



Hexaprotodon (Mammalia: Hippopotamidae) from the Pinjor Formation of Bhimber, Azad Kashmir, Pakistan

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ABSTRACT

The Siwalik Plio-Pleistocene faunas are characterized by the sporadic presence of a hippopotamid taxon, referred to the genus *Hexaprotodon* and the species *Hex. sivalensis*. Due to rarity of this taxon, its morphological characters are incompletely known. Hippopotamid material recently excavated in the middle Pleistocene locality of Bhimber (Azad Kashmir, Pakistan) includes an almost complete mandible that provides a better knowledge of the taxon morphology. *Hexaprotodon sivalensis* is reported for the first time from the Bhimber Pleistocene locality of Azad Kashmir, Pakistan.

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Palaeontology, Hippopotamids,
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INTRODUCTION

Fossil mammal remains are very abundant in the Siwalik Group (Colbert, 1935; Akhtar, 1992; Khan *et al.*, 2010, 2012, 2015, 2016, 2017), and most notably in the Pleistocene deposits of the Upper Siwalik Subgroup. The Pleistocene mammalian faunas represent the end of the record of the Siwalik vertebrate faunas (Nanda, 2002, 2008; Dennell *et al.*, 2006, 2008; Dennell, 2008). The Pinjor Formation (Pleistocene) yielded the geologically youngest fauna of the Siwaliks, including *Proamphibos*, *Bubalus*, *Boselaphus*, *Indoredunca*, *Axis*, *Elephas*, *Stegodon*, *Rhinoceros*, *Sivatherium* and *Equus* (Colbert, 1935; Akhtar, 1992; Nanda, 2002; Basu, 2004; Ghaffar *et al.*, 2012, 2017).

Hippopotamid fossils are rare in the Upper Siwalik Subgroup of the Indian subcontinent. Falconer and Cautley (1836) described *Hexaprotodon* as a subgenus for the Siwalik primitive hippopotamids of the subcontinent, and Owen (1845) elevated *Hexaprotodon* to genus rank. *Hexaprotodon* comprises most of the extinct Eurasian and African species, and one extant Liberian species *Hex. liberiensis*. *Hexaprotodon sivalensis* is the only species recorded so far from the Siwalik Group of Pakistan (Lydekker, 1884; Colbert, 1935; Hooijer, 1950). The oldest record of the Siwalik hippopotamid dates from the boundary of the late Miocene – early Pliocene boundary and comes from the Tatrot Formation (Barry *et al.*, 2002).

This article describes a mandible of a primitive

hippopotamid, the first such specimen belonging to the group to be discovered from the Pleistocene deposits of the Bhimber locality, Azad Kashmir, Pakistan (Fig. 1). The aim of the present work is to present a descriptive account of the hippopotamid material from the Pinjor Formation in the Bhimber district, Azad Kashmir, Pakistan. As the specimen is complete, it provides additional information about the anatomy of *Hex. sivalensis*. Since earlier reports on the fossil hippopotamids from the Siwalik Group were merely based on a brief description (Colbert, 1935). The recovery of new material from the Bhimber locality provides an opportunity to present a more comprehensive description of *Hex. sivalensis*.

Systematic Palaeontology

Hippopotamidae Gray, 1821

Hexaprotodon Falconer and Cautley, 1836

Hexaprotodon sivalensis Falconer and Cautley, 1836

Type specimen

BMNH M2269, a partial skull.

Diagnosis

Like *Hippopotamus amphibius*, but with six incisors of subequal size. First premolar large, brain case relatively small, well developed sagittal crest, lachrymal in contact with orbit but separated from nasal by an extension of the frontal. The anterior premolars diverge from each other (Colbert, 1935, p. 279).

Geographic distribution

Pakistan, India, Sri Lanka, Nepal, Bhutan, Indonesia and Ethiopia (Lydekker, 1884; Colbert, 1935; Hooijer,

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1950; Boissierie and White, 2004; Siddiq, 2015).

