sometimes even white colour with a typical shine, which does not exist in the Nagri sandstones.

The upper portion of the Dhok Pathan Formation is truncated by an angular unconformity near Tatrot village. There is an abrupt lithologic change between the Dhok Pathan and the Tatrot sediments. The unconformity was also noted by Pilgrim (1913, p. 275), Wadia (1928), de Terra & Teilhard de Chardin (1928, pp. 808–810), Cotter (1933, pp. 122, 126) and Lewis (1937, p. 198). It may be noted that this unconformity has only been recorded near Tatrot village. Its existence all over the area of the Siwalik sediments is not known. Along the Salt Range flank the formation is about 2,000 feet thick while to the south of Tammen the maximum figure goes to 3,000 feet. In southeast direction the Dhok Pathan Formation is gradually becoming thinner.

The Dhok Pathan fauna is the richest of all formations. The most abundant genus recorded in the Dhok Pathan is *Hipparion* which acquires its maximum evolutionary development in these layers.

4.3. Upper Siwaliks

"The beds form an easily recognizable series and may be known as Upper Siwaliks. They can be traced in an almost continuous outcrop, by their lithological character and by their fossil contents, from the Salt Range through the Pabbi Hills" (PILGRIM, 1910B, pp. 191, 192).

In general the passage from the Middle Siwaliks to the Upper Siwaliks is gradual. GILL (1952A, p. 391) "The paleontological and strike-mapping evidence shows that the Middle/Upper Siwalik boundary lies within a thick homogeneous group of sandstone and clay alternations and is marked neither by unconformity nor a basal conglomerate." MIDDLEMISS (1890) included the Upper Siwaliks in his Siwalik conglomerate and sand-rock stages. The Upper Siwalik sediments consist of soft, grey and coarse sandstones parted by pinkish clays. Sandstones are not very compact as they are in the Middle Siwaliks. The upper portion of these sediments mainly contains conglomerates and boulder beds.

PILGRIM (1910B, p. 192) reports the maximum thickness of the Upper Siwaliks as 10,000 feet. The average thickness of this bulk of sediments is between 6,000 to 7,000 feet.

A tendency is going on amongst the local geologists to introduce a new lithostratigraphic unit, the Soan Formation, which would include all the lithologic units previously referred to as Tatrot, Pinjor and Tawi Formations.

Equus, *Bos*, *Elephas*, *Camelus* and *Sivatherium* are the characteristic genera of the Upper Siwaliks and can often be found in these beds.

4.3.1. Tatrot Formation

The type locality of the Tatrot Formation is situated at Tatrot village (73°21′ E, 32°52′30″ N) in the north of the Salt Range. This formation further extends northeast of Kalr Kahar and on to the northwest of Bakrala Ridge in Jhelum. An average thickness of 2,000 feet is recorded. Lithologically this formation is composed of soft brownish grey sandstones with intercalated pinkish clay along with conglomerates. At the type locality, as has already been remarked, the base is marked by an angular unconformity. The Tatrot sandstones can be distinguished from the underlying Dhok Pathan sandstones due to their softness and the absence of the characteristic glistening white, typical of the latter.

The fauna in this formation is scarce and intermediate in character between that of Dhok Pathan and Pinjor.

LEWIS (1937, p. 198) "*Equus* first appears in the Tatrot Formation, as far as the Siwalik Series is concerned." It may be noted that LEWIS's Tatrot Formation includes both units previously known as the Tatrot and the Pinjor Formations. It is not clear from which horizon his *Equus* is coming. The recent collections do not show the presence of *Equus* in Tatrot; however, a few rolled specimens of *Hipparion* were collected at the base of the Tatrot Formation.

4.3.2. Pinjor Formation

The type locality is at Pinjor town which is situated to the south of Kalka between the rivers Sutlej and Ghaggar in the Simla foothills. Lithologically this formation is composed of pebble beds and sandstones with intercalated clays. Distinction of the Pinjor from the Tatrot has been denied by LEWIS (1937, p. 198). PILGRIM, however, distinguished a 'Pinjor Zone' between the Tatrot and the Tawi Formations (1913, p. 278). The field observations show that, although there is a very gradual passage between the Tatrot and the Pinjor Formations, Pinjor sediments can still be distinguished from those of all other formations due to their coarseness. True conglomerates appear for the first time in abundance in these layers. In the eastern Potwar the Pinjor Formation is not definitely separable (WADIA, 1928). The thickness of this formation varies between 500 to 1,500 feet. In Potwar and Salt Range the Pinjor sediments reveal *Elephas*, the fossils of which usually occur between 2,000 to 3,000 feet above the top of the Middle Siwaliks.

4.3.3. Tawi Formation

The name was originally proposed by LEWIS (1937, p. 197) as a substitute for the term "Boulder Conglomerate Formation", and is based on the section in the Tawi River Valley (75°10′ E, 33° N) near Udhampur.

This assemblage of rocks forms the topmost formation of the Upper Siwaliks. The Tawi Formation has its maximum development in the central part of the Potwar Plateau. Lithologically the formation is composed of conglomerates with pebbles that range up to 20 inches in diameter, and intercalations of grey or orange clays. WYNNE (1877) first noted that these pebbles were mainly composed of igneous and metamorphic rocks forming an extremely varied assemblage. He further noted the presence of nummulitic limestones amongst these pebbles.

The beds of the Tawi Formation can be distinguished from the sub-recent conglomerates by the presence of structural features such as minorfolds, which do not exist in the latter.

5. DISTRIBUTION OF SOME OF THE FOSSIL MAMMAL GROUPS IN THE SIWALIKS

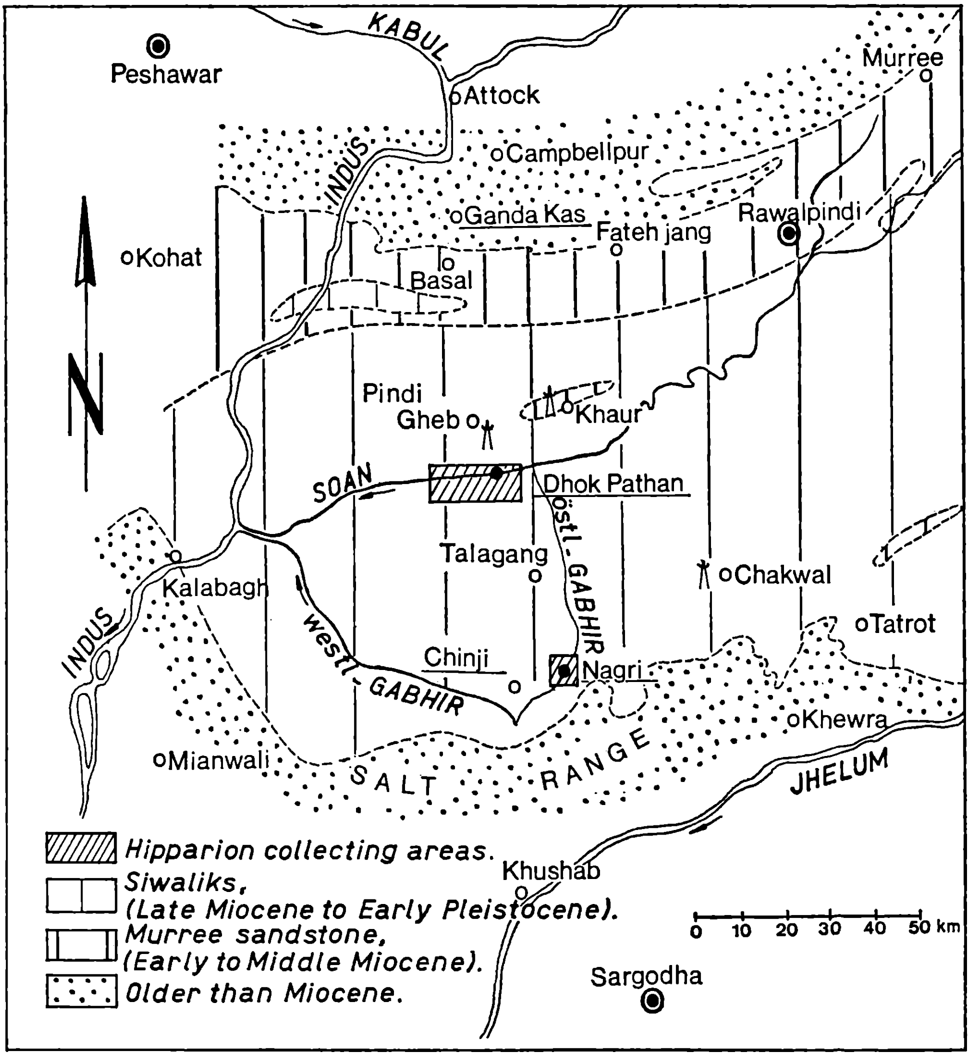
COLBERT (1935C) has given a comprehensive list of the fauna of the Siwalik Group of rocks. I made a general survey of the Utrecht Siwalik collection (1964 and 1966), which mainly comes from the type localities of the Kamlial, Chinji, Nagri, Dhok Pathan and Tatrot Formations. The study of this collection gives a little different view on the distribution of the fauna, which is presented in the following table. Stress is given to the first and the last appearance of certain groups of mammals and for comparative purposes the same were selected from COLBERT'S (1935C) list.

	HUSSAIN	COLBERT, 1935C
Tawi:	Fossils are uncommon. Rarely fragments of *Equus* bones are seen.	
Pinjor:	*Equus**, *Bos**, *Archidiskodon**	*Equus**, *Bos**, *Archidiskodon**
Tatrot:	*Pentalophodon**, *Hippopotamus**	*Pentalophodon**

Dhok Pathan:	*Stegodon**, *Hipparion* is the most abundant genus and reaches its maximum evolutionary development. Two species are recognized: *H. antilopinum* and *H. theobaldi*	*Dinotherium*+, *Hippopotamus**, *Hipparion theobaldi*, *H. antilopinum*, *H. chisholmi*, *H. punjabiense*, *H. perimense*.
Nagri:	*Hipparion nagriensis**, *Dinotherium*+, Giraffidae become large and more advanced, anthracotherids become rare.	*Hipparion theobaldi* and *Giraffokeryx punjabiensis* continue from the Chinji Formation.
Chinji:	Hyaenidae*, Creodonta+, *Chilotherium**, *Tetralophodon**, Giraffidae*, anthracotherids are abundant.	Hyaenidae*, Creodonta+, *Chilotherium**, *Tetralophodon**, *Hipparion theobaldi**, Giraffidae.
Kamlial:	In general fossils are rare but *Listriodon*, *Trilophodon* and *Dinotherium* make general composition of the fauna.	*Listriodon*, *Trilophodon*, *Dinotherium*.

* = First appearance.
+ = Last appearance.

III. SIWALIK HIPPARION



Geological map of Potwar Plateau Northwestern Pakistan, showing Hipparion collecting areas. After Dehm, Oettingen-Spielberg and Vidal, 1958.

1. FOSSIL LOCALITIES

The material of the Siwalik *Hipparion* was studied from four different institutions: Bavarian State Museum for Paleontology and Historical Geology, Munich, W. Germany; Geological Institute, State Universety of Utrecht, the Netherlands; the American Museum of Natural History, New York, U.S.A.; and Yale University Peabody Museum, New Haven, U.S.A. Certain type specimens and the older collections from the British Museum of Natural History, London, were consulted for comparison. The material of European hipparions was consulted from the Museo de Sabadell, Spain; Muséum National d'Histoire Naturelle de Paris and the Geological Institute, Utrecht.

1.1. The Munich collection

The collection was made by Prof. R. Dehm, Th. Princess zu Oettingen-Spielberg and Mr. H. Vidal in 1955–56 in collaboration with the Geological Survey of Pakistan. The *Hipparion* material is from the type localities of the Nagri and the Dhok Pathan Formations. All the specimens from the Nagri Formation come from the Nagri Gorge (type locality) near Nagri village, S.P. map. no. 43 (previously Survey of India, 1930). In view of its thickness Prof. Dehm divided the Dhok Pathan Formation into lower, middle and upper parts in his localities report. The specimens from these three parts were treated separately. All the localities are situated around Dhok Pathan Rest House located at S.P. map no. 43c/8, B-2.

In a personal communication Prof. R. Dehm very kindly supplied the following information about the Dhok Pathan *Hipparion* localities. This information is given below.

"*Hipparion* localities in the region of Dhok Pathan belong only to the Dhok Pathan stage of the Siwalik Series, some belong to the lower parts of this stage, most to the middle parts and some to the higher parts. The Dhok Pathan stage consists of a series of red sandy marls and greyish green sandstones; locally, that is for a distance of about half a mile, one can easily and exactly parallelize the different marl and sandstone horizons. But this is difficult, if not impossible, at greater distances, especially from one side of a broad valley to the other. The sandstones and marls often thin out and change horizontally. A special mapping of the different horizons at a large scale should overcome these difficulties.

All the names of the localities are not marked on the One inch map.

1. Localities North of Soan River

North of the Soan River there is the Dhulian Dome with Chinji layers in its center. From there in the Soan Valley the younger stages, Nagri and Dhok Pathan, are inclined southward from 30° to 15°. So the localities of Dhok Pathan stage North of the Soan belong to the lower parts of the stage:

Gorianwala	1.5	miles northwest of Dhok Pathan Rest House.
Datwal	2	miles westnorthwest of Dhok Pathan Rest House.
Winnewala	1	mile east of Dhok Pathan Rest House.
Kundlawala	2	miles east of Dhok Pathan Rest House.

2. Localities on both sides of Kundvali Kas

(= Kundral Nala) 1–1.2 miles southwest of Dhok Pathan Rest House. The localities 3, 4, and 5 east of Kundvali Kas show their relative stratigraphic positions very clearly;

——— Kundral West and Rattidheri ———
5–8 m (meter)
——— Dhok Pathan 5
1.5–2 m
——— Dhok Pathan 4
8 m
——— Dhok Pathan 3
16 m
——— Kundral Nala, river bed ———

On the other, western side of the Kundvali Kas valley, opposite to locality Dhok Pathan 3, we find the localities Kundral West and Rattidheri; they are stratigraphically higher than Dhok Pathan 5, as far as it is possible to compare both sides of the valley.

These five localities southwest of Dhok Pathan Rest House belong to the middle part of the Dhok Pathan stage, most of the other localities in the west and east of Dhok Pathan Rest House belong to this middle part:

a) East of Dhok Pathan Rest House.

Bharmar	¾ mile east of Dhok Pathan Rest House.
Uchidheri	1.5 miles east of Dhok Pathan Rest House.
Moranwala	2 miles east of Dhok Pathan Rest House.

b) West of Dhok Pathan Rest House.

Dhok Pathan 1 and 2: ½–¾ mile westsouthwest of Dhok Pathan Rest House.

Kundral	to the South of Dhok Pathan 3.
Tappianwali	to the South of Dhok Pathan 3.
"Lalibetscho"	southwest of Dhok Pathan Rest House.
Karpewali	3 miles southsouthwest of Dhok Pathan Rest House, near Loteri.

3. Localities west and southwest of Kundvali Kas

West of Kundvali Kas the layers are inclined to south and southsouthwest; thus above localities Kundral West and Rattidheri follow higher parts of the Dhok Pathan stage:

Dhedari	2 miles westsouthwest of Dhok Pathan Rest House.
Konkrori	near (west of) Dhedari.
Latewali Khan	near (south of) Dhedari.
Parlewali 1–4	3 miles westsouthwest of Dhok Pathan Rest House.
Seanwala	south of Konkrori.
Warwal	2 miles south of Dhedari.
Markhal	6 miles west of Dhok Pathan Rest House."

1.2. The Utrecht collection

The collection was made by Prof. G. H. R. von Koenigswald and Dr. P. Y. Sondaar in 1964 in collaboration with the Panjab University, Lahore, Pakistan, and was later supplemented in 1966 when Mr. A. J. van der Meulen and myself also joined.

Hipparion material comes from the type localities of the Nagri and the Dhok Pathan Formations. All the specimens from the Nagri Formation come from the Nagri Gorge (type locality) near Nagri village, S.P. map no. 43. Most specimens from the Dhok Pathan Formation are from the region around Dhok Pathan Rest House, S.P. map no. 43c/8.

1.3. The American Museum collection

Colbert (1935C, Siwalik Mammals in the American Museum of Natural History) has given a detailed report on all the Siwalik fossil localities. Keeping this in view it was not found necessary to reproduce his localities in this paper. The reader is referred to the above mentioned publication.

The detailed information about the localities of the specimens from the Yale University Peabody Museum will be given, listing them under the respective species. The main part of the collection was made by G. Edward Lewis in 1932 and later on supplemented by de Terra and Teilhard de Chardin in 1935.

2. DENTAL TERMINOLOGY

The patterns of horse teeth and the terminology of their elements has been described by various people. The first description comes from Osborn (1907). In 1918 he described North American Equidae and used his original description while discussing the genesis

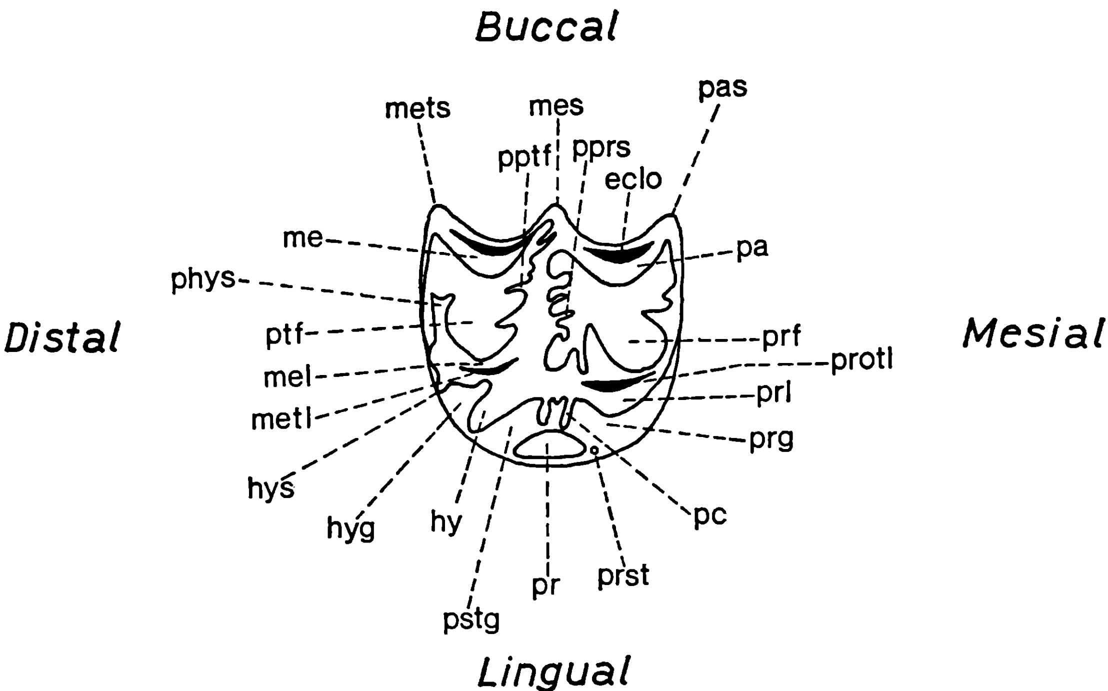


Fig. 1
eclo: ectoloph, hy: hypocone, hyg: hypoconal groove, hys: hypostyle, me: metacone, mel: metaconule, mes: mesostyle, metl: metaloph, mets: metastyle, pa: paracone, pas: parastyle, pc: plicaballin, phys: plihypostyle, pprs: pliprefossette, pptf: plipostfossette, pr: protocone, prf: prefossette, prg: preprotoconal groove, prl: protoconule, protl: protoloph, prst: protostyle, pstg: postprotoconal groove, ptf: postfossette.

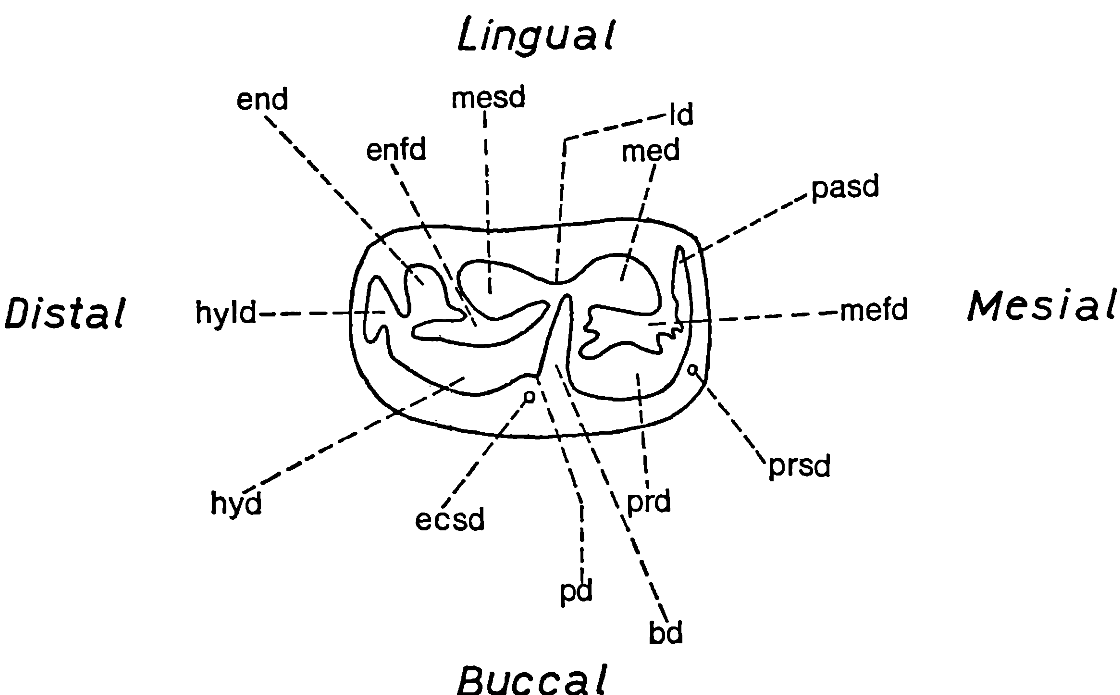


Fig. 2
bd: buccal depression, ecsd: ectostylid, end: entoconid, enfd: entoflexid, hyd: hypoconid, hyld: hypoconulid, ld: lingual depression, med: metaconid, mefd: metaflexid, mesd: metastylid, pasd: parastylid, pd: plihypoconid, prd: protoconid, prsd, protostylid.

and evolution of single dental characters (pp. 5–7). Amendments in OSBORN's basic description have been proposed by HOPWOOD (1937), STIRTON (1941), ARAMBOURG (1947, 1959), COOK (1950) and GROMOVA (1952). No serious changes in the basic terminology have been proposed in this paper, but only a suitable set of terms is selected.

A new term protostyle is suggested by GABUNIJA (1959, p. 106) for a pillar on the lingual side of the upper molars. This is very rarely seen in *Hipparion*. GABUNIJA (1959) notes its presence in *Hipparion tudorovense*. This style arising from the cingulum lies along the anterior margin of the protocone. The protostyle has also been observed in one upper molar of *Hipparion antilopinum* (GIU DP 69) where it does not reach the occlusal surface and in *Hipparion concudense aguirrei* (GIU LM 1054) from Spain where its extension is seen up to the surface of mastication.

3. TAXONOMY

3.1. *Hipparion antilopinum* (FALCONER & CAUTLEY) 1849

Plate 2: figures 1–4, 5, 6; Plate 3: fig. 8; Plate 4: fig. 3; Text fig. 18: e, f.

Hippotherium antilopinum FALCONER & CAUTLEY, 1849, Fauna Antiqua Sivalensis, Pl. LXXXII to LXXXV, fig. 13, 13a.

Hipparion antilopinum, LYDEKKER, 1885 A, Cat. Siw. Vert. Ind. Mus., pp. 57–58.

Hippodactylus antilopinum, PILGRIM, 1910 B, Rec. Geol. Surv. India, XL, p. 201.

Hipparion antilopinum, MATTHEW, 1929, Bull. Amer. Mus. Nat. Hist., LVI, pp. 448, 451, 526–528.

