

***Proamphibos kashmiricus* (Bovini: Bovidae: Mammalia) Lower Case From the Pinjor Formation of Pakistan**

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Abstract. - Newly discovered fossil material of *Proamphibos kashmiricus* from the Plio-Pleistocene of the Pinjor Formation (2.6 – 0.6 Ma) in the Upper Siwaliks (Pakistan) is reported and described here. The new specimen is one opisthocranium of a hornless skull attributed to a female individual of *P. kashmiricus* coming from the Plio-Pleistocene deposits of Rohtas (2.2 Ma) in the Jhelum district, northern Pakistan. The opisthocranium is the largest female individual described so far for this species and the morphology of the present specimen allow examining some skull anatomical features of *P. kashmiricus*. The validity of the genus *Bucapra* is also discussed and the synonymy with *Proamphibos* is proposed.

Keywords: *Proamphibos*, Pinjor Formation, Upper Siwaliks, Plio-Pleistocene, Bovine.

INTRODUCTION

The late Pliocene and early Pleistocene deposits of the Upper Siwaliks have produced several fossil bovine taxa including *Bison*, *Bubalus*, *Proamphibos*, *Leptobos*, *Bos*, *Hemibos* and *Bucapra*. This is a time of important radiation in Bovini (Nanda, 1997, 2002; Masini 1989; Corvinus and Rimal, 2001; Opdyke *et al.*, 1979; Hussain *et al.*, 1992; Pilgrim, 1937, 1939; Colbert, 1935) and also it is thought that there was a high rate of origination for mammal species (Gingerich, 1984).

The Upper Siwaliks (Plio-Pleistocene) of northern Pakistan is divided in three units, the Tatrot, the Pinjor and the Boulder Conglomerate Formations (Pilgrim, 1913; Nanda, 2002; Barry *et al.*, 2002). Of these, the Pinjor Formation, which spans 2.58–0.6 Ma (Dennell *et al.*, 2008), is the longest and most fossiliferous including larger taxa such as *Elephas hysudricus*, *Stegodon insignis*, *Rhinoceros*, *Sivatherium*, *Equus sivalensis*, *Sus* spp., *Hemibos* spp., *Bos acutifrons* and *Cervus palaeindicus* (Nanda, 2002, 2008). Several types of bovinds are known from the Pinjor Formation, of which the commonest are the medium-sized reduncines and the larger ones belonging to *Hemibos*, *Bison*, *Bubalus*, and *Proamphibos*

(Rutimeyer, 1878; Pilgrim, 1937, 1939; Hooijer, 1958; Nanda, 2008).

The unique characteristic of the Pinjor fauna, is its similarity to the living faunas as it is the youngest fauna of the Siwaliks and largely consistent with an open grassland environment. Regarding the bovid composition of the fauna, the forerunners of *Boselaphus tragocamelus*, *Bubalus arnae*, *Bison bison*, *Bos taurus*, *Bibos banteng* and *Antilope cervicapra* are present in the youngest sediments of the Siwaliks.

LOCALITY AND MATERIAL

The material presented in this paper had been unearthed from sediments of the Pinjor Formation near the village Rohtas (32°59 N, 73°38 E) in Jhelum district, northern Pakistan (Fig. 1). The main access to the site is by the Grand Trunk Road (GT Road), the road that connects the cities of Lahore (provincial capital) and Islamabad (country capital). The Rohtas site belongs to the Upper Siwalik subgroup and comprises fluvial deposits of fine-grained sands, silts and clays representing floodplains, gullies and abandoned channels. The type area of the Pinjor Formation is situated in India near Chandigarh, where the Pinjor type locality is located whereas the other type localities of the Siwaliks are located in Pakistan. The Pinjor Formation is mainly characterized by Pleistocene sands and variegated clays (Dennell, 2008). Magnetostratigraphically and biochronologically,

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the upper part of the Pinjor Formation is dated 0.6 Ma while the lower boundary of the Formation is considered to be dated at 2.58 Ma (Ranga Rao *et al.*, 1988, 1995; Cande and Kent, 1995; Hussein *et al.*, 1992; Nanda, 2008).