Temporal distribution

Late Miocene – Pleistocene (Colbert, 1935; Barry *et al.*, 2002).

Material

AZKB 01, a mandible with incisors, canines, premolars and molars (AZKB-Azad Jammu and Kashmir, district Bhimber).

Repository

The specimen has been stored in the house of Master Riaz, a schoolteacher from Bhimber, Azad Kashmir, Pakistan who was so kind to allow us the publication.

Locality

Kas Chanater, district Bhimber, Azad Kashmir, Pakistan (Fig. 1). The outcrops consist of pale-pinkish to brown claystone, brown gray siltstone and fine to medium grained siltstones (Dennell *et al.*, 2006).

Horizon and age

Upper Siwalik Subgroup, Pinjor Formation; middle Pleistocene, ca 1.8 Ma (Dennell *et al.*, 2006).

Description

Mandible

The mandibular corpus is relatively thick, robust and the anterior root of the ascending ramus originates opposite to m3. The mandibular corpus height increases posteriorly. The mandibular symphysis is wide and massive, with strong incisor alveolar process (Fig. 2A, B). The symphyseal plane is inclined sagittally. The symphysis is higher posteriorly. The symphysis sagittal section is robust. Laterally, the ramus height is gradually decreased (Fig. 2C). The gonial angle of the mandible is well developed and bears no hook. The canine process is comparatively compact. The canine has a shallow lingual groove. The canine and incisors are placed in sub-rectilinear pattern with a short diastema. The premolar row is almost equal in length to the molar row (Fig. 2D, E).