Additional references:

OWEN, R. 1846, p. 395.
FALCONER, H. 1868 A, pp. 186–189, 527–532.
LYDEKKER, R. 1880, p. 31; 1882, pp. 75–80, pls. XI, XII, XIII; 1883 B, pp. 83, 91; 1886 A, pp. 59–64.
VON MEYER, H. 1865, p. 17.
GAUDRY, A. 1873, p. 40.
COPE, E. D. 1888, p. 449.
COLBERT, E. H. 1935 C, pp. 129–131, 136–159.
GROMOVA, V. 1952, pp. 248–251.

Synonyms:

Hipparion perimense PILGRIM, 1910 A, Rec. Geol. Sur. Ind., XL, 66 = *H. punjabiense* LYDEKKER (PILGRIM, 1913, ibid., XLIII, p. 321).

Hipparion punjabiense LYDEKKER, 1886, Brit. Mus. Cat. Foss. Mam., III, p. 60.

Hippodactylus chisholmi PILGRIM, 1910 A, Rec. Geol. Surv. Ind., XL, p. 67.

MATTHEW (1929, pp. 526–528) has proposed that the above mentioned species are synonyms of *Hipparion antilopinum* (FALCONER & CAUTLEY). After re-examining the material MATTHEW's statement was found satisfactory.

Holotype:

BM. No. M 2647, right maxilla with P^2–M^3, Fauna Ant. Siva., Pl. LXXXII, figs. 13, 13a.

Paratypes:

BM. Nos. M 16170, a portion of a cranium; M 2652, a mandible; M. 2653, a mandible; M 2648, fragment of an upper molar; various limb bones figured by FALCONER & CAUTLEY, 1849, Pls. LXXXIII–LXXXV.

Type locality:

Probably from the Salt Range, Punjab.

Horizon:

Dhok Pathan Formation (upper part of the Middle Siwaliks).

Diagnosis:

An average-sized *Hipparion*, characterized by small and very hypsodont teeth, oval protocone, complicated enamel plications of the upper molars, well-developed preorbital fossa, short snout and slender metapodials.

Differential diagnosis:

The upper first and second molars range from 19.3–22.2 and 19.8–25.0 mm in length and width respectively. In *H. theobaldi* these measurements vary from 23.0–25.8 and 23.1–26.7 mm and in *H. nagriensis* from 22.1–23.2 and 22.6–25.0 mm. By comparison the teeth of *H. antilopinum* on the average give the smallest measurements amongst the Siwalik species. For details see tables 6, 7 and figs. 4 to 11. The hypsodonty index for M^{1-2} of this species varies between 242–292 (9 spec.) while the same figures for *H. theobaldi* and *H. nagriensis* range between 192–279 (14 spec.) and 183–234 (7 spec.) respectively. So *H. antilopinum* on the average has the most hypsodont teeth among the Siwalik *Hipparion* species. For detailed figures the reader is referred to table 1. Slenderness of the metapodials is one of the important distinguishing characters for this species. The massivity figure for this species was calculated in the metatarsals III, AMNH 19667 and BSM H 573, 10 and 11 respectively, while in *H. theobaldi* this figure varies from 14–16 (5 specimens).

3.1.1. Material studied

P^2

BSM H67, H149 (Moranwala); H80, H86, H87 (Konkrori); H127 (Parlewali 2); H100 (Parlewali 3); H161, H162 (Dhok Pathan 3); H340, H382 (Uchidheri); H183 (Karpewali); H228 (Kundlawala).

YPM 19429, 19539, 19542, 19831, 19852, 19862, 19137 (S.P. map no. 43 H/5); 19121, 19563, 19568, 19587 (S.P. map no. 43 C/8).

P^{3-4}

BSM H144, H178, H180 (Winnewala); H65, H68, H147, H148, H392, H396 (Moranwala); H90, H138, H199 (Rattidheri); H119 (Karpewali); H204, H379 (Uchidheri); H214, H215 (Kundral); H223 (Kundral West); H269, H281 (Dhok Pathan 3); H76, H82, H83 (Konkrori); H130 (Parlewali 2); H103 (Parlewali 3); H139 (Parlewali 4); H302 (Latewali Khan); H452 (Dhedari).

YPM 19421, 19427, 20188 (S.P. map no. 43 H/5 B–2); 19559, 19571 (Naragghi, S.P. map no. 43 C/8 C–2); 19981 (Dhok Pathan, S.P. map no. 43 C/8 B–2); 20187 (1¾ miles S.E. Ganghal, Punjab); 20191 (1½ miles N.W. of Hasnot, Punjab).

GIU DP20, 39, 64, 250 (around Dhok Pathan village).

M^{1-2}

BSM H66, H70, H72, H150, H394, H397 (Moranwala); H75, H78, H79, H84, H370 (Konkrori); H91, H96, H97, H98, H137, H190, H193, H238 (Rattidheri); H104, H107 (Parlewali 3); H231 (Parlewali 4); H121, H234 (Karpewali); H159, H268, H278 (Dhok Pathan 3); H136 (Dhok Pathan 5); H207 (Uchidheri); H220, H221 (Kunral West); H255 (Winnewala); H301 (Latewali Khan).

YPM 19384, 19388, 19447, 19713, 19100 (S.P. map no. 43 H/5 B–2); 19540 (S.P. map no. 43 H/5 A–3); 19573, 19575, 19593, 19594 (S.P. map no. 43 C/8 C–2); 19131, 19990 (S.P. map no. 43 C/8 B–2); 20177 (2 miles east of Hari Talayanger, Punjab).

GIU DP18, 26, 33, 43, 42, 46, 49, 63, 65, 67, 69, 70, 77, 79, 83, 239, 240 (around Dhok Pathan village).

M^3

BSM H176 (Winnewala); H89, H200 (Rattidheri); H246, H247 (Karpewali); H73, H395 (Moranwala); H205, H381 (Uchidheri), H210 (Kundral); H216 (Kundral West); H81 H474 (Konkrori); H129, H133 (Parlewali 2); H140, H230, H447 (Parlewali 4); H415 (Dhedari); H265 (Latewali Khan).

YPM 19308, 19564 (S.P. map no. 43 C/8 B–2, C–2); 19398, 19712 (S.P. map no. 43 H/5 B–2); 19481 (S.P. map no. 43 H/5 B–3).

GIU DP36, 58, 74, 251, 252, 253, 254 (around Dhok Pathan village).

P_2

BSM H470 (Parlewali 2); H110, H363 (Parlewali 4); H264, H267 (Latewali Khan); H292, H293 (Winnewala); H346 (Karpewali).

YPM 19596 (Naragghi, S.P. map no. 43 C/8 C–2).

GIU DP264 (Padri, S.P. map no. 43 H/5).

P_{3-4}

BSM H352 (Parlewali); H132 (Parlewali 2); H449, H453, H454, H458 (Parlewali 3); H109, H355, H443 (Parlewali 4); H154, H158, H385 (Moranwala); H291 (Winnewala); H295, H296, H347 (Karpewali); H208, H337, H343, H383, H425 (Uchidheri); H371, H373, H475 (Konkrori); H439 (Bhermar); H313, H323 (Dhedari); H368 (Dhok Pathan 2); H304 (Latewali Khan); H423 (Gorianwala).

YPM 19855, 19154 (S.P. map no. 43 H/5 A–3, B–2); 19985 (S.P. map no. 43 C/8 B–2).

GIU DP151, 152, 154, 158, 159, 162, 164, 173, 177, 178, 179, 180, 181, 185, 189, 193 (around Dhok Pathan village).

M_{1-2}

BSM H465, H466, H467, H472 (Parlewali 2); H456, H461, H462, H464 (Parlewali 3); H108, H359, H361 (Parlewali 4); H 153, H155, H386, H388 (Moranwala); H184, H185 (Karpewali); H378 (Dhok Pathan 1); H241, H273, H273A, (Dhok Pathan 3); H255, H256, H403, H404, H406, H408 (Winnewala); H283 (Jhalarwali Dhok); H309, H411, H412, H413, H416 (Dhedari); H334, H480, H483, H484 (Rattidheri); H336, H338, H339, H341, H342 (Uchidheri); H374,H375,H477, H478 (Konkrori); H427, H428 (Datwal); H434 (Kundral West).

YPM 19432, 19433, 19434, 19441 (S.P. map no. 43 H/5 C–2); 19576, 19578, 19581, 19598, 19602, 20010, 19991, 19146 (S.P. map no. 43 C/8 B–2); 19155, 19173 (S.P. map no. 43 H/5 B–2); 19545, 19835 (S.P. map no. 43 H/5 A–3).

GIU DP101, 103, 104, 106, 109, 111, 112, 113, 114, 122, 126, 133, 134, 136, 138, 139, 141, 143, 144, 225, 228, 229, 230, 231, 232, 233, 234, 235, 236, 237, 124, 125, 226, 227 (around Dhok Pathan village).

M_3

BSM H344 (Uchidheri); H438, H440 (Bhermar); H253 (WSW Dhok Pathan 1); H367 (Dhok Pathan 2); H471 (Parlewali 2); H362 (Parlewali 4); H387, H393 (Moranwala); H345 (Karpewali); H212 (Kundral); H305, H306, H307 (Latewali Khan); H321, H324 (Dhedari).

GIU DP117, 215, 258, 259, 260, 261, 262, 263 (around Dhok Pathan village).

Skull and jaw fragments

BSM H689, H690 (Dhok Pathan 3); H493, H501, H510, H513 (Dhok Pathan 4); H227, H519 (Dhok Pathan 5); H248 (Lalibetscho); H389–391 (½ mile W of Dhok Pathan Rest House).

GIU DP269, 268, 270 (around Dhok Pathan village).

The Post Cranial Skeleton

BSM H573 (Metatarsal III) Dhok Pathan 1.

BSM H523 (Distal end of humerus), H524 (Distal end of humerus), H534 (Proximal end of radius), H537 (Distal end of radius), H594, H625, H629 (Metacarpals III, distal extremities), H529, H542 (Tibiae distal extremities), H552 (Astragalus), H634 (Metatarsal III, proximal extremity) Dhok Pathan 3.

BSM H561 (Tibia distal extremity) Parlewali 2.

BSM H538 (Distal end of radius), H582 (Metacarpal III, distal extremity), H675 (Second anterior phalanx of the third digit), H581 (Metararsal III, distal extremity), H685 (Second posterior phalanx of the third digit) Parlewali 4.

BSM H539 (Distal end of radius), H551, H556 (Astragali), Karpewali.

BSM H646 (Second anterior phalanx of the third digit) ½–¾ mile WSW of Dhok Pathan Rest House.

BSM H560 (Calcaneum) Rattidheri.

BSM H558 (Astragalus) Latewali Khan.

BSM H653 (Astragalus) Winnewala.

BSM H570 (Metatarsal III) Datwal.

BSM H574 (Metatarsal III, proximal extremity) Dhok Pathan 5.

In addition the material in the American Museum of Natural History, New York, was also critically re-examined. For the list of these specimens the reader is referred to COLBERT (1935C, pp. 130–131).

3.1.2. Description

Upper teeth

Upper teeth are characterized by their oval or suboval protocone and complicated enamel folds of the fossette borders. MATTHEW (1929) assigns these characters to the Old World hipparions in general. The teeth are very hypsodont. It may be said that in *Hipparion antilopinum* the teeth on the average are the highest crowned amongst the Siwalik species. See table 1. The teeth are of moderate size, their respective measurements can be recorded from the individual descriptions.

P^2 Anteroposterior measurements (length) fall between 29.5 and 32 mm. The oval-shaped protocone and complicated enamel folds are found (general character for Siwalik hipparions). One sometimes sees the hypocone with a constricted neck (BSM H100). Open fossettes, which are sometimes seen in the European forms, are not observed here.

P^{3-4} Length of the teeth ranges from 21.4–23.9 mm. Extremely complicated enamel plications and rounded protocone are usual (BSM H281). The hypocone with constricted neck is also occasionally observed (BSM H147). In little-worn teeth the triangular protocone may also be found. In specimen no. BSM H144 exceptionally large and bean-shaped protocone is present which in general is typical for American hipparions. The length of the protocone in this particular case reaches to 10.5 mm. The index of hypsodonty varies between 193 and 288 (6 spec.). The protocone shape index was calculated as 530 (8 spec.) and 426 (3 spec.) in the medium and little-worn teeth respectively.

M^{1-2} Length varies from 19.3–22.2 mm. The same general pattern of the enamel is found as in the previous teeth. In specimen no. GIU DP69 the protostyle is present which is rarely seen in *Hipparion*. The protocone shape index in the medium-worn teeth comes to 513 (9 spec.) while in little-worn teeth the figure reaches to 493 (10 spec.). The figure for hypsodonty index varies from 242 to 292 (9 spec.).

M^3 The teeth measuring between 20 and 23.6 mm are assigned to this species. The protocone is usually a little bit compressed.

Lower teeth

All the accessory elements are well developed. The double knot (metaconid and metastylid) is typically *Hipparion*-like. In the milk teeth the protostylid and ectostylid are very well pronounced. Different frequencies of the ectostylid and plihypoconid are found in the premolars and molars.

P_2 The teeth measuring between 25 and 28.6 mm are grouped under this species. The plihypoconid is very common. In 78% of the cases its presence was recorded, while in none of them was the ectostylid observed. Total number of specimens studied 10.

P_{3-4} Length varies from 20.7–24.5 mm. The plihypoconid is usually present. This was seen in 72% of the cases (total 50 specimens). Occasionally a double plihypoconid was also observed (BSM H371, GIU DP173). The ectostylid is very rare in the permanent teeth, where it was only observed in 3 specimens (BSM H343, H368 and H385). Its frequency in these teeth reaches to 7%. The hypsodonty index varies from 186 to 263 (10 spec.).

M_{1-2} The teeth measuring in length between 20.1 and 23.5 mm are designated to this species. Occasionally a bifid protostylid is found (BSM H464 and H477). The ectostylid is not common. In 12% of the cases its presence was recorded. The pli-hypoconid was found in 10% of the cases (total 99 specimens). The index of hypsodonty ranges from 220–295 (18 spec.).

M_3 These teeth range between 25.1 and 28.4 mm in length. The protostylid is quite pronounced. In little-worn and unworn teeth it was found that it does not reach the occlusal surface.

The skull

There is one nearly complete skull of a young individual in the collection of the Bavarian State Museum, Munich, no. BSM H689 and a good cast of another skull, no. BSM H690, the original of which is stored in the Geological Survey of Pakistan, Quetta. These two skulls as far as different dimensions are concerned come close to skull no. AMNH 19761 assigned by COLBERT (1935C) to *Hipparion antilopinum*. The teeth of these two skulls also fall in the variation of *Hipparion antilopinum*.

BSM H689, skull of a young individual is very much distorted by crushing and as a result was found to be tilted toward the right side. The skull is nearly complete, except for some of its posterior part. Both zygomatic arches are broken. All the incisors and canines on both sides are present. Amongst the cheek teeth P^1 is present while M^3 had not yet erupted. The right cheek teeth series shows unworn permanent P^2, dP^3, dP^4, M^1 and just worn M^2. The left cheek teeth series contains a part of dP^2, dP^3, dP^4, M^1 and just worn M^2.

BSM H690 is of a fully adult individual. This is broken from the anterior end of the preorbital fossa, but, the teeth from P^2–M^3 are well-preserved. At the posterior end it is broken from the temporal bone. The right zygomatic arch is also broken. The skull is a little bit distorted owing to crushing and is tilted toward left side.

The orbit in both of the specimens is placed well back in the skull. The infraorbital foramen is situated right above the anterior end of the P^3 and below the preorbital fossa. It was difficult to make observations of more detailed anatomical features due to distortion which if made might lead to wrong conclusions.

BSM H689 (skull)

Basilar length (from alveolus of I^1 to the back of occipital condyle)	375.4 mm?
Facial width between zygomatic ridges of superior maxillary bones	119.2 mm
Width of Snout at maxillary crests	150.9 mm?
Width of Snout at points between dP^4 and M^1	134.1 mm
Width of Snout at anterior ends of alveoli of P^2	71.5 mm
* { Height of maxilla above M^1 (right side)	96.2 mm
* { Height of maxilla above M^1 (left side)	116.7 mm
Distance between post. edge of preorbital fossa and ant. edge of orbit	26.6 mm?
Length of preorbital fossa	55.0 mm?
Width of preorbital fossa above dP^4	29.2 mm?
Height of preorbital fossa at M^1	61.2 mm?
Vertical line from alveolar border of maxillaries, immediately behind M^3, to plane of upper profile line of skull (left side)	113.0 mm
Length P^2–M^2	128.5 mm
Length P^2–dP^4	81.0 mm
Length M^1–M^2.	47.5 mm

Length P^2–C (diastema)	48.3 mm
Length C–I^3	18.5 mm
Length I^1	18.1 mm
Width I^1	8.8 mm
Length dI^2	12.6 mm
Width dI^2	6.3 mm
Length dI^3	10.6 mm
Width dI^3	6.1 mm
Length C	7.2 mm
Width C	4.5 mm
Height of C (above alveolus)	6.6 mm
Length P^1	13.9 mm
Width P^1	8.0 mm
Height of P^1 (above alveolus)	6.6 mm
Length P^2	31.3 mm
Width P^2	16.6 mm
Length dP^3	24.8 mm
Width dP^3	23.1 mm
Length dP^4	24.9 mm
Width dP^4	22.1 mm
Length M^1	23.9 mm
Width M^1	20.9 mm
Length M^2	23.6 mm
Width M^2	15.3 mm

BSM H690 (skull)

Facial width between zygomatic ridges of superior maxillary bones	135.4 mm
Width of Snout at maxillary crests	146.1 mm
Width of Snout at points between P^4 and M^1	146.1 mm
Width of Snout at anterior ends of alveoli of P^2	72.8 mm
* Height of maxilla above M^1 (right side)	134.8 mm
* Height of maxilla above M^1 (left side)	128.3 mm
Distance between post. edge of preorbital fossa and ant. edge of orbit.	61.4 mm
Length of preorbital fossa	58.1 mm
Width of preorbital fossa above P^4	48.1 mm
Height of preorbital fossa at M^1	73.8 mm
Vertical line from alveolar border of maxillaries, immediately behind M^3, to plane of upper profile line of skull (left side)	126.9 mm
Length P^2–M^3	161.0 mm
Length P^2–P^4	88.8 mm
Length M^1–M^3	72.2 mm
Length P^2	34.6 mm
Width P^2	23.4 mm
Length P^3	27.9 mm
Width P^3	25.4 mm
Length P^4	26.3 mm
Width P_4	25.4 mm
Length M^1	24.1 mm
Width M^1	24.8 mm
Length M^2	24.2 mm
Width M^2	24.4 mm
Length M^3	23.9 mm
Width M^3	20.4 mm

* = approximate, difference on two sides is due to crushing.

Fragments of upper and lower jaws

Several fragments of upper and lower jaws are available for study in the Bavarian State Museum, Munich collection. Separate descriptions of them are not considered necessary; however, their measurements are given.

BSM H227 (Milk Dentition)

Right upper series containing dP^2–dP^4. The teeth are kept together with the rock. The teeth are just worn and little bit crushed, especially dP^2.

Length dP^2–dP^4 at the occlusal surface	77.4 mm
Length dP^2 at the occlusal surface	26.9 mm
Width dP^2 at the occlusal surface	15.6 mm?
Length dP^3 at the occlusal surface	24.9 mm
Width dP^3 at the occlusal surface	17.2 mm
Length dP^4 at the occlusal surface	25.6 mm
Width dP^4 at the occlusal surface	18.0 mm

BSM H248

A part of the right lower ramus with P_3–M_1. P_3 and P_4 have ectostylids. All the teeth are thickly covered with cement.

Length P_3–M_1	66.8 mm
Length P_3	23.4 mm
Width P_3	13.3 mm
Length P_4	22.5 mm
Width P_4	14.1 mm
Length M_1	20.9 mm
Width M_1	11.3 mm

BSM H493

A part of lower left ramus with M_1 and M_2. The teeth are little worn.

Length M_1–M_2	50.0 mm
Length M_1	25.2 mm
Width M_1	9.5 mm
Length M_2	24.8 mm
Width M_2	8.2 mm

BSM H501

Lower right M_1 and M_2 embedded partly in bone and partly in rock. M_1 has slipped down.

Length M_1	24.3 mm
Width M_1	7.4 mm
Length M_2	25.7 mm
Width M_2	9.0 mm

BSM H519

Part of upper jaw with P^2–M^3 on the left side and P^2–M^1 on the right side.

Total length of the left series (P^2–M^3)	139.8 mm
Length P^2–P^4	75.0 mm
Length M^1–M^3	64.8 mm
Length P^2	28.8 mm
Width P^2	21.9 mm
Length P^3	23.4 mm
Width P^3	23.3 mm
Length P^4	22.8 mm
Width P^4	24.1 mm

Length M^1	21.4 mm
Width M^1	22.2 mm
Length M^2	21.2 mm
Width M^2	21.1 mm
Length M^3	22.2 mm
Width M^3	18.2 mm

The Post Cranial Skeleton

Amongst some distal ends of humeri, BSM H524 and H523 are assigned to this species on account of their small size (table 9). Similarly the measurements on the proximal and distal ends of the radii classify BSM H534, H537, H538 and H539 as *Hipparion antilopinum*. The diameter width index at the distal end of the radii was calculated to be ranging between 612 and 651 (4 spec.).

Study of the distal ends of the metacarpal III gives the impression of a slender bone. This fact was further proved in the metatarsal III where more complete material is available. The sagittal crest and the tuberosities are moderately pronounced. The distal ends measuring 30.6–35.3 mm in width and 25.4–27.1 mm in diameter are assigned to this species.

The second anterior phalanx of the third digit gives the smallest measurements of all the species of the Siwalik hipparions (table 13). No morphological differences were observed when compared with the rest of the Siwalik species other than their smallest size.

In the BSM collection there are some distal extremities of tibiae. The width and diameter measurements were made and the specimens BSM H529 (young individual), H542 and H561 were classified as *Hipparion antilopinum*. AMNH 29823 a right tibia followed by tarsus and pes, perhaps, belongs to this species on account of its small size, rather than to *Hipparion theobaldi* as originally mentioned by Colbert (1935 C, p. 135). See table 14.

The calcaneum BSM H560 gives the total length 99.2 mm and maximum width in projection 38.6 mm, thus showing the smallest dimension amongst the Siwalik species. The incurving of the calcaneum at the distal lateral end is rather straight and represents an open arc (fig. 18: f).

The astragali do not show any morphological differences except their smallest size when compared with the other Siwalik forms. See table 15 and fig. 15. AMNH 29829, 29803 C, 29803 D and 29803 E are assigned to this species on account of their small dimensions. Colbert (1935 C, p. 135), however, classified them as *Hipparion theobaldi*.

The metatarsals III are characterized by their slenderness, see Plate 4, fig. 3. Massivity in case of AMNH 19667 and BSM H573 was calculated as 10 and 11 respectively. AMNH 29823 may be assigned to this species on account of its small dimensions. The facets for the cuboid and cuneiform II are well developed and are placed well above the proximal surface of articulation. The surfaces for the attachment of the lateral metatarsals are very clearly seen on both sides of BSM H573 which reach up to the distal extremity. At the distal articulation surface the metatarsal III has a strongly developed sagittal crest which reaches quite far on the volar surface. The tuberosities on the sides and the depression on the dorsal surface are very much pronounced (Plate 4, fig. 3).

AMNH 29823, a first posterior phalanx of the third digit may be assigned to this species. The maximum length and proximal width in this particular case reach 53.1 and 42.4 mm respectively. This is the smallest length so far observed in the Siwalik forms. The V-shaped scar on the ventral surface was found to be less developed in the above mentioned specimen when compared with the rest of the material from the American Museum.

BSM H685, a second posterior phalanx of the third digit gives the smallest length width measurements (table 18) and was classified as *Hipparion antilopinum*. No diagnostic morphological differences were found when compared with its counterparts in the rest of the Siwalik species.

3.1.3. Discussion

Unfortunately no description has been given by the original authors, which makes it difficult to understand the basis on which they raised the species. There are some figures available in the Fauna Antiqua Sivalensis the measurements of which were later given by MURCHISON (1868). LYDEKKER (1880) has already shown that the bones of these figures go to *Equus sivalensis* FALCONER & CAUTLEY, 1849, while the teeth belong to *Hipparion*.