The material was discovered in 1971 and since then it was stored unpublished in the Palaeontology Laboratory of the Punjab University, Lahore, Pakistan. It consists partial skull and a more specifically the opisthocranium of a large female bovid. This specimen is compared with the most common Siwalik genera *Hemibos*, *Bison*, *Bubalus* and a rare specimen of *Bucapra* as they represent the larger known Plio-Pleistocene genera of the tribe Bovini. The subject of this paper is the description of the newly recorded opisthocranium of the female *P. kashmiricus*.

SYSTEMATIC PALAEOLOGY

Bovidae Gray, 1821

Bovinae Gray, 1821

BUBALINA Pilgrim, 1939

Proamphibos Pilgrim, 1939

Proamphibos kashmiricus Pilgrim, 1939

Bucapra daviesii Rutimeyer, 1878

(Fig. 2, Table I)

Original diagnosis

A more advanced species of *Proamphibos* than *P. lachrymans*; skull lower in every part than that of *P. lachrymans*; frontal bone more arched, with an incipient transverse ridge; lachrymal fossa slight; horn-cores somewhat more slender and divergent, with sharper postero-internal keel, more extended inward than in *P. lachrymans*, so that the distance between it and the outer face equals or exceeds that between the primary keels; female hornless; weak temporal crests in female; parietal more reduced; brain case shorter; occipital concave in the vertical plane; condyles larger and projecting more to the rear; basioccipital shallower, with gently rounded surface, more triangular on account of the greater expansion of the posterior tuberosities (Pilgrim, 1939).

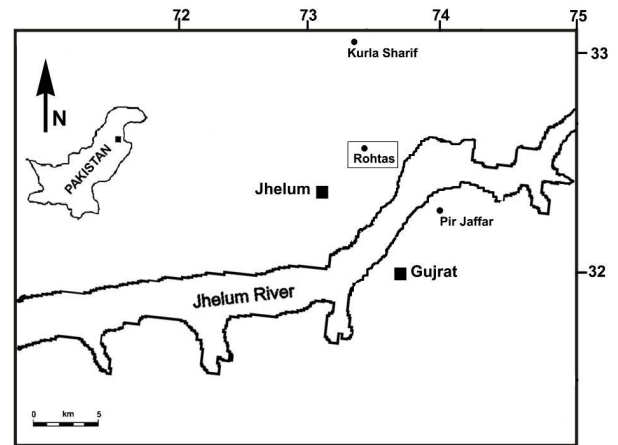


Fig. 1. Map showing the position of the locality (encircled) in the Jhelum district, Punjab, northern Pakistan.

Emended diagnosis

Auditory bullae variable; large basisphenoid; mastoid larger than *Hemibos*. The temporal crests in female are reduced and run almost parallel.

Referred material

PUPC 71/57, opisthocranium (PUPC-institutional abbreviation; Punjab University Palaeontological Collection).

Age

Late Pliocene to Early Pleistocene, ca 2.6-0.6 Ma (Dennell *et al.*, 2006).

Description

PUPC 71/57 is part of the original skull, basically the opisthocranium, which makes it an incomplete specimen retaining only the following: occipital region, occipital condyles, paraoccipital process, part of the parietals, the auditory bullae and the basisphenoid (Fig. 2). The opisthocranium is not compressed dorso-ventrally but the facial part and the dentition are missing. The sutures separating the various bones are almost invisible. Obliterating of suture lines in adults is a characteristic of *Bubalina*. However, the suture line between the parietal and the supraoccipital is visible. The brain case cast is exposed due to the breakage of the parietal bones and the coronal suture line is visible on the brain

Table I.- Comparison of the cranial measurements (mm) of *Proamphibos*, *Bucapra* and *Hemibos*.

Description	<i>P. kashmiricus</i> female (PUPC 71/57) this paper	<i>P. kashmiricus</i> female (GSI B817) Pilgrim, 1939	<i>Bucapra daviesii</i> (BMNH 36677, Rutimeyer, 1878) Pilgrim, 1939	<i>H. triquetricornis</i> (BMNH 39565, holotype) Pilgrim, 1939
Breadth of skull at mastoid	200	?164	160	189
Height of occipital from bottom of occipital condyles to summit of occipital crest	107	?105	-	106
Distance between outer edges of occipital condyles	105	-	92	102
Width of the braincase	114	112	105	118
Width of posterior tuberosities on basi-occipital	73.0	-	-	82
Width of anterior tuberosities on basi-occipital	30	-	-	-
Distance between fronto- parietal suture to summit of occipital crest	90	-	-	-
Distance between Bregma and lambda	72	-	-	-
Length of interparietal suture	32.2	-	-	-
Length of temporal fossa	114	110	109	120
Length of basi-occipital between anterior and posterior tuberosities	44.5	-	-	-
Depth: occipital crest to top of foramen magnum	66.5	-	-	-
Depth: occipital crest to lower border of foramen magnum	109	-	-	-
Width of foramen magnum	39	-	-	-
Height of foramen magnum	42.2	-	-	-
Length of auditory bulla	67.6	-	-	-
Width of auditory bulla	45.0	-	-	-
Approximated length of parietal	70.0	-	-	-

