PROAMPHIBOS (BOVINI, BOVIDAE, MAMMALIA) FROM THE TATROT FORMATION IN THE UPPER SIWALIKS OF PAKISTAN

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ABSTRACT

Proamphibos was a bovine present only in the fresh water deposits of the Upper Siwaliks and its tertiary fossil record is poorly known. New fossil remains of the Bovini genus Proamphibos are described. It includes a maxillary ramus bearing P3-M3. The analysis of the dental characters was allowed individual variations and contributes knowledge about the primitive bovine.

Key words: Proamphibos, Bovine, Tatrot Formation, Upper Siwaliks, Pliocene.

INTRODUCTION

The Bovini are defined by horn cores that are less upright, less angular cross section (with an especially weaker anteriorly keel) and a less marked sagittal crest on the occipital. They have horn cores that are divergent, curved and closer to the back of the skull. Pachyportax is considered the common ancestor of bovines and known from the Upper Miocene in South Asia (Pilgrim, 1913; Stackhouse et al., 1990; Akhtar, 1992 and Khan, 2008). The tribe Bovini includes Eurasian genera Leptobos, Bison, Bos, Proamphibos-Hemibos and Bubalus, and Proamphibos is the earliest among them. Supposed phyletic relationships of tribe Bovini are Leptobos – Bibos – Bos and Proamphibos – Hemibos – Bubalus + Anoa (Geraads, 1992).

By reconstructing ancient proteins of extinct bovids; it is suggested that the two extinct genera from the Pliocene, Proamphibos and Ugandax, appear to correspond to the most ancient members of (respectively) the Bubalus (water buffalo), and Syncerus (African buffalo) branches of the Bovini tree following their divergence, while Leptobos may be ancestral to Bos (cattle, bison) (Stackhouse et al., 1990).

The genus Proamphibos is known only from the Upper Siwalik deposits of the subcontinent. Pilgrim (1939) described two valid species of the genus, P. lachrymans and P. kasmiricus, in the Upper Siwaliks and one provisional species P. hasticornis in the Dhok Pathan level. The author was not confident about the validity of the genus that time because of the fragmentary state of the generic holotype. Later, Geraads (1992) confirmed the validity and stratigraphic level of the genus. He confirmed that P. kashmiricus (Pilgrim, 1939), and P. lachrymans (Pilgrim, 1939), are collected from the Pliocene of Tatrot of the Siwaliks or probably from the sediments of the same level.

The described material is collected from the Pliocene of the Tatrot Formation of the Jari Kas, district Mir Pur, Azad Kashmir (Fig. 1). The lithostratigraphic unit comprises Parmandal Sandstone, sand dominated sequence of sandstone-mudstone couplets (Roa et al., 1988; Agarwal et al., 1993). The unit is well known for its rich mammalian fossil assemblages (Akhtar, 1992, Basu, 2004; Dennell, 2008; Khan et al., 2008). The study is an attempt to describe Proamphibos specimen in situ from the Tatrot Formation of the Upper Siwaliks and subsequently is described below.

Fig. 1. Location map.

The catalogue number of the PUPC specimen consists of series i.e., yearly catalogued number and serial catalogued number, so figures of the specimen represent the collection year (numerator) and serial number (denominator) of that year (69/641). All
measurements are given in mm. The dental length (L) and width (W) were measured at occlusal level. As tooth height (H) is considered the height of the metacone on the upper molar (M) and the height of the protocone on the upper premolar (P). Uppercase letters for upper teeth.

Institutional abbreviations: PUPC – Punjab University Palaeontological Collection, GSI – Geological Survey of India,

**SYSTEMATIC PALAEONTOLOGY**

**BOVIDAE**   Gray, (1821)
**BOVINAE**   Gray, (1821)
**BOVINI**   Gray, (1821)
**PROAMPHIBOS**   Pilgrim, (1939)

**Diagnosis**

*Original*: Pilgrim, 1939, p. 270.

*Referred Material*: PUPC 69/641, left maxillary ramus with P3-M3 collected from Jari Kas (Tatrot Formation), district Mir Pur, Azad Kashmir.

*Age*. – 3.5-2.6 Ma (Hussain *et al*., 1992; Barry *et al*., 2002; Dennell *et al*., 2008; Nanda, 2008).

**Description**: The upper molars are extremely hypsodont and narrowly crowned (Fig. 2). The enamel is thick and crenulated. The central cavities are wide and moderately deep. A large spur (hypoconal spur) projects on the posterior side of the posterior central cavity. A small spur also projects on the anterior side of the anterior central cavity. The cement is well developed on the lingual as well as on the buccal side. The entostyles are well developed, rather thick and attached to the main body of the molars. The styles and ribs are strongly developed, compressed and prominent; the metastyle and the paracone rib prevail over them. The hypsodonty index can not be precisely assessed because all preserved molars are in medium wear stage. The Premolars reflect crown morphology clearly. The P3 is slightly longer than P4. The P4 is narrower and have the antero-posteriorly compressed fossette.