GROMOVA (1952) states that the skull AMNH 19761 should belong to *Hipparion theobaldi* (LYDEKKER), 1877, which is originally assigned to *Hipparion antilopinum* (FALCONER & CAUTLEY), 1849 by COLBERT (1935C, p. 140). It may be remarked that she did not study the material but made this conclusion from the literature. Between the two skulls in the American Museum no. AMNH 19761 and AMNH 19466 there is considerable difference in size. The former being about 15% smaller than the latter. It might be pointed out that the latter is of a young individual in which the growth is still incomplete. GROMOVA (1952, p. 253) also finds similarities of AMNH 19761 to *H. dermatorhinum* SEFVE, 1927 from China.

GROMOVA (1952, p. 251) reports that the smallest teeth of *Hipparion antilopinum* correspond in size to the teeth of *Hipparion elegans* GROMOVA, 1952, and *Hipparion moldavicum* GROMOVA, 1952. The teeth of the type specimen BM no. 2647 (a right maxilla with P^2 to M^3) represent one of the smallest individuals of this species. The protocone shape index comes close to that of *H. elegans* and of *H. moldavicum*, as has already been pointed out by GROMOVA (1952). Discussing the enamel folds of the upper cheek teeth GROMOVA (1952, table 122) pointed out that the animals with the slender feet usually have a smaller number of plications, whereas the massive forms show a higher frequency of enamel folds. Her inference is based upon two figures (65 and 70) of COLBERT (1935C). It is hardly possible to count enamel plications correctly from fig. 65, whereas in fig. 70 there are two teeth of *Hipparion theobaldi* from the "Chinji" and two of *Hipparion antilopinum* from the Middle Siwaliks, which seems to be too poor evidence for such a statement. In our material the plications were counted in medium-worn teeth of different Siwalik species and there does not seem to be any possible relationship between the slenderness of the limbs and the number of plications (table 8). The Siwalik species in general have a high number of plications when compared with other hipparions. Amongst the European forms the number reaches close to *H. koenigswaldi* SONDAAR, 1961 from Spain. See table 8.

Study of AMNH 19761, BSM H689 and a cast of the cranium BSM H690 gives the impression of medium-sized skulls. COLBERT (1935C, p. 140) finds AMNH 19761 closely comparable to the skull of *Hipparion 'gracile'* (KAUP), 1833. COLBERT (1935C) had already noted the short and heavy zygomatic arch which is typical for *Hipparion*. An expanded brain case which is a character of the Late Tertiary horses is also found in *H. antilopinum*.

The available postcranial skeletal parts remind one of an animal of medium size when compared with the other *Hipparion* species.

Different parts of the humeri, radii and tibiae do not show any point of interest; however, their measurements are given in tables 9, 10 and 14.

GROMOVA (1952, p. 254) doubted the characters of slenderness for *Hipparion antilopinum* and of massivity for *Hipparion theobaldi*. She further thought that the metatarsal III

AMNH 19667 might belong to a young individual which consequently gave an impression of slenderness. Re-examination of the American Museum material has shown that the above mentioned metatarsal III is of an adult animal.

There is in fact a difference in the degree of massivity in the metapodials of *Hipparion antilopinum* and of *Hipparion theobaldi* as COLBERT (1935C, p. 141) has already shown. There are two complete metatarsals III in the collection of the Bavarian State Museum, Munich, which belong to *Hipparion antilopinum*. Their comparison with the metatarsals III of *Hipparion theobaldi* further demonstrates that *Hipparion antilopinum* had slender metapodials while *Hipparion theobaldi* had massive and heavy metapodials (Plate 4, figs. 1 and 3). The figures for massivity were calculated for AMNH 19667 and BSM H573 *(H. antilopinum)* as 10 and 11. In *H. theobaldi* this figure varies between 14 and 16 (5 specimens). COLBERT (1935C) compares this slenderness in *H. antilopinum* with *Neohipparion whitneyi* (GIDLEY), 1903 and *H. 'gracile'* (KAUP),1833. He considers *Hipparion antilopinum* to have long and slender metapodials. The comparative studies, however, show that the metapodials of *Hipparion antilopinum* on the average are not longer than those of *H. theobaldi* (table 16). They only apparently look long owing to their slender built.Their absolute length is nearly the same as those of *Hipparion theobaldi*. A very pronounced depression on the dorsal surface of the distal end shows a free movement of the first phalanx in the forward and backward directions. The significance of the cavity has already been discussed by GROMOVA, 1952, while comparing the metapodials of *Hipparion* and *Equus*.

There is not enough material of the phalanges to discuss any points of morphological interest.

3.2. *Hipparion theobaldi* (LYDEKKER) 1877

Plate 1: figs. 7–10; Plate 2: figs. 7,8; Plate 3: figs. 1–3; Plate 4: figs. 1, 2; Text fig. 18a, b.

Sivalhippus theobaldi LYDEKKER, 1877, Rec. Geol. Surv. India, vol. X, pt. I, pp. 31–32.

Hippotherium theobaldi, LYDEKKER, 1882, Pal. Ind., Ser. X, vol. II, pt. III, pp. 81–87, Pl. XI, figs. 3, 4; XII, figs. 2, 4; XIII, figs. 1–3.

Hipparion theobaldi, LYDEKKER, 1885, Cat. Siw. Vert. Indian Mus., pp. 58–60.

Additional References:

LYDEKKER, R., 1877 B, p. 82; 1880, p. 31; 1883 B, pp. 83–91; 1886 A, pp. 64, 65.
PILGRIM, G. E., 1910 B, p. 201; 1913, pp. 284–296.
MATTHEW, W. D., 1929, pp. 448, 450, 524–526.
COLBERT, E. H., 1935 C, pp. 133–159.
GROMOVA, V., 1952, pp. 251–255.

Holotype: IM. no. C. 153, left maxilla of young individual with dP^{2-4}, fig. by LYDEKKER 1882, Loc. cit., Pl. XI, fig. 4.

Type locality: Kaipar in the Punjab.

Horizon: Dhok Pathan Formation (upper part of the Middle Siwaliks).

Diagnosis: A very large and heavily built *Hipparion*, characterized by large and moderately hypsodont teeth, oval protocone, complicated enamel plications of the upper molars, well-developed preorbital fossa, extremely heavy metapodials, large angle between the facets for the magnum and the hamatum (155°, 13 spec.) and ridge-shaped tuberosity at the volar surface of the proximal extremity of the metacarpal III.

Differential diagnosis:

The upper first and second molars range from 23.0–25.8 and 23.1–26.7 mm in length and width respectively. In *H. antilopinum* these measurements vary from 19.3–22.2 and 19.8–25.0 mm and in *H. nagriensis* from 22.1–23.2 and 22.6–25.0 mm. By comparison the teeth of *H. theobaldi* on the average, give the largest measurements in the Siwalik species. For details see tables 6, 7 and figs. 4 to 11. The hypsodonty index for M^{1-2} of this species varies between 192–279 (14 spec.) whereas the same figures in *H. antilopinum* and *H. nagriensis* range between 242–292 (9 spec.) and 183–234 (7 spec.) respectively. So *H. theobaldi* on the average, has moderately hypsodont teeth among the Siwalik *Hipparion* species. For detailed figures the reader is referred to table 1. Extremely heavy metapodials are characteristic for this species. The massivity figure in the metatarsals III for this species varies from 14–16 (5 specimens), and in *H. antilopinum* this figure is 10 and 11 in two individuals. The angle between the facets for the magnum and the hamatum in the metacarpal III of this species varies between 153° and 158° (13 spec.) whereas in *H. nagriensis* the same angle ranges between 145° and 147° (3 spec.). See table 19. In the metacarpal III of *H. theobaldi* there is a ridge-shaped volar tubercle at the proximal end and a shallow concavity for the placement of the interosseous muscle, whereas in *H. nagriensis* the volar tubercle is a rounded tuberosity and the concavity for the placement of the interosseous muscle is deep.

3.2.1. Material studied

P^2

BSM H74 (Konkrori); H94 (Rattidheri); H142 (Winnewala); H426 (Datwal); H99 (Parlewali 3); H229 (Parlewali 4); H219, H224 (Kundral West).

YPM 19579 (Naragghi, S.P. map no. 43 C/8 C–2).

P^{3-4}

BSM H141, H145, H179, H209, H242 (Winnewala); H69, H71 (Moranwala); H88, H92, H192, H194, H196 (Rattidheri); H512 (Dhok Pathan 4); H135 (Dhok Pathan 5); H182 (Karpewali); H217 (Kundral West); H126, H468 (Parlewali 2); H102 (Parlewali 3); H118, H188 (Parlewali 4); H315 (Dhedari).

YPM 19466 (Pind Savidha); 19574 (Naragghi, S.P. map no. 43 C/8 C–2); 19122, 19123 (S.P. map no. 43 C/8 B–2); 19151 (S.P. map no. 43 H/5 B–2); 19364 (no locality).

GIU DP245, 246, 247, 248, 249 (around Dhok Pathan village).

M^{1-2}

BSM H77, H369, H372 (Konkrori); H93, H95, H195 (Rattidheri); H436 (Parlewali); H101 (Parlewali 3); H232 (Parlewali 4); H143, H175, H181 (Winnewala); H211 (Kundral); H218 (Kundral West); H233 (Karpewali); H252 (westsouthwest of Dhok Pathan 1); H163, H186, H239 (Dhok Pathan 3); H285 (Jhalarwali Dhok); H152 (Moranwala); H206 (Uchidheri).

YPM 19426, 19428 (S.P. map no. 43 H/5 B–2); 19580, 19588, 19589 (S.P. map no. 43 C/8 C–2).

GIU DP1, 4, 55, 68, 17, 19, 30, 54, 26, 241, 242, 243, 244 (around Dhok Pathan village).

M^3

BSM H420 (Gorianwala); H177 (Winnewala); H189, H191, H198 (Rattidheri); H203 (Uchidheri); H377 (Dhok Pathan 1); H271 (Dhok Pathan 3); H124 (Seanwala); H85 (Konkrori); H287 (Jhalarwali Dhok); H128, H131 (Parlewali 2); H106 (Parlewali 3).

YPM 19860, 19479, 19672 (S.P. map no. 43 H/5); 19984 (S.P. map no. 43 C/8).

GIU DP61, 255, 256, 257 (around Dhok Pathan village).

P_2

BSM H366 (Dhok Pathan 5); H463 (Parlewali 3); H320, H322 (Dhedari).

YPM 19787, 19422 (S.P. map no. 43 H/5); 19982 (S.P. map no. 43 C/8).

P_{3-4}

BSM H469 (Parlewali 2); H105 (Parlewali 3); H111, H112, H262, H353, H356, H357, H445, H446, H469 (Parlewali 4); H213 (Kundral); H431 (Kundral West); H308, H450 (Dhedari); H400, H401, H410A (Winnewala); H506 (Dhok Pathan 4); H435 (Dhok Pathan 5); H473 (Konkrori); H122 (Seanwala); H419 (Tappianwala); H348 (Karpewali); H398 (Moranwala); H197, H201, H481, H485 (Rattidheri); H424 (Uchidheri).

YPM 19262, 19585 (Naragghi, S.P. map no. 43 C/8 C–2); 19156 (S.P. map no. 43 H/5 B–2).

GIU DP153, 165, 169, 170, 182 (around Dhok Pathan village).

M_{1-2}

BSM H350, H437, H444 (Parlewali); H460 (Parlewali 3); H113, H115, H358 (Parlewali 4); H123 (Seanwala); H236, H237, H333, H482 (Rattidheri); H240 (Dhok Pathan 3); H518 (Dhok Pathan 5); H266, H300 (Latewali Khan); H310, H314, H316, H318 (Dhedari); H380, H384 (Uchidheri); H254, H402 (Winnewala); H421, H422 (Gorianwala); H364, H365, H476 (Konkrori); H288 (Jhalarwali Dhok).

YPM 19425, 19848 (S.P. map no. 43 H/5); 19987, 19557, 19572, 19583 (S.P. map no. 43 C/8).

GIU DP142, 238 (around Dhok Pathan village).

M_3

BSM H257, H258, H259 (Winnewala); H429 (Datwal); H272 (Dhok Pathan 3); H120 (Karpewali); H332, H335 (Rattidheri); H433 (Kundral West); H156 (Moranwala); H311, H317, H414 (Dhedari); H455, H457, H459 (Parlewali 3); H116, H354 (Parlewali 4); H289 (Jhalarwali Dhok).

YPM 19978, 19986, 20000 (S.P. map no. 43 C/8); 20194 (Hasnot area).

GIU DP212, 264 (around Dhok Pathan village).

The skull and jaw fragments

YPM 103 (Dhok Pathan Formation).

BSM H146, H376 (Dhok Pathan 3); H499, H500, H503, H511 (Dhok Pathan 4); H225, H226, H491, H515 (Dhok Pathan 5); H290 (Uchidheri); H410 (Winnewala).

GIU DP265, 266, 267, 271 (around Dhok Pathan village).

The Post Cranial Skeleton

BSM H541 (Part of scapula), H525 (Distal end of humerus), H536 (Radius proximal end), H532, H533, H546 (Radii distal ends), H587, H498, H602, H609, H614, H615, H616, H619, H623, H639, H631, H628 (Metacarpals III, proximal ends.), H596, H601, H613, H622 (Metacarpals III distal ends.), H643, H644, H645 (Second anterior phalanges of the third digit.), H545 (Femur distal end.), H526, H527, H528, H530, H531, H543, H544 (Tibiae distal ends.), H553, H554, H557 (Astragali), H578 (Metatarsal III), H586, H589, H590, H591, H593, H600, H604, H608, H610, H611, H612, H618, H621, H626, H627, H637, H642 (Metararsals III, proximal ends.), H588, H592, H595, H597, H599, H603, H606, H620, H630, H636, H641, H640, H632 (Metatarsals III, distal ends.) Dhok Pathan 3.

BSM H575 (Metacarpal III, distal end.), H584 (Metatarsal III), H576 (Metatarsal III, distal end.) Dhok Pathan 4.

BSM H580 (Metacarpal III, distal end.), H571 (Metatarsal III), H676, H678 (First posterior phalanges of the third digit.) Dhok Pathan 5.

BSM H679 (First anterior phalanx of the third digit.) Kundral West.

BSM H550 (Radius, distal end.), H682 (First anterior phalanx of the third digit.), H683 (First posterior phalanx of the third digit) Moranwala.

BSM H579 (Astragalus) Parlewali.

BSM H562 (Tibia, distal end.) Parlewali 2.

BSM H555 (Femur, distal end.) Parlewali 4.

BSM H559 (Tibia, proximal end.), H583 (Astragalus) Konkrori.

BSM H540 (Calcaneum) Datwal.

BSM H585 (Metatarsal III, proximal end.) Dhedari.

BSM H687 (First posterior phalanx of the third digit.) Winnewala.

BSM H686 (Second posterior phalanx of the third digit.) Karpewali.

In addition the material in the American Museum of Natural History, New York, was also critically re-examined. For the list of these specimens the reader is referred to COLBERT (1935 C, pp. 133–135).

3.2.2. Description

Upper Teeth

The dental pattern is more or less the same as described in the previous species, i.e. oval protocone and complicated enamel folds. The teeth are very large and on the average less hypsodont than those of *Hipparion antilopinum*.

P^2 The minimum length in these teeth is 34.2 mm and the maximum is 37.2 mm. The hypocone is sometimes with a constricted neck, and it may be pointed or rounded in shape at the posterior margin. The enamel plications are fairly complicated.

P^{3-4} The length ranges between 24.6 and 27.7 mm. The index of hypsodonty varies from 187–255 (9 spec.). The protocone shape index in the medium and little-worn teeth was found to be 532 (7 spec.) and 433 (3 spec.) respectively. The protocone in early stage of wear is triangular which later on changes into an oval or suboval shape.

M^{1-2} The length of the teeth measures between 23.0 and 25.8 mm. The figure for hypsodonty index ranges between 192 and 279 (14 spec.). The protocone shape index has been calculated in the medium and little-worn teeth as 522 (5 spec.) and 492 (7 spec.) respectively. The shape of the protocone follows the same general pattern as in the premolars.

M^3 The length ranges between 24.6 and 26.6 mm. In general the protocone is compressed as compared to the other teeth. The index of hypsodonty was calculated for one just worn right tooth no. BM 15396 as 271. The specimen as indicated by the British Museum notes comes from the Tatrot layers (basal part of the Upper Siwaliks).

Lower Teeth

There does not seem to be any diagnostic difference in the dental morphology when compared with those of *Hipparion antilopinum*. The criteria of distinction is on the basis of size. There are also differences in hypsodonty and in the frequency of accessory elements of different teeth. The exact figures will be mentioned in the descriptions of the respective teeth. The elongated and pointed metastylid was sometimes noted too. The ectostylid was not observed in this species.

P_2 The length of the teeth ranges between 30.3 and 30.9 mm. In 29% cases the plihypoconid is present. The ectostylid was not seen in these teeth (total number of specimens 7).

P_{3-4} The length of these teeth varies between 26.1 and 29.7 mm. The index of hypsodonty varies between 186 and 250 (10 spec.). This figure was found as high as 247 in one just worn premolar from Tatrot no. BM 15396. The ectostylid was not observed in these teeth. The plihypoconid was found in 37% cases (total number of specimens 37). Bifid plihypoconid was seen in BSM H431. This condition is repeated in rare cases.

M_{1-2} The length ranges from 24.7–28.0 mm. The index of hypsodonty in these teeth ranges from 198–277 (9 spec.). In 26% specimens the plihypoconid is present whereas the ectostylid is absent altogether (total number of specimens 38). Rarely is there a tendency toward bifid protostylid (BSM H444). This condition is repeated in a few cases. In AMNH 19505 exceptionally well-developed protostylid was observed.

M_3 The length of these teeth varies between 29.6 and 33.7 mm.

The skull

AMNH 19466, skull of a young individual with fourth premolar just erupting, is considerably larger in size than the AMNH 19761, BSM H689 and H690. However, it does not differ anatomically from the other skulls. COLBERT (1935 C, p. 145) has assigned this specimen to *Hipparion theobaldi*. The measurements of this specimen are also given in the same publication by COLBERT on pages 148 and 149.

YPM 103, a part of skull is assigned to *Hipparion theobaldi* on account of its large size. The teeth are little worn. The preorbital fossa is exceptionally large. The anterior edge of the preorbital fossa lies above the anterior border of P^3.

Length P^2–M^3	174.0 mm
Length P^2–P^4	98.4 mm
Length M^1–M^3	75.6 mm
Length P^2	37.5 mm
Width P^2	27.7 mm
Length P^3	31.2 mm
Width P^3	29.2 mm
Length P^4	29.7 mm
Width P^4	23.4 mm?
Length M^1	25.3 mm
Width M^1	25.8 mm
Length M^2	25.3 mm
Width M^2	24.1 mm
Length M^3	25.0 mm
Width M^3	19.1 mm
Length of preorbital fossa	84.7 mm
Maximum width of preorbital fossa	56.6 mm

Jaw fragments

BSM H146

Part of a right upper jaw with P^4–M^2. At the anterior end it is broken from the center of P^3.

Length P^4–M^2	80.6 mm
Length P^4	28.4 mm
Width P^4	24.7 mm
Length M^1	25.0 mm
Width M^1	23.1 mm
Length M^2	27.2 mm
Width M^2	20.0 mm

BSM H225 (Milk Dentition)

Part of an upper jaw of a young individual with 6 deciduous teeth on both sides. On right side M^1 is already erupted.

Length R.dP^2–dP^4	96.8 mm
Length R.dP^2	37.4 mm
Length R.dP^3	29.9 mm
Length R.dP^4	29.5 mm
Length L.dP^2–dP^4	96.6 mm
Length L.dP^2	37.1 mm

Length L.dP^3	29.9 mm
Length L.dP^4	29.6 mm

BSM H226 (Milk Dentition)

Right dP^3 and dP^4 embedded in rock.

Length dP^3–dP^4	59.6 mm
Length dP^3	29.5 mm
Width dP^3	18.4 mm
Length dP^4	30.1 mm
Width dP^4	18.3 mm

BSM H376 (Milk Dentition)

Fragment of a right lower jaw with dP_2 and dP_3. The teeth are just worn.

Length dP_2–dP_3	62.5 mm
Length dP_2	33.4 mm
Width dP_2	9.5 mm
Length dP_3	29.1 mm
Width dP_3	8.3 mm

BSM H410

A fragment of right lower ramus with P_2 and P_3. P_3 has exceptionally pronounced protostylid.

Length P_2	32.1 mm
Width P_2	14.0 mm
Length P_3	29.0 mm
Width P_3	16.1 mm

BSM H491

A right and left cheek teeth series of a young individual. The right cheek teeth series contains unworn P^2, half portion of dP^3 underneath which the permanent P^3 is seen, unworn P^4, little worn M^1, just worn M^2 and unworn M^3 which has not yet reached at the level of mastication.

The left series has unworn P^2, dP^3 and dP^4 underneath which their respective permanent teeth can be seen. Little worn M^1, just worn M^2 and unworn M^3 (which is not yet at the level of mastication) are also present.

Length L.P^2–M^3	174.1 mm
Length L.P^2	39.1 mm
Width L.P^2	22.3 mm
Length L.dP^3	28.8 mm
Width L.dP^3	24.6 mm
Length L.dP^4	29.6 mm
Width L.dP^4	24.4 mm
Length L.M^1	26.8 mm
Width L.M^1	24.0 mm
Length L.M^2	25.8 mm
Width L.M^2	20.7 mm
Length L.M^3	24.0 mm
Width L.M^3	15.9 mm

BSM H499 (Milk Dentition)

A left upper series of deciduous teeth containing dP^2–dP^4. The teeth are unworn and are placed together in the rock.

Length dP^2–dP^4	88.1 mm
Length dP^2	31.3 mm
Width dP^2	15.2 mm
Length dP^3	28.3 mm
Width dP^3	17.2 mm
Length dP^4	28.5 mm
Width dP^4	18.0 mm

BSM H500 (Milk Dentition)

Left lower series of deciduous teeth containing dP_2–dP_4. The teeth are supported by the rock. All the teeth are unworn.

Length dP_2–dP_4	89.8 mm
Length dP_2	34.5 mm
Width dP_2	10.0 mm
Length dP_3	29.1 mm
Width dP_3	9.5 mm
Length dP_4	26.2 mm?
Width dP_4	7.5 mm

BSM H503 (Milk Dentition)

Right upper series of deciduous teeth glued together. All the teeth are unworn.

Length dP^2–dP^4	98.5 mm
Length dP^2	38.2 mm
Width dP^2	17.4 mm
Length dP^3	30.6 mm
Width dP^3	18.3 mm
Length dP^4	29.7 mm
Width dP^4	18.6 mm

BSM H515 (Milk Dentition)

A fragment of upper jaw of a young individual containing milk molars and the first true molar just erupted on the right side, while on the left side only dP^2 is present. The deciduous teeth are just worn. The teeth are kept together with the matrix.

Length dP^2–dP^4	99.9 mm
Length dP^2	40.1 mm
Width dP^2	22.6 mm
Length dP^3	29.9 mm
Width dP^3	22.6 mm
Length dP^4	29.9 mm
Width dP^4	19.4 mm
Length M^1	26.5 mm
Width M^1	19.4 mm?

BSM H511

Part of the left lower ramus with dP_3 and dP_4. M_1 is just erupting. Pronounced ectostylids are seen in the deciduous teeth.

Length dP_3–dP_4	64.5 mm
Length dP_3	30.9 mm
Width dP_3	14.9 mm
Length dP_4	33.6 mm
Width dP_4	12.9 mm

The Post Cranial Skeleton

One distal end of humerus BSM H525 was classified as *H. theobaldi* on account of its large size. All the humeri in the AMNH belong to this species. COLBERT (1935C, p. 153) has given the articular lengths of these bones.

Some complete and a few distal ends of the radii are available for study in the AMNH and BSM collections. The diameter width index (at the distal end) varies between 566 and 600 (5 spec.). There are four complete radii available in the AMNH collection which belong to this species and from them it can be seen that the ulna is complete and extends over the whole length of the radius. The articular length of these bones is given by COLBERT (1935C, p. 153).