case cast as well. The temporal crests are weak. The length of the interparietal suture line is 32.2 mm and judging from the opisthocranium it should correspond to a large and massive skull (Table I). The occipital crest is very prominent and thick. It forms a low and wide arch with a short flattened portion at its summit. Below the occipital crest there is a prominent occipital tuberosity and an external occipital crest continues downwards till the upper border of the foramen magnum. The basioccipital is triangular. The paroccipital processes are large and stout. The occipital condyles are well preserved and projected in lateral view. A deep notch separates them from the paroccipital processes. The end of the paroccipital process is broken. The foramen

magnum is large and subcircular in shape. The temporal crests are reduced and run almost parallel.

The occipital surface is slightly concave in vertical plane, broad and has an ovoid shape, bordered dorsally and dorsolaterally by a very well marked nuchal ridge. The basioccipital has a prominent median ridge and the posterior tuberosities are large and much expanded laterally. The anterior tuberosities are small but prominent. They lie behind the anterior ends of the auditory bullae. The basisphenoid is attached to the basioccipital with a weak angle. The auditory bullae are well preserved, large and well inflated (Table I).

The temporal fossa is short and high with a length of 114 mm from occipital crest to the anterior

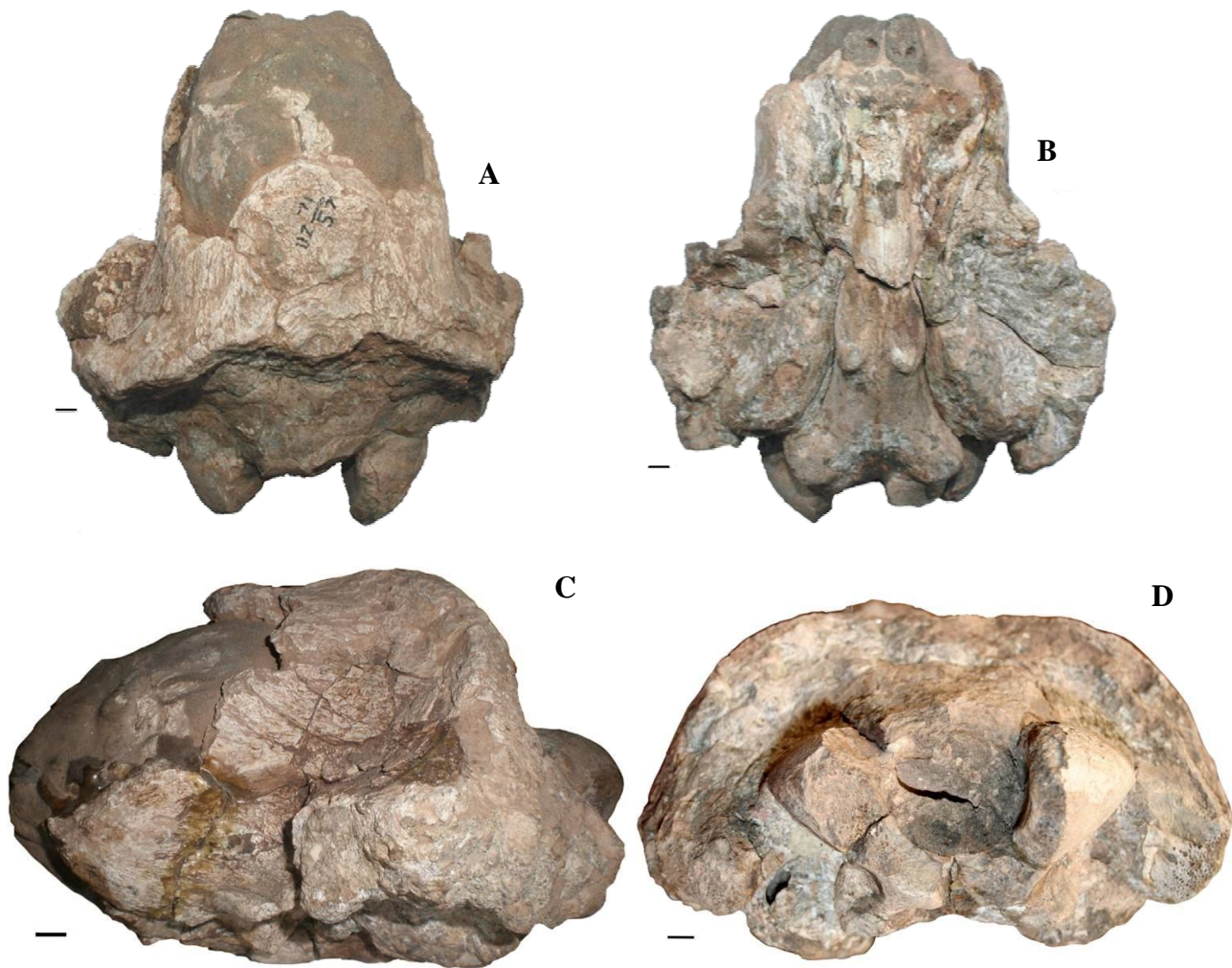


Fig. 2. *Proamphibos kashmiricus*: 1. PUPC 71/57 damaged skull. A, dorsal view; B, ventral view; C, lateral view; D, occipital view. Scale bar 10 mm.

border of the temporal fossa. It opens widely above on to the parietal and the supraoccipital. The supraoccipital extends antero-posteriorly on the upper surface of the brain case. Laterally, the supraoccipital lies on the same plane as the hinder surface of the parietal and it is inclined at somewhat more than a right angle to the occipital plane.

Comparisons

The opisthocranium is characterized by the slightly concave occipital in vertical plane, an expansion of the posterior tuberosities, the large auditory bulla, the triangular shaped basioccipital