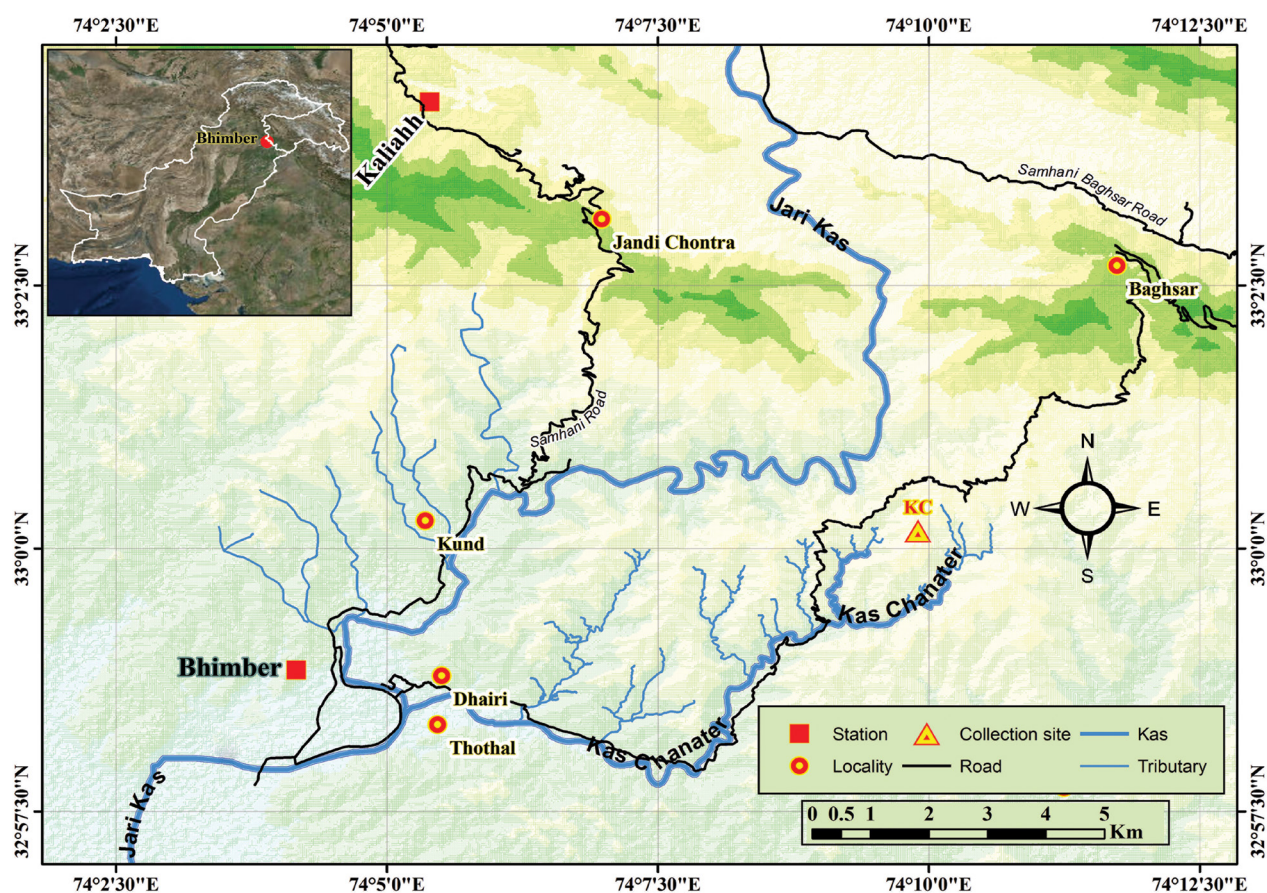


Fig. 1. Map of Pakistan showing the Pleistocene Bhimber locality in Azad Kashmir, Pakistan.

Table I.- Mandible Measurements (in mm) of *Hex. sivalensis* from the Pinjor Formation of Bhimber, Azad Kashmir, Pakistan. The measurements follow Rakotovao *et al.* (2014).

Description	Measurements
Caudal Gonion Infradentale	547
Caudal Gonion Alveolus	529
Infradentale-Condyle	464
M3-caudal Gonion	91.0
Infradental-m3	480
P ₂ -caudal Gonion	450
Length c-m3	372
Length p1-m3	340
length p2-m3	310
Length m1-m3	162
Length p1-p4	183
Length p2-p4	155
Length m3	61.0
Width m3	35.0
Length i2-p2	77.0
Symphysis Length	185
Ventral condyle-gonion	220
Indentation-Gonion Ventrally	228
Coronion-Gonion Ventrally	268
Body height at m3	138
Body height at m1	144
Body height at p2	152
Canine-Canine width	300
External Width canine teeth	415
Incisive Width	194
Width mesial level p1	120
Width distal level m3	100
Lateral Gonion	270
Width Condyle-Condyle	-
Coronion-Coronion	193
Grand Canine diameter	56.0
Alveolus diameter i2	40.0
Alveolus diameter i3	48.0
Smallest mandible width	207
Height of vertical ramus	241
Length of right mandible	249
Length of left mandible	249

Incisors

Most of the incisors are missing (Fig. 2A). The preserved incisors are subequal. The poorly preserved incisors are fragile and stout, with variable crown height. The crown appears chisel-shaped and the apical cutting edge points lingually. The enamel is smooth and thin. The irregular cingulum is present at the base of the crown. The central incisor is lower than the lateral one. The incisors

reflect tip to tip wear pattern. The i3 is larger than the i2. The root is long and circular in cross section. The incisors alveoli are thick.

Canines

The canines are bilaterally compressed and recurved backwardly (Fig. 2B). The canines present a D-shaped cross section. The lateral face is convex and the medial face is slightly concave. The crown is posterolaterally furnished with a shallow longitudinal groove. The enamel is fine and shiny, covering the anterior, medial and lateral sides. The canines are in early wear, which are concentrated posteriorly.