The metacarpal III is heavily built. The articular lengths of different metacarpals III are given by Colbert (1935C, p. 153). The maximum width and diameter at the proximal end vary from 41.7–49.5 and 27.2–34.4 mm (17 spec.) respectively. The proximal surface of articulation is very much specialized when compared with the other hipparions. The angle between the facets for the magnum and the hamatum ranges between 153° and 158° (13 spec.) which is quite high for the genus. See table 19. The volar tubercle for the attachment of the interosseous muscle is not a real tuberosity but it more or less acquires the shape of an elongated ridge like that in *Equus* (plate 3, fig. 1b). The concavity for the placement of the interosseous muscle is shallow and the lateral metacarpals are heavy, and go all along the length of the central metacarpal. The laterals are heavy but they are in proportion to the central metacarpal. This is thought reasonable for animals of heavy built. The distal extremity shows similarities to that in *Equus* and *Hipparion* both. The sagittal crest is very well-developed and so are the tuberosities. This together gives the distal articulation surface the general shape of a pulley where only one-sided movement is pronounced.

The first anterior phalanx of the third digit is also relatively large. The maximum length reaches to 63.9 mm in AMNH 19491 and the minimum to 60.8 mm in AMNH 19685 (7 spec.). The V-shaped ligamentary scar on the volar surface reaches little more than half the length of the phalanx (table 12). The index of length of the V scar and the total length of the phalanx was calculated as ranging between 532 and 638 (3 spec.). The groove on the proximal surface of articulation is well-pronounced (plate 3, fig. 3c).

The second anterior phalanx of the third digit is also very heavy. They can easily be distinguished from the other two species on account of their large dimensions.

Study of the three femora in the AMNH collection gives the impression of an animal with exceptionally heavy extremities.

There is a big variation in the thickness of the tibiae. However, the specimens stored in the AMNH seem to be exceptionally heavy (table 14).

The calcaneum BSM H540 measures 112.8 mm in length and its maximum width in projection is 45.9 mm. The incurving of the calcaneum at the distal lateral end is very straight and shows a large angle (fig. 18b).

The astragali can readily be separated from the other Siwalik species on the basis of their large dimensions (fig. 15).

The metatarsal III is exceptionally heavy. The massivity figure varies from 14–16 (5 specimens), this can also be compared in plate 4, figs. 1 and 3. The facets for the cuboid and the cuneiform II are well-developed and are placed above the articulation surface of the cuneiform III. The lateral metatarsals are very heavy but they are in proportion to the central one, as the skeleton on the whole is heavy. The general built of the distal end suggests a strong fixation with the first phalanx as it shows a very pronounced sagittal crest. The tuberosities at the distal extremity are also very well-pronounced. A deep concavity is observed at the dorsal distal end (Plate 4, fig. 1b).

Beside their large size the first posterior phalanges of the third digit show a deep groove at the proximal surface of articulation. The general configuration of BSM H683 gives the impression that this specimen belongs to a very heavy foot. The phalanx is very heavy, the V-shaped ligamentary scar on the volar surface is less developed and the central scar is quite pronounced (plate 4, fig. 2). The V-shaped ligamentary scar on the volar surface is also not very much developed in BSM H687, but in AMNH 19466 and 29822 it reaches more than half the length of the phalanges.

The second posterior phalanx can be differentiated on the basis of its large size (table 28).

3.2.3. Discussion

The species is originally based upon a left maxilla of a young individual with dP^2–dP^4, described by LYDEKKER (1882). Later he assigned more maxillas and teeth to this species. LYDEKKER could not give other valid clues to differentiate between *H. antilopinum* and *H. theobaldi* than the difference in size. In general the teeth do not show pronounced difference in morphology from the other Siwalik species. The differences in hypsodonty are well pronounced. On the average the teeth of *H. theobaldi* give lower hypsodonty index figures than those of *H. antilopinum* and higher values than those of *H. nagriensis*, table 1.

GROMOVA (1952, p. 252) discussed the skull AMNH 19466 and thinks that its premolar length corresponds to *Hipparion giganteum* and to the largest Chinese hipparions. She further states that the length of the dental series also comes close to the large specimens of *Hipparion crassum*.

The available skull material does not show any difference in morphology between *H. theobaldi* and *H. antilopinum*. However, there is a considerable difference in size which may be used as criteria for differentiation in skulls.

LYDEKKER (1882) described the teeth and foot bones of *H. theobaldi*, but he did not present any systematic description of the skeleton.

The foot bones of this species show morphological differences when compared with the other species from the Siwaliks. Starting from the humerus and the femur downward all the bones are very heavy. This can very nicely be seen on the metapodials where ample material is available. The metapodials are very massive and heavy (plate 4, fig. 1). At this stage it may be pointed out that the lateral metapodials are heavy in proportion to the central since the whole skeleton is heavily built.

In the anterior limbs the metacarpal III shows some interesting features. The large angle between the facets for the magnum and the hamatum (see table 19) provides a more or less flat base to the proximal surface of articulation, which ultimately helps in the transmission of more weight on the central metapodial. The average figure for this angle in *Hipparion theobaldi* is 155° (13 spec.). In one specimen of *Hipparion crassum* this figure reaches to 155°. *Hipparion crusafonti* which is considered to be a Pleistocene form, shows an angle of 164° (1 spec.). See table 19 for comparison of this angle in stratigraphically older and younger *Hipparion* species. It is seen that in stratigraphically older hipparions this angle is relatively smaller whereas in geologically younger hipparions it becomes larger and larger to provide a uniform plane at the proximal surface of articulation. *Neohipparion occidentale* (LEIDY) 1856, from North America, which is considered to be the nearest form to the Old World hipparions (COLBERT, 1935 C), gives the lowest figure for this angle (130°, 1 spec.).

A second point of interest at the proximal end of the metacarpal III is the presence of a ridge-shaped volar tubercle for the attachment of the interosseous muscle (plate 3, fig. 1 b). The ridge-shaped volar tubercle is usually found in monodactyl horses (SONDAAR 1968, p. 23). It seems to be suitable for the attachment of the fibres of the interosseous tendon. Amongst recent mammals the interosseous tendon is found in *Equus* only (CAMP & SMITH, 1942, p. 71). Explaining the function of the interosseous tendon CAMP & SMITH (1942, p. 71) state, "The interosseous tendon, in conjunction with the great sesamoid ligaments, contributes powerfully to the automatic springing of the foot. Muscular tissue, by weakening the tendon, would tend to enfeeble, this action." Presence of the ridge in *H. theobaldi* recalls similarities to that in *Equus*. In this species the interosseous muscle was, perhaps, already on its way to change into interosseous tendon for better adaptation. Presence of a shallow concavity on the volar surface of the metacarpal III in *H. theobaldi* throughout its length indicates that the respective muscle may not have had a fleshy tissue (Plate 3, fig. 1b). In *Hipparion* type foot the interosseous muscle is in close contact with the bone because of more dorsal flexion of the first phalanx. So in case of a thick muscle one should expect a deep concavity for its lodging. In *H. theobaldi* this is different. The shallow concavity suggests the presence of a thin interosseous muscle. This, along with the ridge-shaped volar tubercle, gives an indication of a tendinous muscle, as already suggested. Recession of the interosseous muscle (see CAMP & SMITH 1942) presumably accompanied the enlargement of the inferior sesamoidean ligaments in the Miocene horses. Its complete change into the interosseous tendon is seen in the modern horse. CAMP & SMITH (1942) further state that both *Hipparion* and *Pliohippus* had the ligamental springing mechanism in the foot. SHOTWELL (1961, p. 216) "The three-toed springing foot of *Hipparion* is functional. It provides the additional traction necessary to make sudden change of direction by lunging." SONDAAR'S (1968, p. 7) opinion concerning this problem is somewhat different. "The degeneration of the muscle interosseous into a tendon took place relatively late in the phylogeny of the horse. Only in monodactyl horses is the tendification complete."

The springing foot depends on the presence of the interosseous tendon. Shape of the metapodial in *Hipparion* in general is not in favour of its presence, which makes it difficult to think of a springing foot in *Hipparion*. CAMP & SMITH (1942) and SHOTWELL (1961), however, conclude to its presence in *Hipparion*. Some of the geologically younger hipparions such as *H. theobaldi* and *H. crusafonti*, had a type of metacarpal which, perhaps, indicates the presence of a tendinous muscle. It was assumed that there was still incomplete tendinosity in these animals. They acquired some of the characters of monodactyl horses for better adaptation. At this point one may have to agree with SONDAAR (1968) where he says that the complete tendinosity is only seen in monodactyl horses.

The distal extremity of the metacarpal III shows mixed characters when compared with that in *Equus*. The pronounced sagittal crest gives a better fixation to the metacarpal III with the first phalanx which would minimise the possibility of lateral dislocation (Plate 3, fig. 2). GROMOVA (1952) and SONDAAR (1968) state that this crest is most pronounced in *Equus*. SONDAAR (1968) remarks that development of the sagittal crest, lengthening of the central phalanx and reduction of the laterals are synchronous changes in the phylogeny of horse. He is further of opinion that it also controls most of the lateral dislocation of the fetlock joint. The concavity at the ventral distal end of the metacarpal III is quite pronounced and divided into two by the sagittal crest (Plate 3, fig. 2b). GROMOVA (1952) regards this concavity as produced by the pressure of the laterals. This is very well demonstrated in *Hipparion theobaldi* as it has very heavy lateral metapodials. Well-pronounced tubercles at the distal end of the metacarpal III in *Hipparion theobaldi* show higher figures for width as compared to the width at the distal surface of articulation. GROMOVA (1952) in comparing *Hipparion* and *Equus* metapodials assigns the character of pronounced tuberosities to *Hipparion* whereas in *Equus* she did not observe any such tuberosities. SONDAAR (1968) relates this difference to tridactyl and monodactyl horses. *Hipparion theobaldi* in its characters like elongated ridge on the ventral side of the proximal extremity and pronounced sagittal crest at the distal end of the metacarpal III shows similarities to *Hipparion crusafonti* and to *Hipparion crassum*.

The deep groove on the proximal surface of articulation in the first anterior phalanx of the third digit in *Hipparion theobaldi* shows better fixation of the sagittal crest of the metacarpal III with the first phalanx (Plate 3, fig. 3c). GROMOVA (1952), explaining the differences between *Hipparion* and *Equus*, reports that the sagittal crest on the distal end of the metapodial and consequently the groove on the proximal surface of articulation of the first phalanx help in preventing lateral dislocation at the fetlock joint. The V-shaped scar on the first anterior phalanx which is very well-developed in *H. theobaldi* also is in favour of the better fixation of the ligaments and prevents lateral dislocation. See Plate 3, fig. 3b, and Table 12.

Femora and tibiae of *Hipparion theobaldi* do not give much information other than their large size. COLBERT (1935 C) has reported that the femur is of ordinary form and the fibula extends about half way down the tibia. The calcaneum in having a large angle of the incurve at the lateral distal end resembles more or less to that of *Equus* (Fig. 18b), whereas in geologically older hipparions this curve generally resembles a half circle.

The metatarsal III is a very heavy and massive bone. Pronounced sagittal crest at the distal end gives a better fixation with the first phalanx. Exceptionally pronounced concavity at the dorsal distal end provides more space for the movement of the first phalanx. GROMOVA (1952) has already evaluated this character while comparing the characters of *Hipparion* and *Equus*. The short and stout first phalanx indicates a heavy foot. The pronounced groove at the proximal surface of articulation of the first phalanx gives a better fixation at the fetlock joint and ultimately reduces the possibility of lateral movement.

The lateral digits of *Hipparion theobaldi* seem to be exceptionally heavy when compared with the other hipparions. COLBERT (1935 C, p. 149 and 152) has very clearly shown that the laterals are only proportionally heavy. To quote "the lateral digits are heavy, but this is due to the fact that the entire foot is heavy. One of the most reliable methods of comparison, when working with various genera and species of mammals, is that whereby the ratios of homologous parts are considered. A certain skeletal element may seem to show considerable variations in two separate species when the comparisons are made on the basis of that element alone, but when it is considered in its relation to some other element of functional affinities the supposed differences often turn out to be more apparent than real.

For instance, the lateral digits of *Hipparion theobaldi* seem to be very heavy as compared to the lateral digits of other species of *Hipparion*, say *Hipparion whitneyi*. But when the lateral digits are compared to the medial digit it is seen that they are proportionately about the same in the two species. That is to say, the lateral digits of *Hipparion theobaldi* are heavy by virtue of the fact that the entire foot and limb is heavy, but proportionately they are no larger than in other more slender species of the genus."

As the increase in size of the animal is followed by increase in width and massiveness of the bones, *Hipparion theobaldi* which is a large species should have heavy limbs and foot bones. COLBERT (1935 C) considered *Hipparion theobaldi* as large as a small wild *Equus*. Our study of the material shows that this animal not only reached the size of an average sized *Equus*, but also acquired some morphological characters of it, which we have already discussed in the study of the metapodials. MATTHEW (1929) considered the Old World *Hipparion* as progressive, but rather aberrantly specialized. *Hipparion theobaldi* acquired similarities to *Equus* which might have been necessary to cope with changing ecological conditions.

3.3. *Hipparion nagriensis* new species

Plate 1: figs. 1–6; Plate 2: figs. 9, 10; Plate 3: figs. 5–7; Plate 4: figs. 4, 5; Text. fig. 18c, d.

Holotype: BSM H15, a right medium worn M^{1-2}, Plate 1, fig. 1.
length: 22.6 mm.
width: 23.6 mm.

Paratypes: Figured specimens:

GIU Ng12, a left upper P^{3-4}; GIU Ng7, a left upper M^{1-2}; BSM H13, a right lower M_{1-2}; BSM H10, a left lower P_{3-4}; GIU Ng27, a right lower M_{1-2}; BSM H17, a left upper M^{1-2}; GIU Ng17, a right lower M_{1-2}; GIU Ng53, a left proximal end of metacarpal III; GIU Ng52, a distal end of metacarpal III; BSM H43, first anterior phalanx of the third digit; BSM H61, distal end of metatarsal III; GIU Ng70, first posterior phalanx of the third digit; GIU Ng62, a right astragalus; GIU Ng90, a right calcaneum.

Unfigured specimens:

BSM H12, H22 and GIU Ng28 (upper second premolars); BSM H2, H6, H7, H8, H11, H16, H18, H25, H29 and GIU Ng2 (third or fourth upper premolars); BSM H9, GIU Ng1, Ng3, Ng4, Ng6, Ng13 (first or second upper molars); GIU Ng5, Ng8, Ng10, Ng11, Ng32, Ng37, Ng38 (upper third molars); GIU Ng24, Ng33, Ng35, and Ng36 (lower second premolars); BSM H1 (lower second milk molar); BSM H14, GIU Ng15, Ng18, Ng21, Ng26, Ng29 and Ng31 (lower third or fourth premolars); BSM H3, H19, H21, GIU Ng14, Ng16, Ng19, Ng22 and Ng23 (lower first or second molars); BSM H5, GIU Ng20, Ng25, Ng30, and Ng34 (lower third molars); BSM H40, part of left lower ramus with M_2 and M_3; YPM 19119, part of left ramus with P_2–M_3 (this specimen does not come from the Nagri gorge, see the description page 50); GIU Ng60, Ng61 and BSM H41 (astragali); GIU Ng54 (metacarpal III distal); BSM H49 (young individual), H60 (metacarpals III proximal); GIU Ng51 (metatarsal III distal); BSM H42, GIU Ng71, Ng72, Ng73, Ng74 (first posterior phalanges of the third digit); BSM H44, H45, GIU Ng80 (second anterior phalanges of the third digit); BSM H55, H53, H46 and GIU Ng81 (second posterior phalanges of the third digit); some distal ends of the lateral metapodials and phalanges.

Type locality: Nagri gorge near Nagri village.

Horizon: Nagri Formation, stratotype (basal Middle Siwaliks). About 1,000 feet above the lithologic boundary of the Nagri Formation.

Diagnosis: A large *Hipparion*, characterized by moderately large and less hypsodont teeth than those of *H. antilopinum* and of *H. theobaldi*, oval protocone, complicated enamel plications at the fossette borders of the upper molars, small angle between the facets for the magnum and the hamatum (146°, mean of 3 specimens), and rounded tuberosity at the volar surface of the proximal extremity of the metacarpal III.

Differential diagnosis:

The upper first and second molars range from 22.1–23.2 and 22.6–25.0 mm in length and width respectively. In *H. antilopinum* these measurements vary from 19.3–22.2 and 19.8–25.0 mm and in *H. theobaldi* from 23.0–25.8 and 23.1–26.7 mm. By comparison the teeth of *H. nagriensis* on the average, give the intermediate measurements of the Siwalik species. For details see tables 6, 7 and figs. 4–11. The hypsodonty index for M^{1-2} of this species varies from 183–234 (7 spec.) while the same figures in *H. antilopinum* and *H. theobaldi* range between 242–292 (9 spec.) and 192–279 (14 spec.) respectively. So *H. nagriensis*, on the average, has less hypsodont teeth in the Siwalik *Hipparion* species. For detailed figures the reader is referred to table 1. The angle between the facets for the magnum and the hamatum in the metacarpal III of this species varies from 145–147° (3 spec.), whereas in *H. theobaldi* the same angle ranges between 153° and 158° (13 spec.). In the metacarpal III of *H. nagriensis* the volar tubercle at the proximal extremity is a rounded tuberosity and the concavity for the placement of the interosseous muscle is deep, whereas in *H. theobaldi* this tubercle is ridge-shaped and the concavity for the placement of the interosseous muscle is shallow.

3.3.1. Description

Upper Teeth

The general morphology of the teeth does not differentiate them clearly from the previously described two species. The constricted neck hypocone is more frequently seen than in the last two species (17 out of 30 specimens). It is hard to say whether this character should be considered of any specific value or not because it changes with wear. In general the teeth can be separated from those of *Hipparion antilopinum* and of *Hipparion theobaldi* on the basis of size. Length of most of the teeth is intermediate between the two previously described species and they, on the average, give the lowest figures for index of hypsodonty amongst the Siwalik species. The oval protocone and the complicated enamel plications which may be considered as general characters for Siwalik *Hipparion* are also observed in this species.

P^2 The length of these teeth varies between 33.2 and 33.7 mm. In two out of three teeth from the BSM collection the hypocone is with constricted neck. In one specimen (BSM H12) the protocone is very large and flat instead of being rounded or oval.

P^{3-4} They measure in length between 23.8 and 25.1 mm. The figure for the index of hypsodonty varies from 166–222 (5 spec.). The average protocone shape index in the medium and little-worn teeth was calculated 590 (4 spec.) and 430 (2 spec.) respectively. The hypoconal groove in general seems to be a bit more deeply invaginated than in the previously described species. No specific value to this character is given as it varies with wear.

M^{1-2} The specimens fall between 22.1 and 23.2 mm when measured anteroposteriorly. The index of hypsodonty for these teeth varies from 183–234 (7 spec.). The average figures for protocone shape index are 510 (4 spec.) and 438 (5 spec.) in medium and little-worn teeth respectively. The type specimen BSM H15 is one of the typical molars of this species with oval protocone and constricted neck hypocone. An extreme development of constricted neck hypocone was seen in GIU Ng7 (Plate 1, fig. 2), where it appears in the form of an isolated island. Isolated hypocone was also observed in both the upper third molars of a skull of *H. dietrichi* WEHRLI, 1941, from Samos no. AMNH 20596.

M^3 The specimens when measured in length fall between 23.3 and 24.6 mm. The protocone of M^3 in this species is also compressed. This may be considered as a general character for the third molars.

Lower teeth

Lower teeth again are not morphologically different from the previously described two species except for their dimensions and their low index of hypsodonty. These figures will be mentioned in the description of the specific teeth. The double knot (metaconid and metastylid) is typical of *Hipparion*. The protostylid is quite pronounced.

P_2 Out of the four teeth three range between 28.5 and 29.1 mm in length whereas the fourth one GIU Ng33 is measured 32.1 mm. The tooth is unusually large and its whole surface was not in contact with the opposite tooth. This resulted in its uneven wear and finally made a wedge-shaped structure. For further details the reader is referred to HUSSAIN & SONDAAR (1968) where they consider it to be an anomalous feature. In the same tooth there is an indication of presence of the plihypoconid on the occlusal surface, but it cannot be seen on the buccal side because the tooth is covered with cement. The other three teeth do not show its presence. The ectostylid is lacking in all the four.

P_{3-4} They vary in length between 24.7 and 26.0 mm. All the teeth show very pronounced protostylid. GIU Ng15 has cranulated enamel and this is the only specimen which bears the ectostylid. In the BSM collection three out of eight teeth show the presence of the plihypoconid, thus the frequency goes to 38%. The index of hypsodonty for little-worn and unworn teeth varies from 158–211 (5 spec.).

M_{1-2} They fall between 22.9 and 25.0 mm when measured in length. These teeth show considerable overlap with those of the other two species. Only one out of 11 specimens from the BSM collection showed the presence of the ectostylid, whereas in none of them was the plihypoconid observed. The index of hypsodonty for little-worn and unworn teeth was calculated as ranging between 170 and 227 (7 spec.).

M_3 Out of the five teeth the length of the four varies between 28.7 and 29.2 mm and the fifth one GIU Ng25 is exceptionally large and measures 31 mm.

Jaw fragments

BSM H40, a part of left lower jaw with M_2 and M_3.

Total length M_2 and M_3	49.2 mm
Length M_2	22.1 mm
Width M_2	14.8 mm
Length M_3	27.1 mm
Width M_3	12.5 mm

YPM 19119, a part of left lower ramus with P_4–M_2. This specimen comes from South of Pari, Darweza. LEWIS (1932) has mentioned in his field notes that the age of these beds is basal Middle Siwaliks. This is the only specimen that does not come from the type locality of the Nagri Formation.

Length P_4	26.9 mm
Width P_4	16.1 mm
Length M_1–M_2	48.4 mm
Width M_2	13.2 mm

The Post Cranial Skeleton

The width and diameter (maximum) at the proximal end of the metacarpal III range from 34.1–37.1 and from 23.9–29.1 mm respectively (3 spec.). The angle between the facets for the magnum and the hamatum varies from 145–147° (3 spec.). The volar tubercle for the attachment of the interosseous muscle is a rounded tuberosity (Plate 3, fig. 5b). The concavity for the placement of the interosseous muscle is deep (Plate 3, fig. 5b). The distal extremity in two specimens measures 32.6, 33.5 and 26.0, 28.1 mm in width and diameter respectively. The sagittal crest is weakly developed.

The first anterior phalanx gives the impression that it belongs to a slender metapodial (Plate 3, fig. 7). The central groove at the proximal surface of articulation is moderately developed. The V-shaped ligamentary scar is not well-developed and reaches nearly one third of the total length of the phalanx (Plate 3, fig. 7b). Length of the scar was measured in BSM H43 as 16.1 mm. The ratio of length of the ligamentary scar and the total length of the phalanx was calculated as 298.

The second anterior phalanges of the third digit occupy an intermediate position in length width relation (table 13). The comparison of morphology with the other Siwalik species does not give clear-cut differences.

The calcaneum GIU Ng90 measures 101.3 mm in length. The incurving at the lateral distal end shows an arc-shaped structure (fig. 18d).

The astragali did not show any pronounced morphological differences, except that they occupy an intermediate position when their length width measurements are plotted against those of *Hipparion theobaldi* and of *Hipparion antilopinum* (fig. 15).

The concavity at the dorsal distal surface of the metatarsal III is moderately pronounced and so is the sagittal crest (Plate 4, fig. 4a). The width and diameter at the distal extremity in two specimens measure 35.8, 36.3 and 29.5, 31.8 mm respectively. The tuberosities on the sides of the distal end are not very pronounced.

GIU Ng70, a first posterior phalanx of the third digit, shows a fairly deep groove on the proximal surface of articulation (Plate 4, fig. 5c). Length and proximal width for the first posterior phalanx range between 54.9–58.3 and 35.3–39.6 mm respectively (4 spec.). The V-shaped ligamentary scar on the volar surface hardly reaches half the length of the phalanx (table 17). In GIU Ng70 the perforatus scars are particularly pronounced (Plate 4, fig. 5b). Index of the length of the V-scar and the total length of the phalanx ranges between 342 and 485 (4 spec.).