**Discussion**: The teeth are large, strongly hypsodont, broad with a relatively short premolar to molar row and presence of basal pillars and goat folds on the lower molars would suggest affinities with the Bovini. The teeth of Alcelaphini are hypsodont but in alcelaphine teeth the basal pillars and goat folds on the lower molars are absent (Gentry, 1978).

Broad upper molars are the characteristic of Bovinæ and Boselaphinae than the other subfamilies of Bovidae. But in Bovinæ teeth are extremely hypsodont, accompanied by the formation of cement, the disappearance of the wrinkles on the enamel and the enlargement of the basal pillars on the inner and outer sides respectively of the upper and lower molars (Pilgrim, 1939). Excessive anterior – posterior compression of Bovinæ molars has produced median ribs of extraordinary strength. This type of development has taken place also in Bopselaphini genera *Selenoportax* and *Pachyportax*.

![FIG. 2. – Proamphibos sp.: 1. PUPC 69/641. a = Crown view, b = buccal view, c = lingual view. Scale bar 10 mm.](image)

**FIG. 2.**

The presence of cement, the disappearance of the wrinkles on the enamel and the enlargement of the entostyles and excessive anterior – posterior compression confirm the specimen of Bovinæ. In bovinæ the quadrate shape of the upper molars is a characteristic of *Proleptobos, Proamphibos* (Fig. 3) and equally some elongation has taken place in *Leptobos, Hemibos* and in a much less degree in *Bubalus*. In *Proleptobos* P3 is much longer than P4 and outer folds rather divergent at the neck. However, in the studied specimen but P3 and P4 almost are equal in length (Table 1). Moreover the P4 is narrower and the fossette is more compressed antero-posteriorly which make the specimen inclusion to *Proamphibos*. The morphometry of the dental remains fit with *Proamphibos lachrymans* (Pilgrim, 1939) but the

![FIG. 3. Bivariate showing quadrate shape of Proamphibos molars.](image)
material is not enough to identify it precisely and the material is referred to Proamphibos sp.

Table 1. Proamphibos sp. Comparative measurements (mm) of the cheek teeth.

<table>
<thead>
<tr>
<th>Specimens</th>
<th>Position</th>
<th>L</th>
<th>W</th>
<th>H</th>
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<tbody>
<tr>
<td>PUPC 69/641</td>
<td>P3</td>
<td>20</td>
<td>24</td>
<td>23</td>
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<td></td>
<td>P4</td>
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<tr>
<td></td>
<td>M3</td>
<td>32</td>
<td>29</td>
<td>27</td>
</tr>
<tr>
<td>PUPC 72/57 (Akhtar, 1992)</td>
<td>P4</td>
<td>20</td>
<td>23</td>
<td>36</td>
</tr>
<tr>
<td>PUPC 84/27 (Akhtar, 1992)</td>
<td>P3</td>
<td>20</td>
<td>19</td>
<td>28</td>
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<tr>
<td></td>
<td>P4</td>
<td>18</td>
<td>19.5</td>
<td>30</td>
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<td></td>
<td>M1</td>
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<td>28</td>
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<td>M2</td>
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<td>M3</td>
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<td>M3</td>
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<td>21.5</td>
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<td>GSI B561 (Pilgrim, 1939)</td>
<td>P4</td>
<td>19</td>
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<td></td>
<td>M3</td>
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Conclusion: According to the evidence, we recognize here that Proamphibos is found in the Pliocene of the Upper Siwaliks. Proamphibos (Tatrot Formation, Early and Middle Pliocene) follows evolutionary lineage leading in the direction of Hemibos which is found in the Plio-Pleistocene of Eurasia and the ancestor of the water buffalo Bubalus (Pilgrim, 1939; Hooijer, 1958; Nanda, 1979; Akhtar, 1992; Martinez-Navarro and Palombo, 2004). The Bubalus is known in the Middle and Upper Pleistocene of Pakistan, India, Indonesia, China and Europe (Berkhemer, 1927; Franzen and Koenigswald, 1979; Van Dam et al., 1997; Schreiber and Munk, 2002). Recently, the first record of Indian bovine Hemibos is reported by Martinez-Navarro and Palombo in 2004 and mentioned its dispersal at the Early – Middle Pleistocene transition.

Proamphibos is only found in the Upper Siwaliks deposits of the subcontinent and its expansion into Europe might have occurred in earlier times during the Pliocene as Lindsay et al. (1980) mentioned three major dispersal events of large mammals during the Pliocene. This should be kept on the paleontological suspense account and wait for the European record.

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REFERENCE