Premolars

The premolar series starts from p2 (Fig. 2A, D), p1 being absent. The p2 is a single conical tooth with early wear. The premolar is recurved posteriorly. The crown is anteroposteriorly long and narrow. A well-developed cingulum is present, forming a continuous shelf around the crown base. A prominent accessory cusp is present posterolingually. The anteroposterior crests are pustulated. The p3 resemble the same version of the p2. The p3 is labiolingually waisted on the posterior side. The p4 is a molariform tooth with a relatively broad crown unlike p2 and p3. A shelf-like cingulum around the crown is prominent in the premolars. The hypoconulid is present posteriorly. An accessory tubercle is present labioposteriorly. The premolars are triangular with continuous cingulum.

Molars

The mandible preserves the complete molar series (Fig. 2A, E). The molars are long, narrow and in early to moderate wear stages. The molars are brachydont. The main conids are low and conical with exposed dentine. The conids represent simple trefoil shape owing to the wear. The anterior lobe is larger and more elevated than the posterior lobe. The main conids are linked by low, rounded crests that pass obliquely. The m3 has a prominent hypoconulid, which is low. The hypoconulid is labio-lingually furnished by two accessory cuspules. The labiolingual cingula are well developed.

The premolars and molars are brachydont and the conids are bunodont (Fig. 2D, E). The anterior lobe conids, protoconid and metaconid are almost equal in size. The preprotocristid and premetacristid are united anteriorly. The postprotocristid and postmetacristid extend linguo-labially. The trigonid and talonid are connected to the prehypocristid and preentocristid by the postprotocristid and the postmetacristid with prehypocristid and preentocristid, respectively. A notch appears at the point where two cristids are fused together.

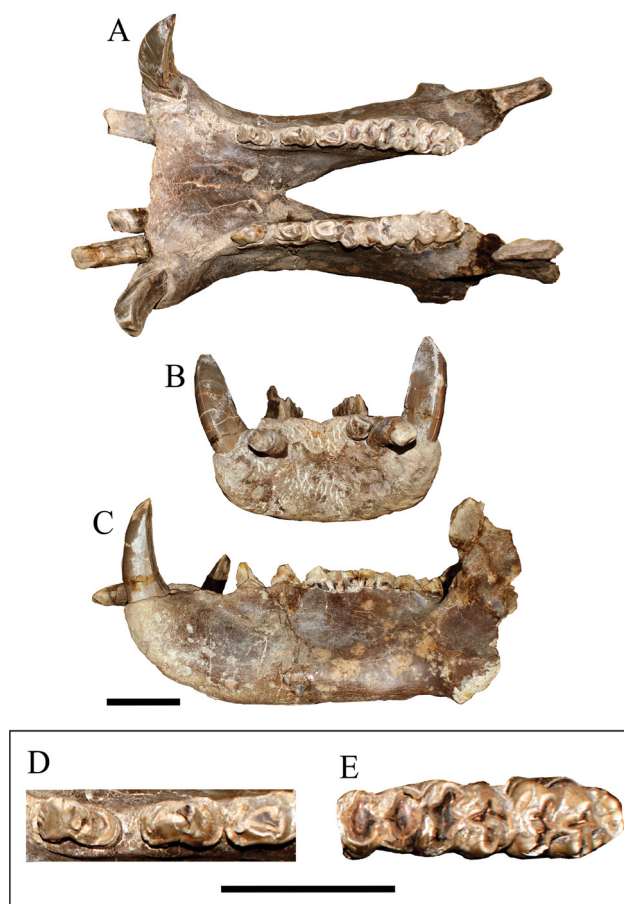


Fig. 2. Mandible of *Hexaprotodon sivalensis* from the Siwalik Pleistocene. **A**, Dorsal view of AZK-B, 01 with incisors, canines, premolars and molars; **B**, Anterior view of AZK-B, 01; **C**, Lateral view of AZK-B, 01; **D**, Occlusal view of p2-4; **E**, Occlusal view of m1-3. Scale bar 10 cm.