The second posterior phalanges of the third digit are intermediate in size between the other species from the Siwaliks.

3.3.2. Discussion

Two points of interest can be observed in the isolated teeth. The upper and lower teeth ranging from the second premolar to the third molar, on the average, are intermediate in size between those of *Hipparion antilopinum* and of *Hipparion theobaldi*. This is demonstrated in figures 4–11. The second difference is that of hypsodonty. *Hipparion nagriensis* from the Nagri Formation, on the average, gives the lowest figures for hypsodonty index when compared with *Hipparion antilopinum* and *Hipparion theobaldi*. See table 1. The morphology of the teeth does not show important criteria to distinguish them from the previously described two species. So all the Siwalik hipparions have the same dental morphology. Constricted neck hypocone is more frequently seen in *Hipparion nagriensis* (17 specimens out of 30 show this feature). It is difficult to evaluate this character as it changes with wear. The isolated hypocone in GIU Ng7 (Plate 1, fig. 2) may induce us to consider it a primitive feature in the Siwalik *Hipparion* species, but such a statement requires more material. In the pattern of the upper teeth *Hipparion nagriensis* more or less resembles *Hipparion catalaunicum* PIRLOT, 1956. In the teeth of the left upper jaw of *H. catalaunicum* (MS VP 100) the oval protocone was observed whereas the enamel plications are not as complicated as in the teeth of *H. nagriensis*. In MS VP156 (part of a skull of *H. catalaunicum*) the constricted neck hypocone was seen in the right series P^2–M^3. In its character of the constricted neck hypocone *Hipparion nagriensis* also resembles *Hipparion koenigswaldi* SONDAAR, 1961 (see SONDAAR, 1961, plate 1, fig. B) where P^2, P^3, P^4 and M^2 show this feature. Lower teeth of *Hipparion nagriensis* are typically *Hipparion*-like and have well-developed dental elements.

Study of different skeletal parts gives a better basis to distinguish *Hipparion nagriensis* from the other Siwalik hipparions. The relatively small angle (146°, mean of 3 spec.), between the facets for the magnum and the hamatum at the proximal surface of articulation of the metacarpal III brings it closer to the stratigraphically older hipparions from Europe. In this respect it comes very close to *Hipparion catalaunicum* where the same angle is measured 145° (one spec.). For detailed comparison see table 19. Small angle gives nearly two separate planes at the proximal articulation surface which contribute to distribute the weight of the animal on the central and the lateral metacarpal IV. In this way some of the weight is being carried by the fourth metacarpal. The rounded tuberosity at the volar side of the proximal extremity and the deep concavity on the ventral surface show the presence of a thick fleshy interosseous muscle in *Hipparion nagriensis* (Plate 3, fig. 5b). In this respect it again resembles *Hipparion catalaunicum* where such features like rounded tuberosity on the volar side of the proximal end and deep concavity on the ventral surface of the metacarpal III along the length are observed. The metacarpal III no. MS VP 120 of *Hipparion catalaunicum* was studied for comparative purposes. Similarities of *Hipparion nagriensis* in the above mentioned features have also been recorded to *Hipparion koenigswaldi* (Plate 3, fig. 4). In the evolution of horse the above mentioned features are considered primitive characters when compared with the ridge-like structure inspite of tuberosity, a shallow concavity instead of deep one and a large angle between the facets for the magnum and the hamatum instead of small. The functional implications of these characters are discussed at greater length by Camp & Smith (1942), Gromova (1952) and Sondaar (1968). The moderately developed sagittal crest at the distal end of the metacarpal III in *Hipparion nagriensis* shows a relatively weak fixation at the fetlock joint if compared with the later Siwalik hipparions. This shows that the fixation against lateral dislocation was not so good in *H. nagriensis* (Plate 3, fig. 6). In *Hipparion theobaldi* the sagittal crest is very strongly developed which gives a better fixation at the fetlock joint.

The relatively shallow groove at the proximal surface of articulation and less-developed V-scar on the volar side of the first phalanx of the third digit also indicate a weak fetlock joint (Plate 3, fig. 7).

There are no morphological differences in the second anterior phalanx of the third digit except for their intermediate size between those of *Hipparion theobaldi* and of *Hipparion antilopinum* (table 13).

An important feature is noted in the calcaneum of *Hipparion nagriensis*. The incurving at the lateral distal end shows a sharp curvature which gives it an arc-shaped structure (fig. 18d). In *Hipparion theobaldi* and *Hipparion antilopinum* this curve is an open arc. Arc-shaped curve was also noted in the calcaneum of *Hipparion catalaunicum* (MS VP 106) from Spain and in *Hipparion forcei* Richey, 1948 (UC 33724) from North America.

The astragali only show their intermediate position in size between those of *Hipparion antilopinum* and of *Hipparion theobaldi* (fig. 15).

Study of the distal extremities of the metatarsal III draws our attention to a slender limbed animal. The sagittal crest and the concavity at the dorsal distal surface are nearly as pronounced as in *Hipparion antilopinum*. The tuberosities on the sides are weak as compared to *Hipparion antilopinum* and *Hipparion theobaldi* (Plate 4, fig. 4).

The first posterior phalanx of the third digit differs from *Hipparion theobaldi* in having very pronounced perforatus scars on the volar surface. Furthermore it does not give the impression of having a heavy foot like we observe in the phalanges of *Hipparion theobaldi*. The less developed ligamentary scar may also add to form a weak fetlock joint where more lateral movement is possible.

LYDEKKER (1884A, pp. 14–16) proposed a new species *Hipparion feddeni* on the basis of a jaw fragment with three right upper teeth, namely P^3–M^1, IM C273 (Paleontologica Indica, Ser. 10, vol. 3, part 1, fig. 4) from the Siwaliks of Perim Island (Southwestern India, in the Gulf of Cambay). The age of the Perim Island beds is questionable. PILGRIM (1913), while discussing the fauna of Perim Island, provisionally correlated it with the Nagri "zone" Later COLBERT (1935C) found its closest affinities with the Dhok Pathan fauna of the Salt Range area. LYDEKKER compared these teeth with those of *Hipparion antilopinum* and of *Hipparion theobaldi*. Most of his comparison is based on the shape of the protocone and the hypocone. These differences are not considered of specific value because the shape of the protocone and hypocone changes with wear. Moreover, the protocones of the Siwalik hipparions are not very different from each other. He further concludes that these teeth are intermediate in size between those of *Hipparion antilopinum* and of *Hipparion theobaldi*, but to base such a statement on a mere three teeth does not seem to be very convincing as there is a great variation in tooth size in the Siwalik species. Furthermore, nothing is known about the post cranial skeleton of this species. Under these circumstances it is preferred to consider *Hipparion feddeni* as ***nomen dubium***.

4. TRENDS IN HYPSODONTY

Increase in hypsodonty is one of the main features observed in the evolution of the Equidae. It becomes more conspicuous after *Merychippus* where it is seen in the phylogenetic lines to *Hipparion* and *Pliohippus*. The subject in general has been discussed from various angles, among others by MATTHEW (1926), SIMPSON (1944 and 1953), STIRTON (1947), WHITE (1959) and VAN VALEN (1960). SIMPSON (1953, p. 16) "Hypsodonty is a single character from a physiological point of view, and it is unquestionably a unit in its interaction with the pressure of natural selection." STIRTON (1947, p. 32) "Origin and evolution in Tertiary mammals, particularly in the hypsodont horses, has usually been correlated with a change in diet. This dietry change probably involved a shift from browsing on softer herbaceous plants to grazing on harsh or siliceous grasses which acted as abrasive agents on the teeth."

STIRTON (1947) has discussed the relation between the root closure and hypsodonty in later Cenozoic horses at some length and has given some figures for illustration. He concludes that there is a slight retardation in root closure and continuation of vertical growth in the cheek teeth of the species ranging from Middle Miocene to Pleistocene. After the theoretical review of hypsodonty by SIMPSON and STIRTON it will be checked how does it

Table 1. Showing hypsodonty index in Siwalik *Hipparion*

	M^{1-2}	P^{3-4}	M_{1-2}	P_{3-4}
H. nagriensis	183(212)234 7 spec.	166(189)222 5 spec.	170(203)227 7 spec.	158(184)211 5 spec.
H. theobaldi	192(251)279 14 spec.	187(222)255 9 spec.	198(234)277 9 spec.	186(226)250 10 spec.
H. antilopinum	242(263)292 9 spec.	193(240)288 6 spec.	220(252)295 18 spec.	186(241)263 10 spec.

fit to the Siwalik Equidae. The figures for hypsodonty index were separately calculated for *Hipparion nagriensis* from the Nagri Formation, for *Hipparion antilopinum* and *Hipparion theobaldi* from the Dhok Pathan Formation. Considering the thickness of the Dhok Pathan Formation it is divided into lower, middle and upper parts, and it was observed that the hypsodonty index figures for the genus are increasing from the Nagri Formation upward. See tables 2–5.

Tables showing hypsodonty index in stratigraphically collected specimens.

Table 2
M^{1-2}

	Nagri	Dhok Pathan		
		Lower	Middle	Upper
H. nagriensis	183(212)234 7 spec.	—	—	—
H. theobaldi	—	192(224)259 3 spec.	233(250)268 7 spec.	260(272)279 4 spec.
H. antilopinum	—	—	242(252)264 4 spec.	254(272)292 5 spec.

Table 3
P^{3-4}

	Nagri	Dhok Pathan		
		Lower	Middle	Upper
H. nagriensis	166(189)222 5 spec.	—	—	—
H. theobaldi	—	187(197)212 3 spec.	218(231)251 4 spec.	231(243)255 2 spec.
H. antilopinum	—	193(200)207 2 spec.	247(249)251 2 spec.	254(271)288 2 spec.

Table 4
M_{1-2}

	Nagri	Dhok Pathan		
		Lower	Middle	Upper
H. nagriensis	170(203)227 7 spec.	—	—	—
H. theobaldi	—	198(202)206 2 spec.	222(229)237 4 spec.	251(262)277 3 spec.
H. antilopinum	—	232	220(239)259 9 spec.	257(269)295 9 spec.

Table 5

P_{3-4}

	Nagri	Dhok Pathan		
		Lower	Middle	Upper
H. nagriensis	158(184)211 5 spec.	—	—	—
H. theobaldi	—	186(202)219 2 spec.	209(211)214 2 spec.	230(239)250 6 spec.
H. antilopinum	—	186(211)237 2 spec.	248(248)249 2 spec.	242(249)263 6 spec.

The differences in hypsodonty indices of the samples were tested by Wilcoxon's two sample test, assuming 5% significance level.

M^{1-2}

H. nagriensis	*H. theobaldi*		
Nagri	Lower Dhok Pathan	Middle Dhok Pathan	Upper Dhok Pathan
HI	HI	HI	HI
183	192	233	260
190	223	240	275
215	259	244	277
219		249	279
223		256	
226		260	
234		268	

	m	n	U	P (two-sided)
Nagri-Lower Dhok Pathan	7	3	7–8	> 0.500
Lower-Middle Dhok Pathan	3	7	5	0.270
Middle-Upper Dhok Pathan	7	4	1–2	< 0.020
Nagri-Middle Dhok Pathan	7	7	1	0.001
Nagri-Upper Dhok Pathan	7	4	0	0.006
Lower-Upper Dhok Pathan	3	4	0	0.057

H. nagriensis	*H. antilopinum*		
Nagri	Lower Dhok Pathan	Middle Dhok Pathan	Upper Dhok Pathan
HI	HI	HI	HI
183		242	254
190		248	261
215		255	265
219		264	291
223			292
226			
234			

	m	n	U	P (two-sided)
Nagri-Middle Dhok Pathan	7	4	0	0.006
Middle-Upper Dhok Pathan	4	5	3	0.111
Nagri-Upper Dhok Pathan	7	5	0	0.003

P^{3-4}

H. nagriensis	*H. theobaldi*		
Nagri	Lower Dhok Pathan	Middle Dhok Pathan	Upper Dhok Pathan
HI	HI	HI	HI
166	187	218	—
174	192	223	
176	212	232	
210		251	
222			

	m	n	U	P (two-sided)
Nagri-Lower Dhok Pathan	5	3	5	0.571
Lower-Middle Dhok Pathan	3	4	0	0.057
Nagri-Middle Dhok Pathan	5	4	1	0.032

M_{1-2}

H. nagriensis	*H. theobaldi*		
Nagri	Lower Dhok Pathan	Middle Dhok Pathan	Upper Dhok Pathan
HI	HI	HI	HI
170		222	251
185		227	259
196		232	277
211		237	
211			
224			
227			

	m	n	U	P (two-sided)
Nagri-Middle Dhok Pathan	7	4	2–3	< 0.042
Middle-Upper Dhok Pathan	4	3	0	0.057
Nagri-Upper Dhok Pathan	7	3	0	0.017

H. nagriensis	*H. antilopinum*		
Nagri	Lower Dhok Pathan	Middle Dhok Pathan	Upper Dhok Pathan
HI	HI	HI	HI
170		220	257
185		221	261
196		224	264
211		227	265
211		245	265
224		251	268
227		252	276
		252	279
		259	295

	m	n	U	P (two-sided)
Nagri-Middle Dhok Pathan	7	9	5–6–7	< 0.008
Middle-Upper Dhok Pathan	9	9	1	0.000
Nagri-Upper Dhok Pathan	7	9	0	0.000

The upper first or second molars of Siwalik *Hipparion* show a significant difference in hypsodonty indices between specimens from the Middle and Upper Dhok Pathan, Nagri and Middle Dhok Pathan and Nagri and Upper Dhok Pathan layers. The P value of the difference in hypsodonty indices of the teeth from the Lower and Upper Dhok Pathan strata is just above the 5% level which may be due to the fewer number of specimens from the Lower Dhok Pathan layers.

The specimens from the Nagri and Lower Dhok Pathan layers do not show significant differences in hypsodonty indices. It is not possible to give any one reason for this insignificant difference. This can either be explained due to the reason that the specimens of *H. nagriensis* come from the upper layers of the Nagri Formation (At the type locality of the Nagri Formation the fossils are found 1,000 to 1,500 feet above the lithologic boundary between the Chinji and the Nagri Formations.) and there is, perhaps, not enough vertical thickness of the sediments, consequently less time to see pronounced differences or the rate of evolution was slow during these times. The few number of specimens from the Lower Dhok Pathan layers may also be equally involved in the whole affair.

More or less similar results were obtained when Wilcoxon's test was applied to the other teeth. The P^{3-4} from the Lower and Middle Dhok Pathan beds show better results than the M^{1-2} from the same layers. In general it may be considered that there is an increase in hypsodonty in Siwalik *Hipparion* during the course of time.

Forsten (1968, p. 92) states that hypsodonty in the genus *Hipparion* did not steadily increase, but by spurts rather. Our figures do not suggest such a trend. It is recommended that one should study all the different lineages of the genus before coming to such a conclusion.

Total height of the crown of the tooth is directly proportional to the size of the animal, but hypsodonty is not. This can be seen in *H. antilopinum* and in *H. theobaldi*, the former being with small teeth and of slender built whereas the latter has large teeth and is of very heavy built. Absolutely, the teeth of *H. theobaldi* may be higher crowned than those of *H. antilopinum*, but on the average they are not more hypsodont than the teeth of *H. antilopinum*. See tables 1–5 and figs. 12, 13. Apparently, from the figures the teeth of *H. antilopinum* look more hypsodont than those of *H. theobaldi* but this cannot be statistically proved due to the few data available. Simpson (1953) and van Valen (1960) state that hypsodonty is positively correlated with the size of the animal. This, however, is not demonstrated by the Siwalik hipparions. *H. antilopinum* may have been living in a different biotope than *H. theobaldi* and may have been eating more hard and siliceous grass, and for better adaptation required more hypsodont teeth.

Comparison of different figures of hypsodonty indices shows that the molars are more hypsodont than the premolars.

There is a change in composition of the fauna in the Dhok Pathan beds compared to the Nagri fauna. In the Dhok Pathan layers we are getting more animals which are adapted to the open country like antelopes and *Hipparion*. This together with the increase in hypsodonty may give an indication of arid climate during sedimentation of the Dhok Pathan beds. On the other hand, it is not clear how such a thick bulk of sediments could be deposited without taking in consideration the action of abundance of water. Seasonal floods separated by long dry spells might be the answer to this question.

Hypsodonty alone cannot be considered a decisive factor in survival, as has already been pointed out by Stirton (1947). *Hipparion* from the upper part of the Dhok Pathan beds had sufficiently hypsodont teeth and it would be too vague to give this as a reason for the extinction of the genus at the end of the Dhok Pathan or in the beginning of the Upper Siwaliks. One has to agree with Stirton (1947) that there are multiple factors which may play as important a part as hypsodonty in the survival or length of the life span, such as hardness of dentine and enamel, mechanical (see Camp & Smith, 1942; Gromova, 1952 and Sondaar, 1968) and physical ability to secure food, to escape enemies, to produce and protect young ones, etc.

5. COMPARISON OF *HIPPARION ANTILOPINUM*, *H. THEOBALDI* AND *H. NAGRIENSIS*

Lydekker (1882) was the first to distinguish between the milk teeth of *H. antilopinum* and *H. theobaldi*. Matthew (1929) agreed that there were two (large and small) forms of *Hipparion* in the Siwaliks but he did not agree with the characters by which Lydekker distinguished them. Later Colbert (1935C) followed Matthew's opinion. For detailed account the reader is referred to the part of this paper dealing with the previous work.

Re-examination of all the available material gives a different picture of the problem. In the light of the descriptions and discussions made under the heads of the different species, the following conclusions may be reached:

1. There are three species of *Hipparion* in the Siwalik Group of rocks. *Hipparion antilopinum* and *Hipparion theobaldi* are restricted to the Dhok Pathan Formation. *Hipparion nagriensis* is limited to the Nagri Formation.
2. *Hipparion antilopinum* is an average sized *Hipparion*. The teeth, on the average, are the smallest amongst all the Siwalik species but very hypsodont. Isolated upper M^{1-2} measure on the average 21.1 mm anteroposteriorly and 21.5 mm transversely. Same measurements in lower M_{1-2} are 22.1 and 12.8 mm respectively. For detailed measurements of all the cheek teeth see tables 6 and 7. The average index of hypsodonty for the upper first or second molars is calculated as 263 (9 spec.) and the same figure for the lower first or second molars comes to 252 (18 spec.). The skulls of *H. antilopinum* distinguish themselves from those of *H. theobaldi* in that they have smaller dimensions. The metapodials are distinguished by their slender built which gives entirely different configuration to the animal when compared with those of *H. theobaldi*. The massivity for the metatarsal III was calculated as 10 and 11 in two specimens. The bones assigned to this species mostly give the smallest measurements when compared with those of the other Siwalik forms.
3. *Hipparion theobaldi* is a very large *Hipparion* comparable in size with a small domesticated horse. The teeth are moderately hypsodont and the largest of all the Siwalik species. Isolated upper M^{1-2} measure on the average 24.0 mm anteroposteriorly and 24.5 mm transversely. These measurements in lower M_{1-2} are 25.4 and 14.3 mm respectively. For detailed measurements of all the cheek teeth see tables 6 and 7. The average index of hypsodonty for the upper first or second molars was calculated as 251 (14 spec.) and the same figure for the lower first or second molars reached to 234 (9 spec.). The skull is very large. All the bones are very large and heavy. The metapodials are very massive. The massivity figure for the metatarsal III was calculated as ranging between 14 and 16 (5 spec.). The metacarpal III, on the average, in having a large angle between the facets for the magnum and the hamatum (155°, 13 spec.); ridge shaped volar tubercle at the proximal extremity; shallow concavity for the placement of the interosseous muscle on the volar side along the length and very pronounced sagittal crest at the distal end shows similarities to that in *Equus*. Thus these characters may be considered as advanced for the genus. The bones are larger than those of the other Siwalik species.
4. *Hipparion nagriensis* is intermediate in size between *Hipparion antilopinum* and *Hipparion theobaldi*. The teeth are intermediate in size too, but, on the average, are less hypsodont. Isolated upper M^{1-2} measure on the average 22.6 mm anteroposteriorly and 23.9 mm transversely. These measurements in lower M_{1-2} are 23.9 and 13.6 mm. For detailed measurements of all the cheek teeth see tables 6 and 7. The average index of hypsodonty for the upper first or second molars was calculated as 212 (7 spec.), this figure in the lower first or second molars reached to 203 (7 spec.). The metapodials seem to be a little heavier than in *H. antilopinum*, but are still of a slender built. The morphology of the metacarpal III reminds us of the stratigraphically older hipparions in showing a small angle between the facets for the magnum and the hamatum (146°, 3 spec.); the volar tubercle in the form of a rounded tuberosity; deep concavity for the placement of the interosseous muscle on the volar surface along the length and moderately developed sagittal crest at the distal end. The bones in general give intermediate measurements between those of *H. antilopinum* and of *H. theobaldi*.

6. COMPARISON OF SIWALIK *HIPPARION* WITH OTHER SPECIES OF THE GENUS

An attempt was made to compare certain morphological features of Siwalik *Hipparion* with the European forms. Comparison of the length width measurements of the upper cheek teeth shows that *H. antilopinum* comes close to *H. concudense* and *H. concudense aguirrei;* those of *H. nagriensis* come near to *H. primigenium* whereas *H. theobaldi* has nearly as large teeth as *H. koenigswaldi*. Nearly a similar picture was seen in the lower teeth. See tables 6 and 7. In the above mentioned forms the enamel plications on the fossette borders are simpler than in the Siwalik species of the genus, except for *H. koenigswaldi* which shows fairly complicated enamel folds.

The metapodials of *H. primigenium* seem to be heavier than those of *H. antilopinum* but are still of slender built when compared with those of *H. theobaldi*. The massivity figures for *H. antilopinum*, *H. primigenium* and *H. theobaldi* were calculated as 10–11 (2 spec.), 13 (1 spec.) and 14–16 (5 spec.) respectively. The data for *H. primigenium* were taken from SONDAAR (1961, table 21). The metapodials of *H. nagriensis* also seem to be a little bit heavier than those of *H. antilopinum* but no exact figures can be given owing to the lack of complete material.

Similarities of *H. theobaldi* were found to *H. crassum* and *H. crusafonti* especially in the metapodials. The volar tubercle on the ventral side of the proximal end of the metacarpal III, for the attachment of the interosseous muscle, is ridge-like in all the three species. Similarly the angle between the facets for the magnum and the hamatum is large in these three forms when compared with the other species of *Hipparion*. This angle reaches to the maximum (164°, 1 spec.) in *H. crusafonti*. For detailed figures see table 19. The sagittal crest at the distal end of the metacarpal III is very pronounced in all three species, which means that they all might have had better fixation at the fetlock joint. Consequently there was less possibility for the lateral dislocation. In all these characters *H. theobaldi*, *H. crassum* and *H. crusafonti* show similarities to *Equus* where all these features are much more pronounced. For comparative purposes the type material of *H. crassum** was studied from the Muséum National d'Histoire Naturelle de Paris and the material of *H. crusafonti* was studied in the Museo de Sabadell, Spain.

H. nagriensis from the Nagri Formation shows some similarities to *H. catalaunicum* and *H. koenigswaldi*. The volar tubercle on the ventral side of the proximal end of the metacarpal III, for the attachment of the interosseous muscle, is a rounded tuberosity. Similarly the angle between the facets for the magnum and the hamatum is relatively small in these three species. The lowest figure for this angle, amongst these three species, was recorded in *H. koenigswaldi* (138°, 1 spec.). For detailed figures see table 19. The con-

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* GERVAIS (1859) introduced *H. crassum* for the first time but did not give any figures of his material. Later in 1869 he presented two figures, one of the metatarsal III and other of the metacarpal III. He also pointed out the characteristics of these metapodials on the basis of which he proposed this species. FORSTEN (1968) took a skull referred to in DEPÉRET (1890) as lectotype for this species, which is not in accordance with the rules of the nomenclature. Moreover, the material of DEPÉRET is not from the same locality as that of GERVAIS. After a survey of the literature it was considered appropriate to select the type specimen out of the two figures of GERVAIS (1869) given in Zoologie et Paléontologie générales. The metatarsal III, Plate 31, fig. 7 may be considered as the type specimen for *H. crassum*. This specimen is also marked as type and is preserved in the Muséum National d'Histoire Naturelle de Paris.

cavity along the length on the volar surface of the metacarpal III is quite deep in all three species, which might lead to the conclusion that they have had a fleshy interosseous muscle.