and the reduced temporal lines. The occipital condyles are large and clearly projected beyond the summit of the occipital crest. The opisthocranium is narrow in shape with a flattened occipital summit. The triangular basioccipital associates the studied specimen to Bovinae (Pilgrim, 1939). The development of temporal lines is correlated with the presence or absence of horn cores. The studied opisthocranium differs from the respective ones of *Bison*, *Bubalus*, *Bos*, *Leptobos* and male *Proamphibos* in the absence of strong temporal lines (Martinez-Navarro *et al.* 2007).

The weak temporal lines of the

opisthocranium are the features found in *Bucapra*, *Hemibos* and female *Proamphibos*. *Bucapra* is characterized by a narrow and high skull, large occipital condyles that do not project beyond the summit of the occipital crest, small anterior tuberosities and large auditory bullae (Pilgrim, 1939). The occipital condyles are very large and they are projected to the rear of the occiput in the studied opisthocranium, unlike in *Bucapra*. The backwardly projected occipital condyles are absent in *Bucapra* but they are present in *Hemibos* and *Proamphibos*. The studied specimen is wider than *Bucapra* and approaches *Hemibos* and *Proamphibos*. The large auditory bullae are absent in *Hemibos* but in some individuals of *Proamphibos* they are quite large. In the studied specimen the auditory bulla is large, long, stout and reaches far below the level of the basioccipital. The flattened occipital surface and reduced temporal lines are present in *H. triquetricornis* and *H. acuticornis* (Pilgrim, 1939; Martinez-Navarro and Palombo, 2004). But the parietal is very short in *Hemibos* (Hooijer, 1958). The studied opisthocranium is distinguished from *Hemibos* being closer to *Proamphibos* in the widened mastoid (Table I). The temporal fossa opens widely on to the parietal as well as on to the supraoccipital than that of *Hemibos*. The opisthocranium is narrower than that of the earlier described skull of *Hemibos* (Pilgrim, 1937; 1939). Furthermore, the small width at the mastoid in the studied skull associates it to *Proamphibos* in distinction from *Hemibos* (Pilgrim, 1937). The anatomy of the specimen confirms that it is a member of the genus *Proamphibos*, a primitive Bubaline.