Comparison

The studied mandible differs from suoids in having more trenchant conids and in lacking minor grooves. *Hexaprotodon* presents a wide and robust symphysis with poorly differentiated canine processes as in the mandible observed (Fig. 2). The presence of smooth enamel is a typical for *Hexaprotodon* (Geze, 1985) as is the tip to tip wear pattern (Hooijer, 1950). *Hexaprotodon sivalensis*, the species reported from the Siwalik Group, is closely related anatomically to two African species: *Hex. garyam* and *Hex. bruneti* (Boisserie, 2005). The i2 and i3 are larger than i1 in *Hex. sivalensis*, unlike *Hex. garyam*, where i2 is the largest (Boisserie, 2005). The incisors seen in the specimen described here are, therefore, similar to those of *Hex. sivalensis*. The continuous incisor series between the two canines forms an overhang relative to the frontal face of the symphysis, representing a character of *Hex. sivalensis*.

The symphysis is inclined anterodorsally. The frontal and ventral faces of the symphysis show a gentle angle, feature shared with *Hex. sivalensis* (Boisserie, 2005).

The canines are comparable to *Hex. sivalensis* in their size, general structure and degree of bilateral compression, contrary to *Hex. garyam* and *Hex. bruneti* (Boisserie and White, 2004). The premolars are like those of *Hex. sivalensis* in being large, bearing accessory tubercles, and diverging anteriorly, unlike in *Hex. garyam*. The lower molars seen in the specimen described here are indistinguishable from those of *Hex. sivalensis*. The molars are comparable in size to *Hex. sivalensis* from the Upper Siwalik Subgroup (Colbert, 1935). The mandibular symphysis proportions, ratio of i3 to i1, length of premolar row, hypoconulid with two anterior lobes, thick incisor and canine processes assess the studied specimen to *Hex. sivalensis* from the Bhimber locality of Azad Kashmir, Pakistan.

DISCUSSION

Hexaprotodon is a hippopotamid genus first reported from the late Miocene of Eurasia that reached a wide geographic range in a short period of time, mostly due to the availability of the unoccupied niche for large semiaquatic herbivores (Falconer and Cautley, 1836; Colbert, 1935; Hooijer, 1950; Barry *et al.*, 2002). The weak extension of the canine process and short diastema in *Hexaprotodon* can be considered the primitive characters of hippopotamids, occurring in taxa known from the late Miocene and early Pliocene (Coryndon, 1977, 1978; Geze, 1980; Harris, 1991). The oldest occurrence of *Hex. sivalensis* is recorded from the late Miocene (Barry *et al.*, 2002) from the Siwaliks. Moreover, it was recorded from the Tatrot Formation of the Upper Siwalik Subgroup, dated 3.4–2.6 Ma, prevailing through to the late Pleistocene (Barry and Flynn, 1989).

Hexaprotodon has been restricted to the Asian lineage and approved to be a peculiar lineage of hippopotamids in Asia (Falconer and Cautley, 1836; Lydekker, 1884; Colbert, 1935; Hooijer, 1950; Coryndon, 1978; Boisserie and White, 2004). *Hexaprotodon sivalensis* is one of the best-flourished species of the genus *Hexaprotodon* (Colbert, 1935; Hooijer, 1950; Barry *et al.*, 2002). *Hexaprotodon sivalensis* is a comparatively large species of hippopotamid, with retention of six irregular incisors (Falconer and Cautley, 1847; Colbert, 1935; Hooijer, 1950). The species represents the sole member of Hippopotamidae in the Siwaliks of Pakistan. *Hexaprotodon sivalensis* was recovered from all of the major stratigraphic units of Tatrot-Pinjor formations, although it occurs less frequently than other associated groups.

CONCLUSIONS

The discovered mandible can be referred to *Hex. sivalensis*, as the specimen is morphometrically indistinguishable from *Hex. sivalensis*. This fossil record provides additional information of the primitive Siwalik hippopotamid, previously known only from the upper jaw and neurocranium, and isolated fragments of the lower jaw (mostly dental specimens). The species is restricted to the late Miocene to Pleistocene in the Siwalik Group of Pakistan.

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Statement of conflict of interest

Authors have declared no conflict of interest.

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