7. STRATIGRAPHIC DISTRIBUTION AND PHYLOGENY OF SIWALIK *HIPPARION*

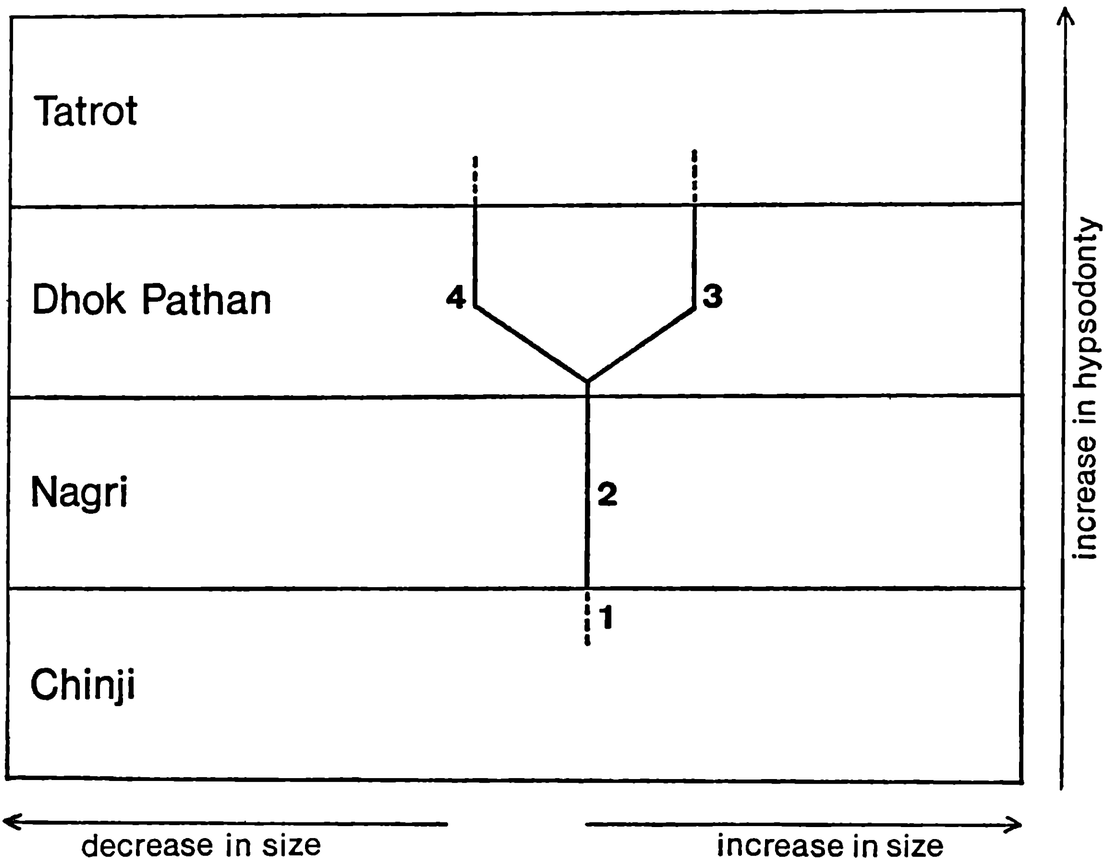

Fig. 3

1. *Hipparion sp.?*
2. *Hipparion nagriensis*
3. *Hipparion theobaldi*
4. *Hipparion antilopinum*

Phylogenetic tree showing the relationships and geological distribution of the Siwalik *Hipparion*.

The solid lines indicate definite presence whereas the broken lines show probable presence of the genus.

MATTHEW (1929), COLBERT (1935 C) and LEWIS (1937) have argued on the first appearance of the genus in the Chinji Formation. This finding is based on certain isolated teeth which are stored in the American Museum of Natural History (AMNH 19555, 19584 and 19590). These teeth cannot morphologically be distinguished from those of the Middle Siwaliks. In size they correspond to the teeth of *H. theobaldi* from the Dhok Pathan beds or the large specimens of *H. nagriensis* from the Nagri Formation. COLBERT (1935 C, p. 33) identifies the "Chinji *Hipparion*" as *H. theobaldi* and gives its range from the Chinji up to the top of the Dhok Pathan Formation. The present study, however, does not suggest the possibility of its presence in the Nagri Formation as the animal at this level has a primitive foot structure which does not coincide with the very specialized foot as that of *H. theobaldi* from the Dhok Pathan beds. For the same reason, the presence of *H. theobaldi* in the Chinji layers is questionable. These layers being stratigraphically even older than the Nagri ones. The foot structure of this species was not met with below the Dhok Pathan level. One may conclude that the "Chinji *Hipparion*" (MATTHEW, 1929, and COLBERT, 1935C), which is known from some isolated teeth cannot be specifically distinguished until its more teeth and especially foot bones are recovered. This makes it difficult to place it in the phylogeny of the genus in the Siwaliks.

DEHM, OETTINGEN-SPIELBERG & VIDAL (1963, pp. 22–25) have doubted the occurrence of *Hipparion* in the Chinji Formation. The argument put forward by them is that some scientific workers get the specimens from local collectors and take their word for stratigraphic data. This might lead to wrong conclusions because Chinji village is built on the Nagri sandstones. The Chinji Formation is exposed further south of the village. If those teeth reported from the Chinji Formation were brought in by the locals, then it should be avoided to draw any conclusions from them.

The genus occurs for the first time in abundance in the Nagri Formation. Its appearance is recorded ± 1,000 feet above the lithologic boundary between the Chinji and the Nagri Formations. *Hipparion nagriensis* from the Nagri beds is less hypsodont with primitive foot structure when compared with the species from the Dhok Pathan layers and is restricted to this Formation. *Hipparion antilopinum* and *Hipparion theobaldi* are abundant in the Dhok Pathan Formation. They reach their maximum evolutionary development in these layers. First appearance of these two species may either be considered in the uppermost layers of the Nagri or the lowermost part of the Dhok Pathan Formation. The present evidence is in favour of the latter possibility. Scarcity of the genus is already noticed in the uppermost part of the Dhok Pathan beds.

Presence of the genus in the Upper Siwaliks is again a matter of controversy. Some isolated teeth have been reported from the basal part of the Tatrot Formation. There is an unconformity between the Middle and the Upper Siwaliks at the type locality of the Tatrot Formation. Some reworked fossils from the Middle Siwaliks are usually found in the basal part of the Tatrot beds, which quite often also include rolled *Hipparion* teeth. Presence of *Hipparion*, however, is not noticed above the basal Tatrot layers. PILGRIM'S (1944, p. 32) statement that *Hipparion* is present up to the top of the Pinjor Formation is not based on any evidence. Its existence in the Pinjor beds is not known from any collection; however, *Equus* is the common genus in these layers.

Change in size, increase in hypsodonty and specialization in locomotion are seen to occur during the course of time required for the deposition of approximately 6,000 feet of sediment. Fossils from the type locality of the Nagri Formation show a uniform composition. Teeth of *H. nagriensis* do not show as great a variation in size as those of *H. antilopinum* and of *H. theobaldi*. A similar picture is seen from the astragali of which comparative material is available.

From the foregoing the following may be concluded:

1. *Hipparion* is guide fossil for the Middle Siwaliks.
2. There seems to be one influx in the Nagri or the Chinji (?) layers, and that later on the genus developed locally.

3. The representatives of the genus stay primitive in their foot structure throughout the Nagri Formation *(H. nagriensis)*.

4. In the uppermost part of the Nagri or the lowermost part of the Dhok Pathan Formations *H. nagriensis* gives rise to two forms: one small with slender metapodials *(H. antilopinum)*, the other large with heavy metapodials and specialized in locomotion *(H. theobaldi)*.

5. There is an increase in hypsodonty in various species throughout the Middle Siwaliks.

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FIGURES AND PLATES

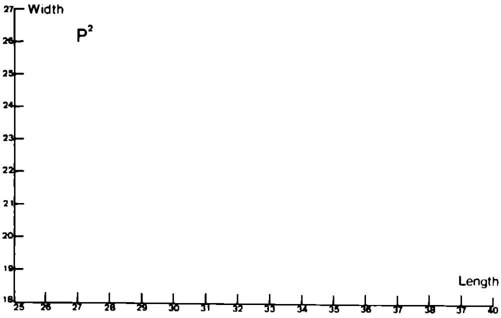


Fig. 4

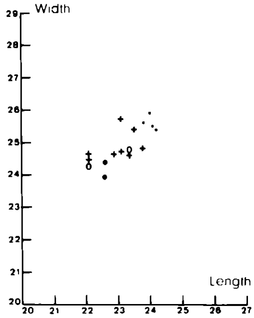


Fig 5

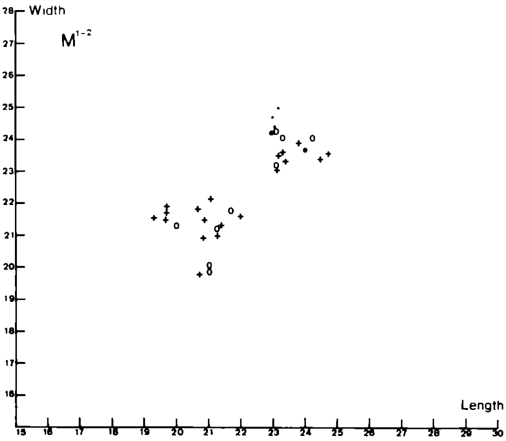
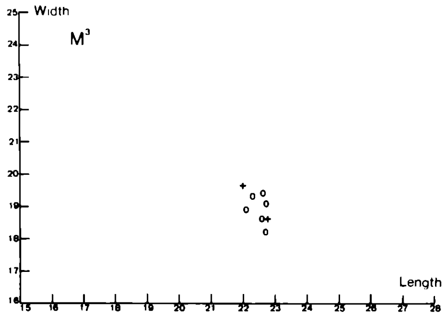


Fig. 6



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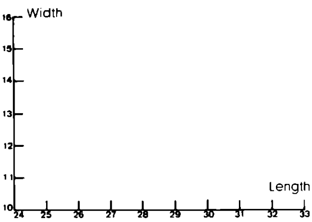

Fig 8

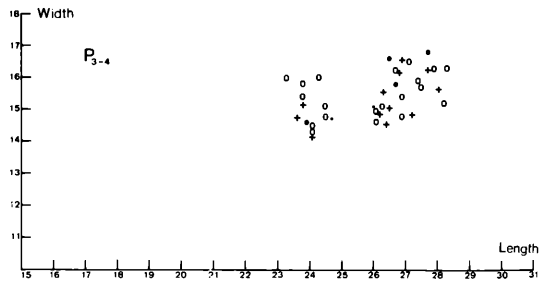

Fig. 9

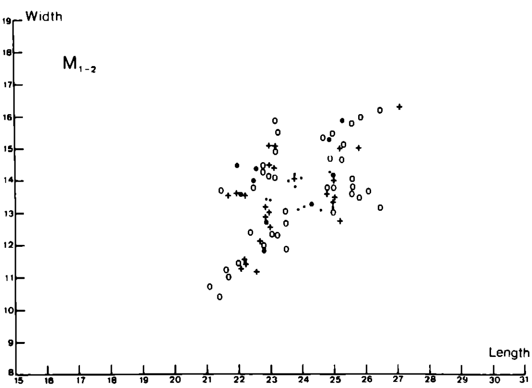

Fig. 10

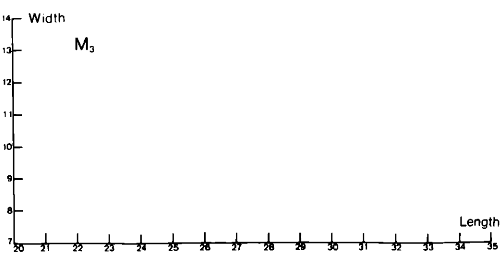

Fig 11

Fig. 4–11: Length-width relationship of various upper and lower cheek teeth in *H. antilopinum*, *H. nagriensis* and *H. theobaldi*. The measurements are in millimeters.

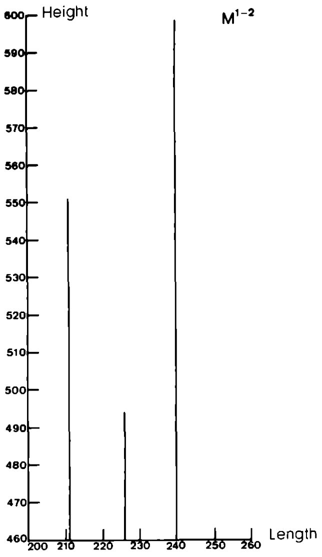

Fig.12

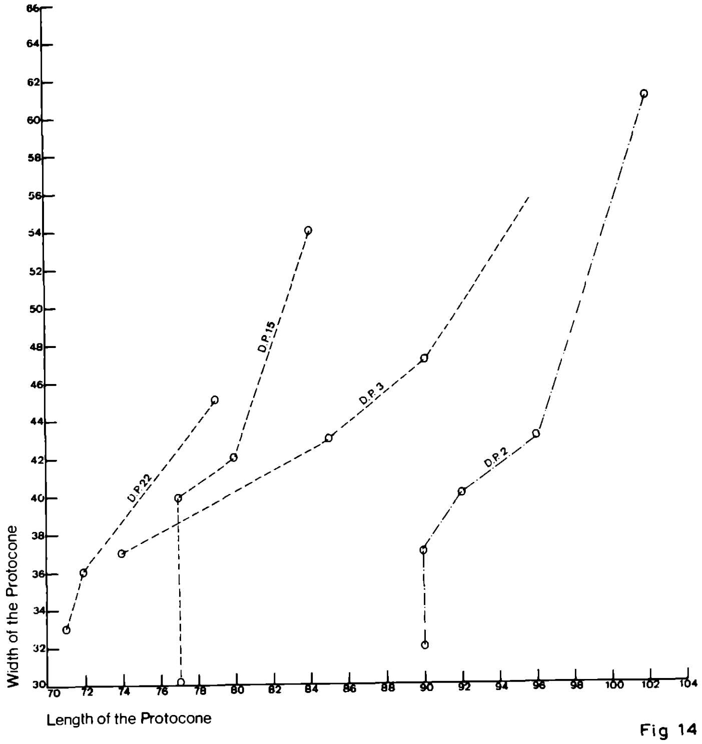

Fig 14

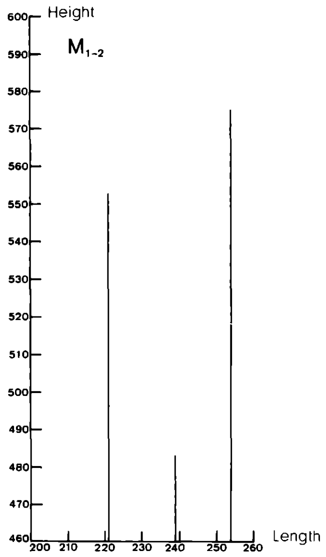

Fig 13

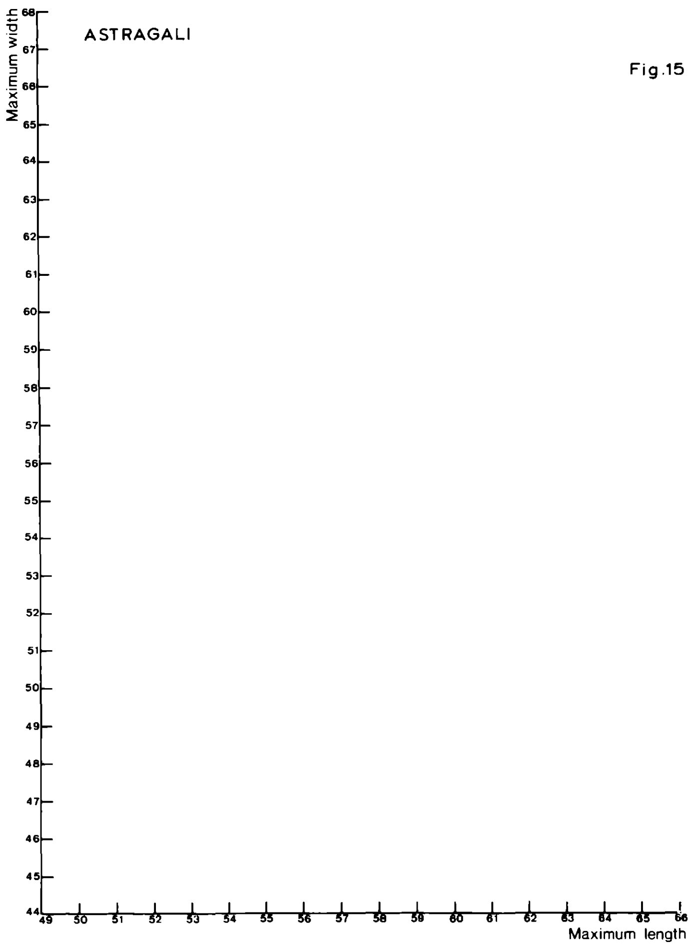

Fig.15

o = Upper Dhok Pathan.
+ = Middle Dhok Pathan.
• = Lower Dhok Pathan.
Nagri.

Fig. 12 and 13: Average height and length relationship of M^{1-2} and M_{1-2} in *H. antilopinum*, *H. nagriensis* and *H. theobaldi*.

Fig. 14: Length-width relationship of protocone at different stages of wear. The teeth were cut approximately at every 1 centimeter.

Fig. 15: Length-width relationship of the astragali in *H. antilopinum*. *H. nagriensis* and *H. theobaldi*.

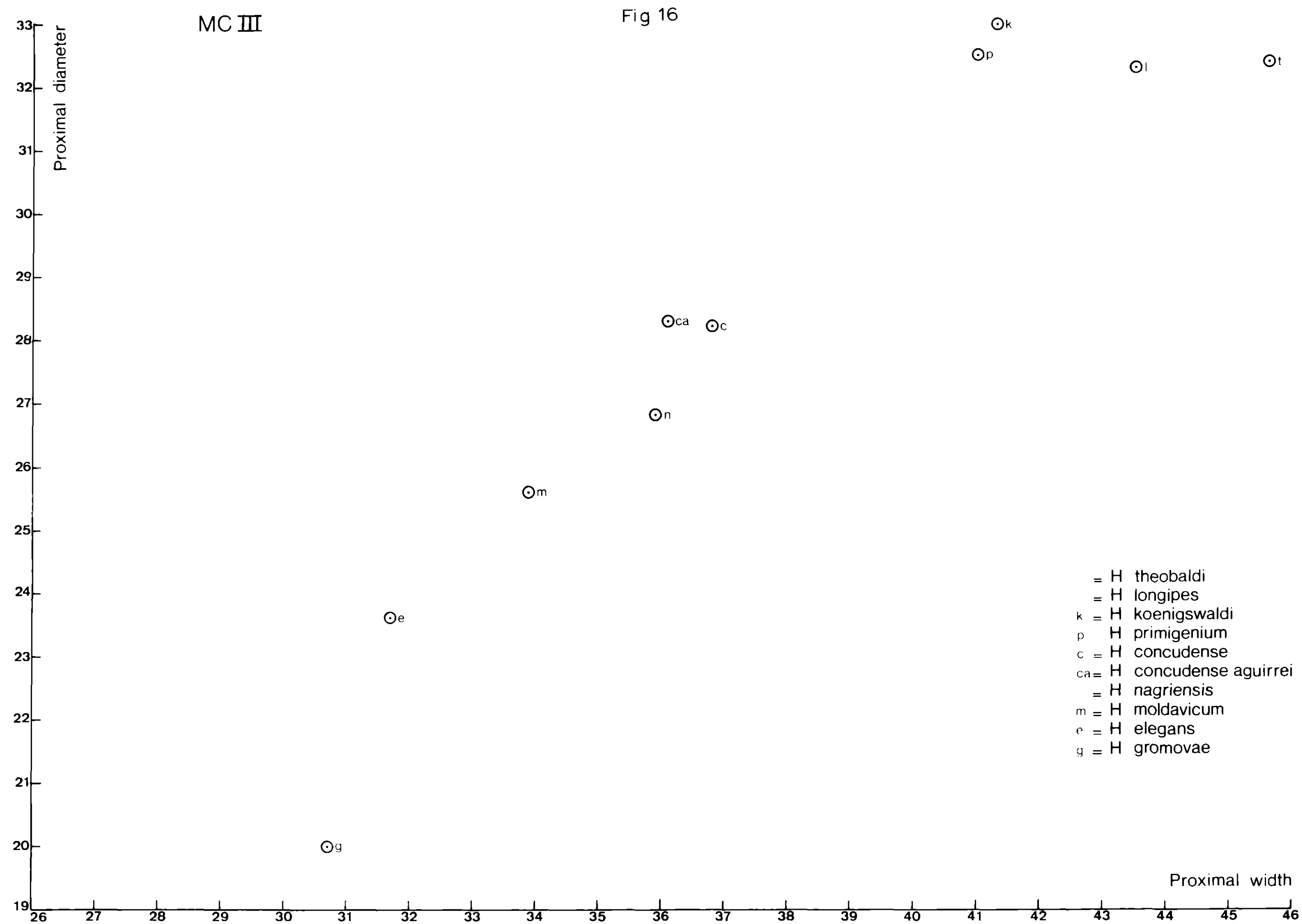

Fig. 16: Width-diameter relationship of the proximal extremity of metacarpal III in various *Hipparion* species. The data other than Siwalik hipparions are taken from GROMOVA (1952) and SONDAAR (1961).

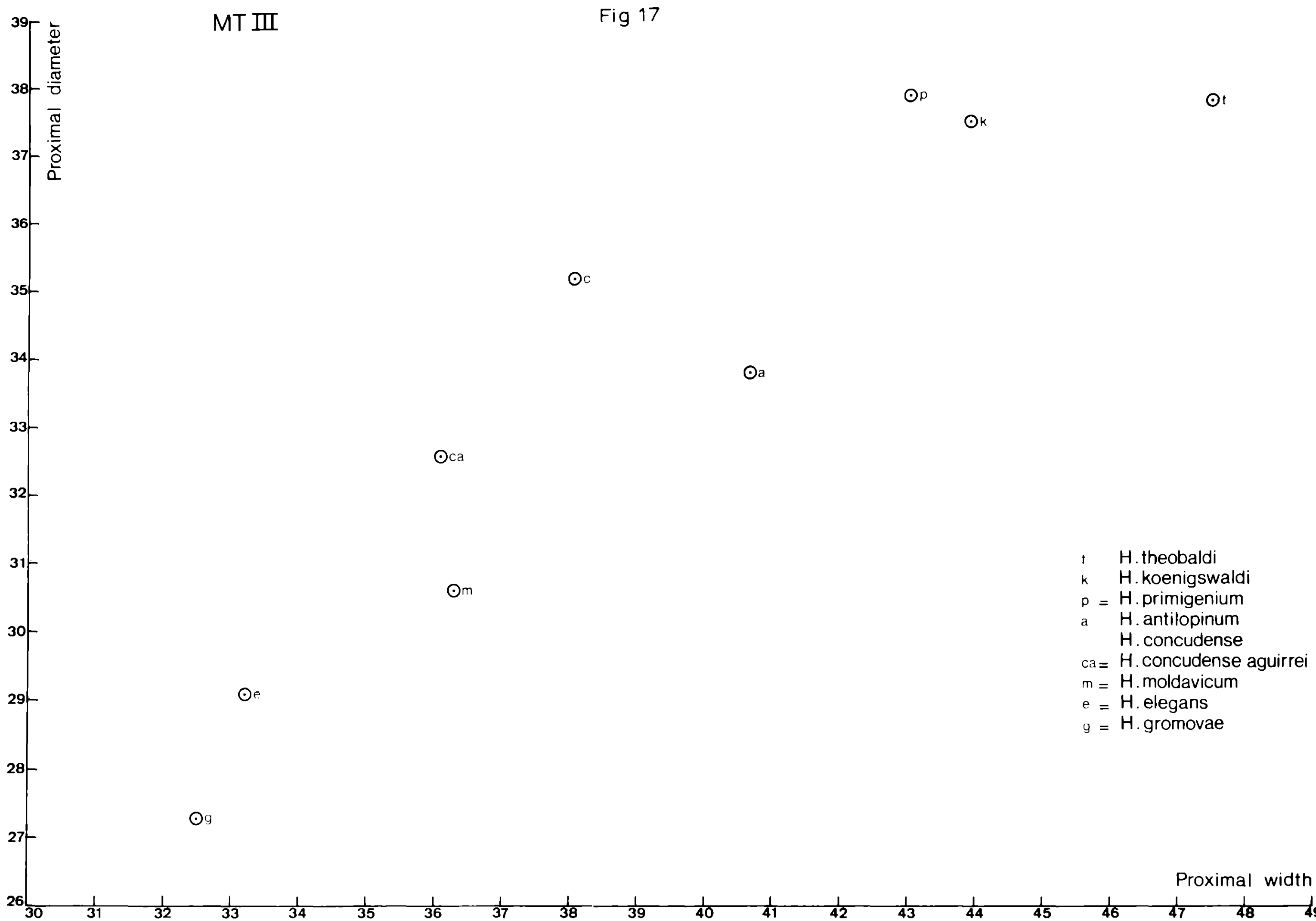

Fig. 17: Width-diameter relationship of the proximal extremity of metatarsal III in various *Hipparion* species. The data other than Siwalik hipparions are taken from Gromova (1952) and Sondaar (1961).