Proamphibos is represented in the Siwaliks by two species *P. lachrymans* and *P. kashmiricus*. *P. lachrymans* occipital condyles are not projected backward in the high degree as those of *P. kashmiricus*. *Proamphibos kashmiricus* and the studied skull have more projected occipital condyles than *P. lachrymans* (Pilgrim, 1939). The minimum distance apart of the two temporal fossae in the studied skull is 34 mm, same as in the holotype GSI B561 of *P. kashmiricus* (Pilgrim, 1939). The surface of the opisthocranium is not rugose because the rugosity is normally absent in the female *P. kashmiricus*. According to its dimensions the

studied skull is of similar size with that of a female *P. kashmiricus* (Table I). In addition, the weak development of the temporal lines indicates that the specimen belongs to a hornless female of *P. kashmiricus*.

Based on the comparison, the studied opisthocranium shares the morphotypical conditions of *Proamphibos* and particularly of the species *P. kashmiricus*. Regarding the width of the skull at the mastoid process, the narrowness of the skull, the height of the occiput, the width of the occipital condyles and the large auditory bulla the specimen PUPC 71/57 fits pretty well with the previously described specimen of *P. kashmiricus* (Table 1 with comparative measures). The animal is somewhat larger with relatively longer and thicker occipital crest than the hitherto described material of a female *P. kashmiricus*.

DISCUSSION

Nobody had described a new *Proamphibos* female skull after Pilgrim (1939). After more than 130 years, a new specimen of *P. kashmiricus* was recovered. *Bucapra* is characterized by a narrow and high skull, large occipital condyles do not project beyond the summit of the occipital crest, small anterior tuberosities of the basioccipital and large auditory bulla (Rutimeyer, 1878; Pilgrim, 1939). These features are variables and can be seen on crania of *Proamphibos* (Pilgrim, 1939). In addition the species *Bucapra daviesii* is a problematic taxon. Rutimeyer (1878) erected this species based on the holotype (broken skull) which does not bear distinguishing characteristics, and he erroneously attributed it to Caprinae, an act criticized by Pilgrim (1939) and placed the specimen in the primitive Bubaline group. Therefore, the systematic status of *Bucapra* is not clear and according to Pilgrim (1939), its systematic status is also uncertain.

The main defining features of *Bucapra* are variables and these are represented in *Proamphibos* skull from the Tatrot and the Hasnot sediments (Pilgrim, 1939). The exhibited features of the studied skull: the parietal and the adjacent bones, the narrow occipital, the temporal fossae that open partially to the parietal and partially to the supraoccipital, the greater expansion of the posterior

tuberosities, the weak temporal crests agree very well with those of the holotype BMNH 36677 of *Bucapra* and the female *Proamphibos* skull (Table I). The only difference of the holotype BMNH 36677 *Bucapra* from the studied skull is the smaller size and the backward projection of the occipital condyles. Rutimeyer's *Bucapra* might be an immature female *Proamphibos*.

CONCLUSIONS

The main characters defining the new fossil skull are: the wide posterior tuberosities of the basioccipital, the large bullae, and the absence of horn cores (according to the plesiomorphic shallow temporal fossae, weak temporal lines, parietals in the dorsal plane). These same characters are documented on the crania of *Hemibos* and *Proamphibos* (to name two bovine taxa with horn cores that are not shifted far posteriorly).

The described opisthocranium (PUPC 71/57, Fig. 2) corresponds fairly with the referred specimen GSI 817 of *P. kashmiricus* and the holotype BMNH 36677 of *Bucapra daviesii* described by Pilgrim (1939) from the sediments of the Tatrot. The opisthocranium is massive than those of *P. kashmiricus* and *B. daviesii*, nevertheless, it defines sufficient similarity with the female *P. kashmiricus* regarding skull anatomy. Comparing the referred specimen GSI 817 of *P. kashmiricus* and the holotype BMNH 36677 of *Bucapra daviesii* with the studied opisthocranium PUPC 71/57, it is clear that the differences should be credited to intraspecific variability. The strong resemblance of the studied skull with *P. kashmiricus* and *B. daviesii* suggest synonymy of *Bucapra* genus with *Proamphibos*. The size and morphology of the studied specimen and *Bucapra* allow us to regard them local races of *Proamphibos*. Nevertheless, the material is insufficient and more material will be required for the confirmation.

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