Plate 1

Fig. 1–6: *Hipparion nagriensis* new species.
Fig. 1: (BSM H15) M^{1-2} dext. (1a occlusal view, 1b lingual view). Holotype.
Fig. 2: (GIU Ng7) M^{1-2} sin. (2a occlusal view, 2b lingual view).
Fig. 3: (GIU Ng12) P^{3-4} sin. (3a occlusal view, 3b lingual view).
Fig. 4: (BSM H13) M_{1-2} dext. (4a occlusal view, 4b buccal view).
Fig. 5: (GIU Ng27) M_{1-2} dext. (5a occlusal view, 5b buccal view).
Fig. 6: (BSM H10) P_{3-4} sin. (6a occlusal view, 6b buccal view).

Fig. 7–10: *Hipparion theobaldi* (LYDEKKER) 1877.
Fig. 7: (BSM H143) M^{1-2} dext. (7a occlusal view, 7b lingual view).
Fig. 8: (BSM H102) P^{3-4} dext. (8a occlusal view, 8b lingual view).
Fig. 9: (BSM H482) M_{1-2} dext. (9a occlusal view, 9b buccal view).
Fig. 10: (BSM H111) P_{3-4} dext. (10a occlusal view, 10b buccal view).

Plate 1

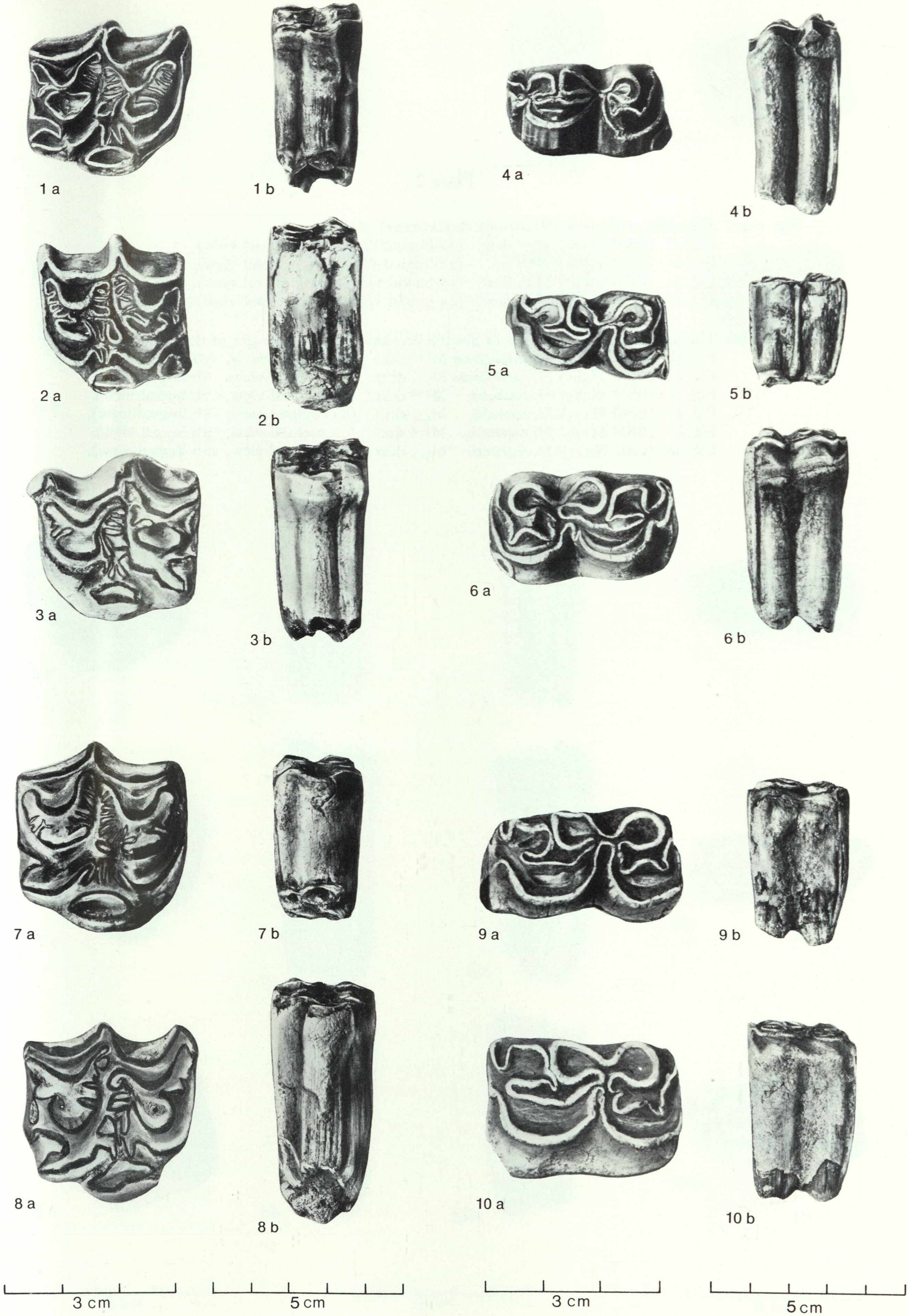
1 a
1 b
4 a
4 b
2 a
2 b
5 a
5 b
3 a
3 b
6 a
6 b
7 a
7 b
9 a
9 b
8 a
8 b
10 a
10 b
3 cm
5 cm
3 cm
5 cm

Plate 2

Fig. 1–4: *Hipparion antilopinum* (FALCONER & CAUTLEY) 1849.

Fig. 1: (BSM H150) M^{1-2} dext. (1a lingual view, 1b occlusal view).
Fig. 2: (BSM H281) P^{3-4} sin. (2a lingual view, 2b occlusal view).
Fig. 3: (BSM H342) M_{1-2} dext. (3a buccal view, 3b occlusal view).
Fig. 4: (BSM H443) P_{3-4} dext. (4a buccal view, 4b occlusal view).

Fig. 5–10: The upper and lower molars of Siwalik *Hipparion* showing height of the crown.

Fig. 5: (BSM H75) *H. antilopinum* M^{1-2} sin. (5a occlusal view, 5b buccal view).
Fig. 6: (BSM H465) *H. antilopinum* M_{1-2} dext. (6a occlusal view, 6b lingual view).
Fig. 7: (BSM H285) *H. theobaldi* M^{1-2} dext. (7a occlusal view, 7b buccal view).
Fig. 8: (BSM H123) *H. theobaldi* M_{1-2} sin. (8a occlusal view, 8b lingual view).
Fig. 9: (BSM H17) *H. nagriensis* M^{1-2} sin. (9a occlusal view, 9b buccal view).
Fig. 10: (GIU Ng17) *H. nagriensis* M_{1-2} dext. (10a occlusal view, 10b lingual view).

Plate 2

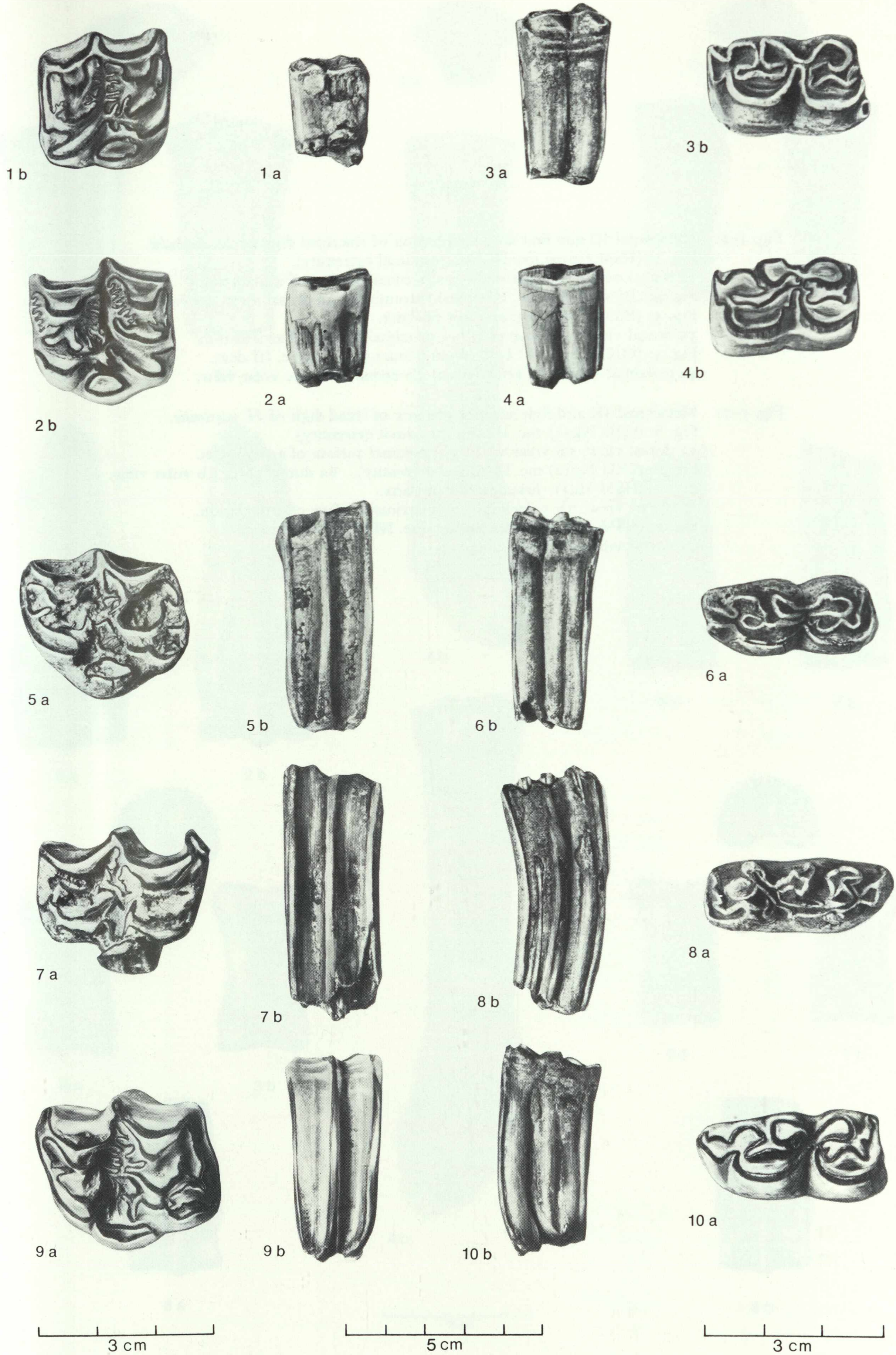
1 b
1 a
3 a
3 b
2 a
4 a
4 b
2 b
5 a
5 b
6 b
6 a
7 a
7 b
8 b
8 a
9 a
9 b
10 b
10 a
3 cm
5 cm
3 cm

Plate 3

Fig. 1–3: Metacarpal III and first anterior phalanx of the third digit of *H. theobaldi*.
Fig. 1: (BSM H619) mc. III sin. (proximal extremity).
1a dorsal view, 1b volar view, 1c proximal surface of articulation.
Fig. 2: (BSM H624) mc. III (distal extremity). 2a dorsal view, 2b volar view.
Fig. 3: (BSM H682) first anterior phalanx.
3a dorsal view, 3b volar view, 3c proximal surface of articulation.
Fig. 4: (GIU 1417) *H. koenigswaldi* SONDAAR 1961, mc. III dext.
4a proximal surface of articulation, 4b dorsal view, 4c volar view.

Fig. 5–7: Metacarpal III and first anterior phalanx of third digit of *H. nagriensis*.
Fig. 5: (GIU Ng53) mc. III sin. (proximal extremity).
5a dorsal view, 5b volar view, 5c proximal surface of articulation.
Fig. 6: (GIU Ng52) mc. III (distal extremity). 6a dorsal view, 6b volar view.
Fig. 7: (BSM H43) first anterior phalanx.
7a dorsal view, 7b volar view, 7c proximal surface of articulation.
Fig. 8: (BSM H594) *H. antilopinum*. mc. III (distal extremity).
8a dorsal view, 8b volar view.

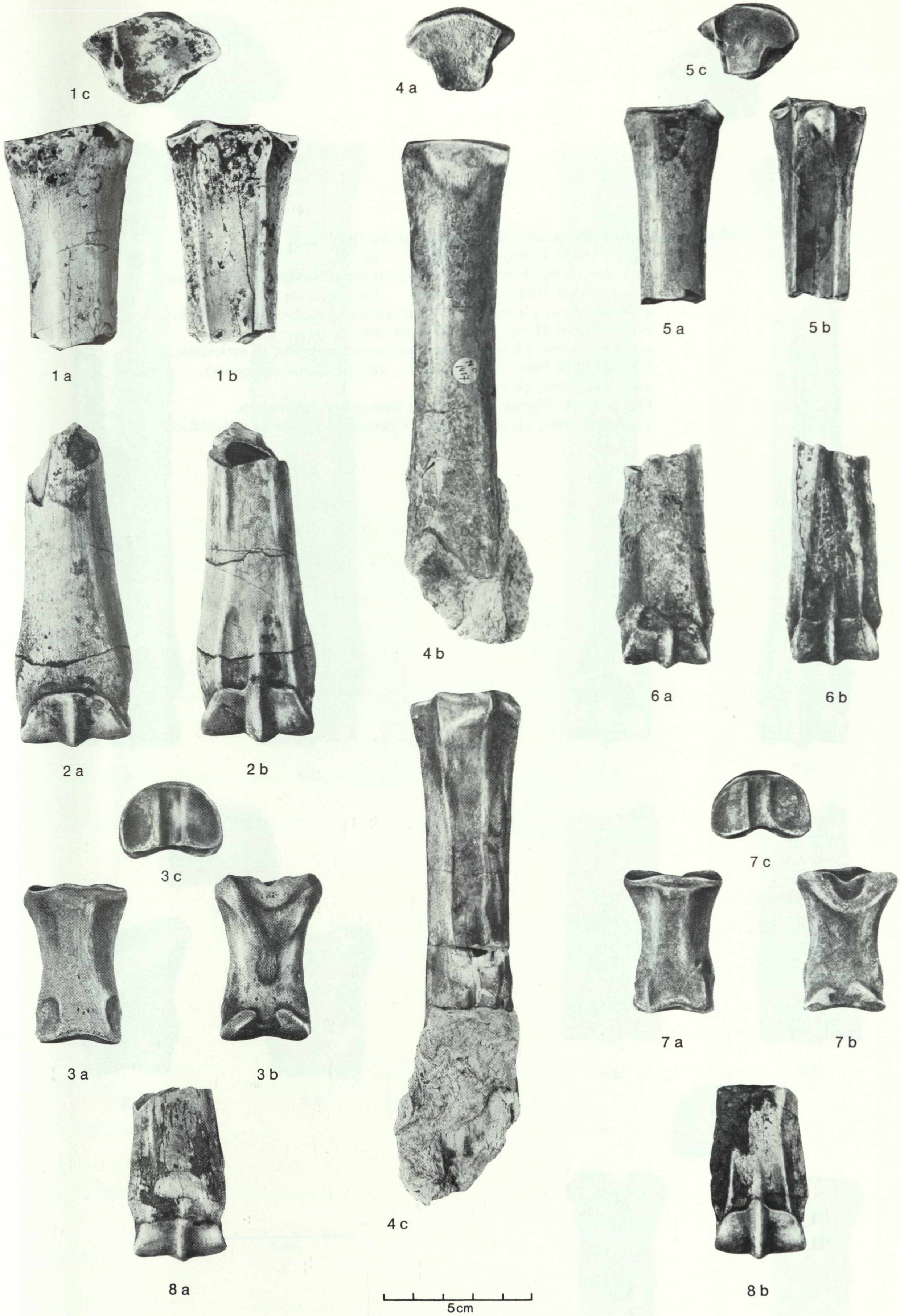
1 c
4 a
5 c
1 a
1 b
5 a
5 b
4 b
6 a
6 b
2 a
2 b
3 c
7 c
3 a
3 b
7 a
7 b
4 c
8 a
8 b
5cm

Plate 4

Metatarsal III and first posterior phalanges of the third digit.

Fig. 1: (BSM H584) *H. theobaldi.* mt. III.
1a volar view, 1b dorsal view, 1c proximal surface of articulation.

Fig. 2: (BSM H683) *H. theobaldi.* first posterior phalanx.
2a volar view, 2b dorsal view, 2c proximal surface of articulation.

Fig. 3: (BSM H573) *H. antilopinum.* mt. III.
3a dorsal view, 3b volar view, 3c proximal surface of articulation.

Fig. 4: (BSM H61) *H. nagriensis.* mt. III (distal extremity).
4a dorsal view, 4b volar view.

Fig. 5: (GIU Ng70) *H. nagriensis.* first posterior phalanx.
5a dorsal view, 5b volar view, 5c proximal surface of articulation.

Plate 4

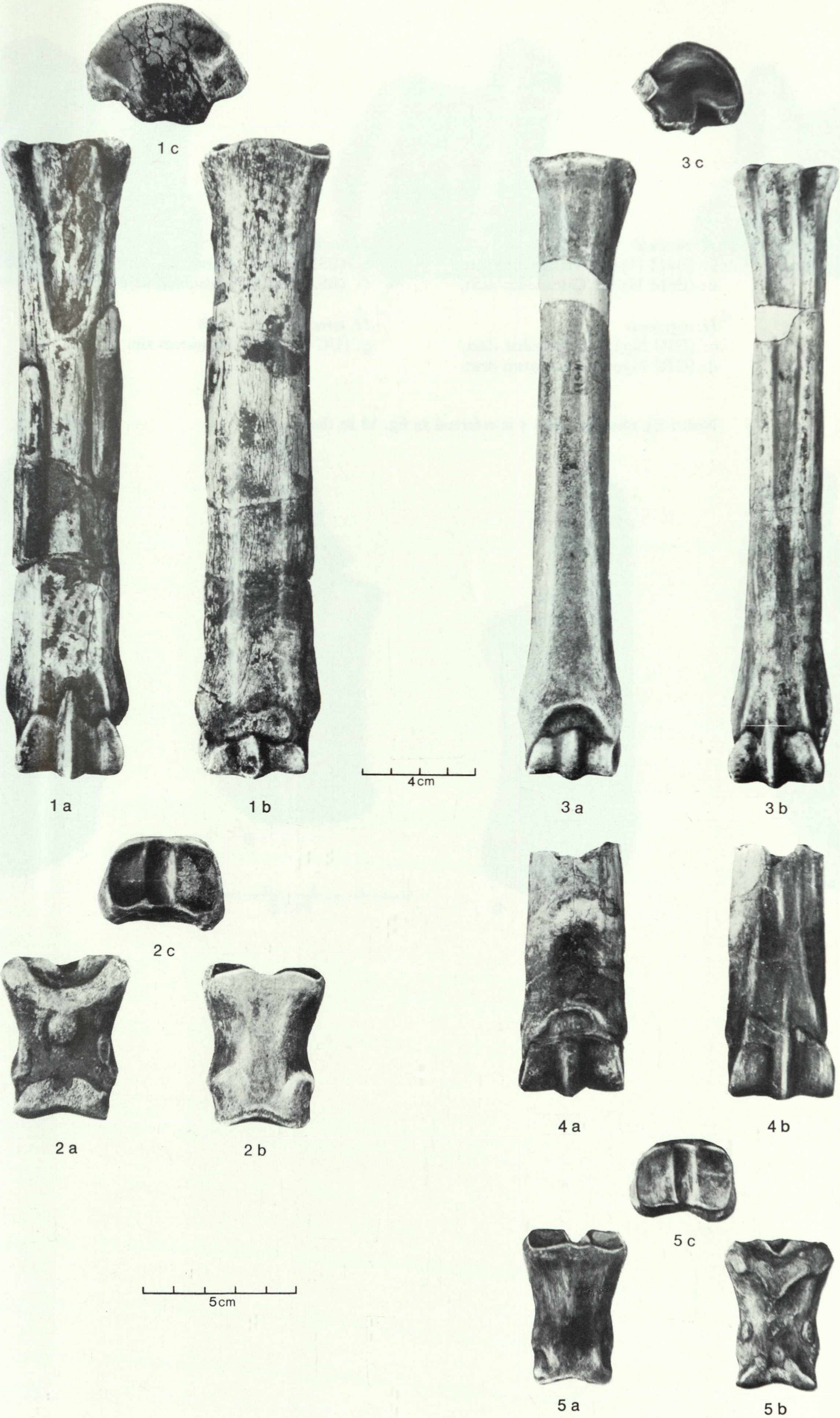

Plate 5

H. theobaldi
a: (BSM H557) Astragalus dext.
b: (BSM H540) Calcaneum dext.

H. nagriensis
c: (GIU Ng62) Astragalus dext.
d: (GIU Ng90) Calcaneum dext.

H. antilopinum
e: (BSM H551) Astragalus sin.
f: (BSM H560) Calcaneum sin.

H. forcei, RICHEY 1948
g: (UC 33724) Calcaneum sin.

Note: By mistake Plate 5 is referred as fig. 18 in the text.

Plate 5

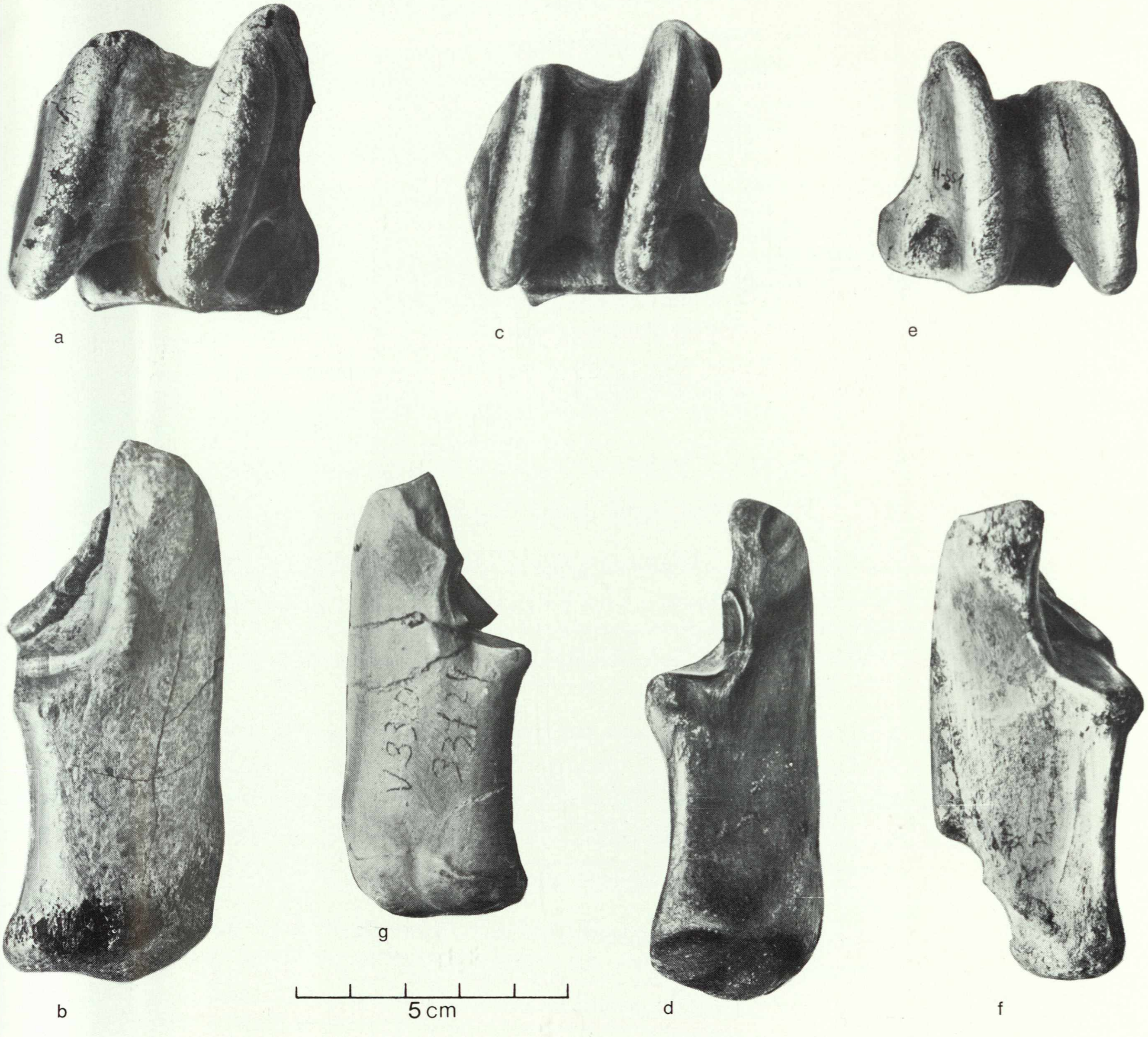

Table 5a: Historical sketch of different species of Siwalik *Hipparion.*

Species of Siwalik hipparions described so far.	*H. antilopinum*	*H. theobaldi*	*H. punjabiense*	*H. perimense*	*H. chisholmi*	*H. nagriensis*
Horizon	Dhok Pathan	Dhok Pathan	Middle Siwaliks	Middle Siwaliks	Middle Siwaliks	Nagri
Described by	Falconer & Cautley	Lydekker	Lydekker	Pilgrim	Pilgrim	Hussain
The species marked x are considered synonyms of *H. antilopinum* by Matthew (1929)			x	x	x	

Table 5a: Historical sketch of different species of Siwalik Hipparion.

Species of Siwalik hipparions described so far.	H. antilopinum	H. theobaldi	H. punjabiense	H. perimense	H. chisholmi	H. nagriensis
Horizon	Dhok Pathan	Dhok Pathan	Middle Siwaliks	Middle Siwaliks	Middle Siwaliks	Nagri
Described by	Falconer & Cautley	Lydekker	Lydekker	Pilgrim	Pilgrim	Hussain
The species marked x are considered synonyms of H. antilopinum by Matthew (1929)			x	x	x	

Table 6: length width measurements of the upper cheek teeth of Siwalik hipparions and some of the European forms.

	P^2		P^{3-4}		M^{1-2}		M^3	
	L	W	L	W	L	W	L	W
H. antilopinum	295(308)320	205(223)242	214(225)239	215(237)264	193(211)222	198(215)250	200(223)236	171(193)222
	13 ex.		28 ex.		33 ex.		20 ex.	
H. theobaldi	342(350)372	221(233)261	246(260)277	228(261)295	230(240)258	231(245)267	246(258)266	212(224)252
	8 ex.		22 ex.		22 ex.		14 ex.	
H. nagriensis	332(333)337	219(233)241	238(242)251	228(247)262	221(226)232	226(239)250	233(240)246	201(213)227
	3 ex.		11 ex.		9 ex.		7 ex.	
H. primigenium after Sondaar (1961)	298(312)336	218(236)257	231(253)270	226(253)278	205(224)252	210(234)263	230(244)267	197(214)234
	18 ex.		35 ex.		30 ex.		15 ex.	
H. koenigswaldi after Sondaar (1961)	301(334)366	232(249)270	243(270)290	248(266)295	227(238)255	230(250)270	246(263)291	205(227)247
	31 ex.		37 ex.		39 ex.		42 ex.	
H. concudense after Sondaar (1961)	282(305)325	204(222)235	208(234)261	217(241)275	190(207)229	199(219)237	207(229)255	174(198)218
	42 ex.		43 ex.		55 ex.		55 ex.	
H.c. aguirrei after Sondaar (1961)	270(289)310	197(212)234	209(229)253	218(234)253	180(199)217	190(210)223	196(217)237	170(191)207
	12 ex.		25 ex.		35 ex.		13 ex.	

Table 7: Length width measurements of the lower cheek teeth of Siwalik hipparions and some of the European forms.

	P_2		P_{3-4}		M_{1-2}		M_3	
	L	W	L	W	L	W	L	W
H. antilopinum	250(270)286	113(124)139	207(231)245	121(139)160	201(221)235	104(128)156	251(266)284	92(104)114
	8 ex.		30 ex.		49 ex.		16 ex.	
H. theobaldi	303(305)309	131(139)149	261(272)297	139(154)168	247(254)280	117(143)163	296(315)337	98(122)137
	4 ex.		29 ex.		30 ex.		19 ex.	
H. nagriensis	285(288)291	131(134)141	247(254)260	138(150)159	229(239)250	131(136)143	287(293)310	107(111)114
	3 ex.		8 ex.		11 ex.		5 ex.	
H. primigenium after Sondaar (1961)	272(284)297	122(138)150	217(246)266	129(149)173	206(222)245	118(130)149	272(287)304	103(109)128
	16 ex.		40 ex.		30 ex.		22 ex.	
H. koenigswaldi after Sondaar (1961)	274(297)322	125(147)171	250(270)292	150(163)185	224(239)253	124(140)158	275(310)347	97(125)133
	38 ex.		44 ex.		41 ex.		41 ex.	
H. concudense after Sondaar (1961)	260(276)302	118(137)158	216(234)258	132(146)174	190(211)232	110(125)152	249(267)292	97(109)133
	37 ex.		45 ex.		56 ex.		41 ex.	
H. c. aguirrei after Sondaar (1961)	241(254)269	120(136)155	210(225)242	128(141)160	190(203)218	104(121)143	240(259)282	92(101)115
	6 ex.		27 ex,		23 ex.		17 ex.	

Table 8: Number of plications in the medium worn teeth of Siwalik <u>Hipparion</u> and <u>H. koenigswaldi</u>.
The plications are counted separately on anterior and posterior margins of the pre- and postfossettes respectively. Figures under the line represent the folds of the plicaballin.

	P^2	P^{3-4}	M^{1-2}	M^3
H. nagriensis	3 ex. 5(5.5)6-4.5(6.5)9-6(6.5)7.5-1.5(2)3 ――― 2(2)3	4 ex. 4.5(6.5)8.5-7.5(8)9-6(6.5)7-2(2)3 ――― 2(3)4.5	3 ex. 5(6.5)7.5-6(7)8-5(6)7-2(2.5)3 ――― 2(3.5)4.5	2 ex. 3.5(4)4.5-7(7)7.5-4(4)4.5-1(1.5)2 ――― 1(1)1
H. antilopinum	5 ex. 4(5)6-3(4)6-3.5(4)7.5-2(2.5)3.5 ――― 1(1)1.5	9 ex. 3(5.5)7-6(8.5)11-5(6)8-2(3)4 ――― 1(2)3.5	4 ex. 4(5)7.5-7(7.5)8-5(5)6-3(3.5)5 ――― 1(1.5)3.5	6 ex. 3(4)5-5(5.5)6-3(4)5-1(2.5)4 ――― 1(1.5)2
H. theobaldi	4 ex. 5(5.5)6-3.5(5)8-2.5(4.5)6-1.5(2.5)3 ――― 1.5(2)3.5	6 ex. 4(5)6-7(7.5)9-6(7.5)9-2(2.5)4 ――― 1.5(2)3	3 ex. 2(3)5.5-6(7.5)10-5(6.5)7.5-2(2.5)3 ――― 2(3)6	2 ex. 3(4)5-6(7)8-3(4)5-0(2)4 ――― 2(2)2
H. koenigswaldi after Sondaar, 1961	10 ex. 3(5.6)8-3(6)8-2(4.1)7-1(2.3)4 ――― 1(1.9)3	15 ex. 2(4)9-4(8.4)13-4(6.1)9-1(2.6)6 ――― 2(2.4)4	14 ex. 2(4.4)8-4(7.8)12-3(6.1)9-1(3.1)6 ――― 2(2.3)3	9 ex. 1(2.3)6-3(6)8-2(4.2)5-1(2.3)4 ――― 1(2)3

Table 9: Humerus.

	H. theobaldi					H. antilopinum		
	AMNH 29825	AMNH 19969	AMNH 19685	BSM H 525	Mean	BSM H 523	BSM H 524	Mean
Total length	244 (Colbert 1935)	260 (Colbert 1935)	240 (Colbert 1935)		248			
Proximal width	112.5	90.6	\		101.5			
Proximal diameter	76.3							
Distal width	72.6	71.5		75.4	73.1	67.8	65.3	66.5
Distal diameter	68.3	69.4	71.4	70.6	69.9	64.2	61.7	62.6

Table 9: Humerus.

	H. theobaldi					H. antilopinum		
	AMNH 29825	AMNH 19969	AMNH 19685	BSM H 525	Mean	BSM H 523	BSM H 524	Mean
Total length	244 (Colbert 1935)	260 (Colbert 1935)	240 (Colbert 1935)		248			
Proximal width	112.5	90.6	\		101.5			
Proximal diameter	76.3							
Distal width	72.6	71.5		75.4	73.1	67.8	65.3	66.5
Distal diameter	68.3	69.4	71.4	70.6	69.9	64.2	61.7	62.6

Table 10 Radius

	H. theobaldi										H. antilopinum				
	AMNH 19685	AMNH 29825	AMNH 29819	AMNH 19969	BSM H 536	BSM H 550	BSM H 546	BSM H 532	BSM H 533	Mean	BSM H 534	BSM H 538	BSM H 539	BSM H 537	Mean
1 Total length	283 (Colbert 1935)	267 (Colbert 1935)	278 (Colbert 1935)	273 (Colbert 1935)						27.5					
2 Proximal width	72.4	72.7	71.9	72.3	72.1					72.2	61.1				
3 Proximal diameter					41.1						31.2				
4 Distal width	71.1	67.2	67.9	71.1		69.1	69.8	70.6	68.6	69.3		56.2	56.6	54.7	55.8
5 Distal diameter	41.2			47.9?		41.5	40.1	40.0	39.5	41.9		36.6	35.5	33.5	35.2
6 Width in the center	38.7	39.7	41.3	41.3						40.2					
Index of 5:4	579					600	574	566	575	578		651	627	612	630

Table 11		Metacarpal III		
		H. nagriensis 3 prox., 2 dist.	H. antilopinum 4 dist.	H. theobaldi 5 comp., 12 prox., 7 dist.
1	Total length			192(207)217 (Colbert (1935)
2	Maximum proximal width	34.1(35.9)37.1		41.7(45.6)49.5
3	Maximum proximal diameter	23.9(26.8)29.1		27.2(32.4)34.4
4	Width of the proximal surface of articulation	32.9(34.7)35.8		40.9(44.0)49.2
5	Diameter of the proximal surface of articulation	21.5(23.2)24.5		24.7(28.4)30.8
6	Width of the facet for magnun	28.5(29.3)30.0		34.6(36.6)39.2
7	Width of the facet for hamatum	08.0(08.9)09.9		09.6(11.8)13.9
8	Width at the distal end	32.6(33.0)33.5	30.6(33.7)35.3	38.2(41.1)43.0
9	Width at the distal tuberosities	36.8(36.9)37.1	33.5(36.4)38.7	41.5(43.3)47.0
10	Diameter at the distal end	26.0(27.0)28.1	25.4(26.6)27.1	29.6(31.2)32.7
	Index of 3:2	700(766)792		665(704)756

Table 12: First anterior phalanx of the third digit.

	H. theobaldi								H. nagriensis
	BSM H 682	BSM H 679	AMNH 19969 (Young)	AMNH 29819	AMNH 29825	AMNH 19685	AMNH 19491	Mean	BSM H 43
1 Maximum length	62.0	61.6	58.6	61.5	62.4	60.8	63.9	62.0	53.9
2 Proximal width	40.0	40.1	38.0	42.9	44.3	45.0	46.6	43.1	37.4
3 Width at the proximal surface of articulation	37.2	38.3	34.7		41.3	41.0	40.4	39.6	35.9
4 Diameter at the proximal end	28.8	30.3	30.3			32.6	35.9	31.9	26.0
5 Diameter at the proximal surface of articulation	24.5	24.1	19.7			25.5	25.7	24.9	21.8
6 Width at the distal end	33.9	34.6	31.1	38.1	38.1	36.8	36.1	36.2	30.7
7 Diameter at the distal end	21.6	21.1	19.9	21.0		23.9	22.7	22.0	18.2
8 Width in the center	27.6	31.2	29.5	32.5	32.5	34.1	32.8	31.7	25.5
9 Diameter in the center	19.6	21.1	19.3	20.5	21.9	19.9	22.6	20.9	16.5
10 Length of the ligamentry scar	39.1		28.6			38.8	34.0	37.3	16.1
Index of 2:1	645	650		697	709	740	729	695	693
Index of 4:1	464	491				536	561	513	482
Index of 4:2	720	755				724	770	742	695
Index of 10:1	630					638	532	600	298

Table 13: Second anterior Phalanx of the third digit.

	H. nagriensis				H. antilopinum			H. theobaldi			
	BSM H 44	BSM H 45	GIU Ng 80	Mean	BSM H 646	BSM H 675	Mean	BSM H 644	BSM H 645	BSM H 643	Mean
1 Maximum length	39.0	38.4	37.5	38.3	34.8	36.6	35.7	44.2	44.1	44.6	44.3
2 Length at the anterior border	32.0	32.1	32.0	32.0	27.4	30.7	29.0	34.7	35.6	34.9	35.0
3 Length at the posterior border	39.0	38.4	37.5	38.3	34.8	36.6	35.7	44.2	44.1	44.6	44.3
4 Proximal width	38.5	39.0	37.1	38.2	36.5	35.1	35.8	44.3	42.1	46.6	44.3
5 Proximal diameter	25.5	24.7	25.1	25.1	22.2	23.0	22.6	29.7	27.1	29.7	28.8
6 Distal width	33.8	37.2	34.0	35.0	33.5	33.1	33.3	39.6	39.3		39.4
7 Distal diameter	20.6	24.7	19.7	21.6	17.3	17.6	17.4	24.0	21.7	24.9	23.5
8 Width in the center	32.6	33.3	31.0	32.3	30.5	29.8	30.1	39.4	38.0	39.8	39.0
9 Diameter in the center	18.2	18.7	17.8	18.2	15.2	17.1	16.1	21.1	20.6	21.3	21.0
Index of 6:1	866	968	906	913	962	904	933	895	891		893
Index of 4:1	987	1001	989	992	1048	959	1003	1002	954	1044	1000
Index of 7:6	609	663	579	617	516	531	523	606	552		579
Index of 8:1	835	867	826	842	875	814	844	891	861	892	881

Table 14

Tibia

	H. theobaldi													H. antilopinum				
	AMNH 29822	AMNH 29824	AMNH 29831	AMNH 29828	BSM H 526	BSM H 527	BSM H 528	BSM H 530	BSM H 531	BSM H 543	BSM H 544	BSM H 562	Mean	AMNH 29823?	BSM H 529 (Young)	BSM H 542	BSM H 561	Mean
1 Total length	335	354	338										342	297				
2 Proximal width	89.5	92.4	99.2										93.7					
3 Proximal diameter	88.4	88.4	87.8										88.2					
4 Width in the center	47.0	43.3	47.2	50.0									46.8	40.0				
5 Diameter in the center	34.6	36.3	36.2	35.6									35.6	32.1				
6 Distal width	72.7	73.4	73.1	76.9	73.3	74.3	71.6	74.4	74.3	72.0	73.3	75.5	73.7	65.2	60.5	62.8	61.7	62.5
7 Distal diameter	48.6	46.1	48.1	50.9	49.8	49.2	45.0	48.7	48.0	51.1	47.8	49.5	48.5	46.0	41.7	42.3	39.8	42.4
Index of 7:6	668	628	658	661	679	662	628	654	646	709	652	655	658	705	689	673	645	678

Table 15

Astragali

	H. nagriensis					H. antilopinum						H. theobaldi					
	GIU Ng 62	GIU Ng 61	GIU Ng 60	BSM H 41	Mean	BSM H 551	BSM H 552	BSM H 556	BSM H 558	BSM H 653	Mean	BSM H 553	BSM H 554	BSM H 557	BSM H 579	BSM H 583	Mean
1 Maximum length to the inferior articulation surface	56.7	56.4	56.1	56.5	56.4	51.9	54.2	50.3	51.4	52.1	51.9	64.2	62.9	65.3	63.5	61.1	63.4
2 Length at the external trochlea	55.7	56.4	53.5	55.7	55.3	50.7	54.1	48.1	51.1	51.9	51.1	62.6	62.2	64.9	61.8	60.5	62.4
3 Length at the internal trochlea	56.6	56.3	56.1	56.5	56.3	49.3	54.2	50.3	49.8	52.0	51.1	62.5	62.6	64.2	63.2	60.9	62.6
4 Maximum width in projection	54.2	51.9	54.8	51.6	53.1	46.5	51.2	45.3	49.7	51.2	48.7	61.2	62.5	58.4	62.4	62.7?	61.4
5 Width of the inferior articulation surface	41.7	41.2	41.2	40.3	41.1	38.7	40.2	34.9	38.1	36.7	37.7	48.3	48.5	48.4	49.2	50.3	48.5
6 Diameter of the inferior articulation surface	32.6	32.6	31.3	31.0	31.8	28.6	30.4	28.5	28.2	30.1	29.1	33.4	34.8	34.6	33.5	33.2	33.9
7 Width of the fossa for cuboid	7.1	10.9	7.4	7.4	8.2	6.4	6.5					11.9	9.1		12.7	9.6	10.8
8 Minimum width at the trochlea	42.1	43.4	42.7	42.5	42.6	40.1	42.0	38.4	42.1	43.0	41.1	51.4	51.5	51.0	49.6	50.7	50.8
Index of 4:3	957	921	996	913	946	943	944	900	909	984	936	979	998	909	987	1002?	974
Index of 6:5	781	791	759	769	775	739	756	816	740	820	774	691	717	714	680	660	692

Table 16

Metatarsal III

	H. nagriensis 2 distal extremities	H. antilopinum 3 comp., 2 prox., 1 dist.	H. theobaldi 10 comp., 21 prox., 17 dist.
1 Total length		230(240)248	230(237)249
2 Maximum proximal width		36.2(39.3)42.9	43.6(47.6)50.5
3 Maximum proximal diameter		33.0(33.6)34.5	35.2(37.8)42.4
4 Diameter of the prox. surface of articulation		29.5(30.9)32.9	32.7(34.7)36.8
5 Width of the proximal surface of articulation		34.7(39.2)42.7	39.2(46.1)49.1
6 Width of the surface of articulation for cuniform III		32.5(36.0)39.7	39.2(42.1)45.6
7 Width of the surface of articulation for cuniform II		05.8(05.8)05.8	04.1(05.9)07.2
8 Width of the surface of articulation of cuboid		07.9(08.9)09.9	10.1(11.5)13.3
9 Width at the distal end	35.8(36.0)36.3	32.2(34.8)36.1	38.2(41.6)44.9
10 Width at the distal tuberosities	37.3(38.2)39.1	37.6(39.9)42.6	40.0(45.1)48.6
11 Diameter at the distal end	29.5(30.6)31.8	28.8(30.4)31.7	31.7(34.7)39.4
Index of 3:2		783(846)898	662(799)853

Table 17: First posterior phalanx of the third digit.

	H. theobaldi									H. nagriensis					H. antilopinum
	BSM H 687	BSM H 683	BSM H 676	AMNH 19466	AMNH 29822	AMNH 29824	AMNH 29831	AMNH 29830	Mean	BSM H 42	GIU Ng 70	GIU Ng 71	GIU Ng 72	Mean	AMNH 29823?
1 Maximum length	62.6	59.5	63.8	62.4	63.8"	61.5"	61.9"	65.0	62.5	58.3	54.9	57.5	56.6	56.8	53.1
2 Proximal width	43.6	45.0	43.9	45.7	44.7"	47.4	46.6	47.9	45.6	39.6	37.6	37.8	35.3	37.5	42.4
3 Width at the proximal surface of articulation	42.0	40.2	39.8	42.6		42.1	43.6	42.9	41.8	36.4	33.6	36.1	34.2	35.0	
4 Diameter at the proximal end	32.5	33.7	33.4	34.6	35.2	35.7	37.5	36.6	34.9	29.0	29.9	30.4	28.0		
5 Diameter of the prox. surface of articulation	26.0	26.0	26.0	22.4			27.2	24.8	25.4	22.9	21.9	24.3	22.2	22.8	
6 Width at the distal end	37.2	34.6	34.2	37.9	38.1	38.1	39.3	37.7	37.1	33.6	28.8	30.4	28.8	30.4	32.8
7 Diameter at the distal end	22.0	19.8	22.0	23.3	24.5	22.8	25.6	24.5	23.0	20.7	19.0	18.0	17.0	18.6	21.0
8 Width in the center	33.5	34.3	33.7	37.7	32.9	34.5	33.8	35.3	34.4	29.8	27.1	28.4	25.8	27.7	33.6
9 Diameter in the center	18.8	21.0	21.9	22.1	23.3	22.0	22.3	23.4	21.8	20.4	18.6	18.2	19.2	19.1	19.5
10 Length of the ligamentary scar				32.2	33.6"				32.9	26.1	20.3	21.1	19.4	21.7	
Index of 2:1	696	756	688	732	700"	770"	752	736	728	679	684	657	623	660	798
Index of 4:1	519	566	523	554	551	580	605	563	557	497	544	528	494	515	
Index of 4:2	745	748	760	757	787	753	804	764	764	732	795	804	793	781	
Index of 10:1				516	526				521	485	369	366	342	390	

"=approximate

Table 18: Second posterior phalanx of the third digit.

	H. nagriensis					H. antilopinum	H. theobaldi
	BSM H 55	GIU Ng 81	BSM H 53	BSM H 46	Mean	BSM H 685	BSM H 686
1 Maximum length	36.3	38.3	37.0	38.4	37.5	34.3	41.9
2 Length at the ant. border	29.3	31.4	29.3	30.5	30.1	28.2	32.5
3 Length at the post. border	36.3	38.3	37.0	38.4	37.5	34.3	41.9
4 Proximal width	37.0	36.0	37.1	34.9	36.2	32.8	37.4
5 Proximal diameter	23.7	24.3	22.6	25.5	24.0	20.9	26.0
6 Distal width	30.9	31.0	30.5	30.7	30.7	26.4	31.9
7 Distal diameter	17.0	17.7	15.8	19.5	17.5	14.9	17.1
8 Width in the center	30.2	29.2	28.7	30.2	29.5	27.9	29.4
9 Diameter in the center	15.6	15.7	15.3	16.9	15.8	14.8	17.5
Index of 4:1	1019	939	1002	908	967	956	892
Index of 6:1	834	809	824	799	816	769	761
Index 7:6	550	570	514	635	567	564	536
Index of 8:1	831	762	775	786	788	813	701

Table 19: Angle between the facets for the magnum and the hamatum in different species of Hipparion.

Neohipparion occidentale	H. koenigswaldi	H. catalaunicum	H. nagriensis	H. concudense	H. concudense aguirrei	H. crassum	H. theobaldi	H. crusafonti
FAM 73901	GIU 1417	MS VP 120	3 ex.	GIU cc 435	GIU LM 1197	Gervais, 1869 Plate 31, fig. 8	13 ex.	MS V 180
130°	138°	145°	145°(146°)147°	151°	152°	155°	153°(155°)158°	164°