Rivista Italiana di Paleontologia e Stratigrafia	volume 119	no. 1	pp. 57-63	March 2013

FIRST RECORD OF MAXILLARY DENTITION OF *POTAMOCHOERUS THEOBALDI* (SUIDAE, MAMMALIA) FROM THE UPPER SIWALIKS OF INDIA

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Received: June 28, 2012; accepted: September 17, 2012

Key words: *Potamochoerus,* Suidae, Pliocene, Tatrot Formation, Upper Siwaliks, India.

Abstract. The present paper describes the maxillary dentition of *Potamochoerus theobaldi*. A well preserved right maxillary fragment with P^4-M^2 was collected from the Tatrot Formation of the Upper Siwaliks exposed northeast of Khetpurali Village near Raipur Rani (Haryana), Northwest India. The specimen was found associated with several other mammalian taxa, which include *Stegodon insignis, Hexaprotodon sivalensis, Camelus sivalensis, Gazella* sp., and yet to be identified Bovini. The mammalian faunal assemblage suggests an Early Pliocene age for the Tatrot deposits of Upper Siwaliks in the area. *P. theobaldi* was probably adapted to a bush land and forest fringe type of habitat. The present discovery is significant in the sense that it represents the first report of the maxillary dentition of *Potamochoerus theobaldi* from the Indian Siwaliks.

Riassunto. Questo contributo descrive un frammento di osso mascellare destro, ben conservato, che conserva P^4-M^2, e che viene attribuito, sulla base delle caratteristiche morfologiche e metriche, alla specie *Potamochoerus theobaldi*. Il reperto proviene da sedimenti della Tatrot Formation (Upper Siwaliks) affioranti a nordest del villaggio di Khetpurali, nei pressi di Raipur Rani (Haryana), nell'India nordoccidentale. L'associazione faunistica che accompagna il reperto qui descritto include diversi mammiferi, tra i quali *Stegodon insignis*, *Hexaprotodon sivalensis*, *Camelus sivalensis*, *Gazella* sp., ed alcuni resti di Bovini il cui studio è tuttora in corso. Quest'associazione a mammiferi, da un punto di vista biocronologico, suggerisce, per i depositi fossiliferi della "Upper Siwaliks, Tatrot Formation" affioranti nell'area di studio, una attribuzione cronologica riferibile al Pliocene Inferiore. Da un punto di vista paleoecologico, *P. theobaldi* era probabilmente adattato a habitat e territori caratterizzati da boschi aperti o da foreste con radure. L'identificazione di questo taxon è particolarmente significativa in quanto rappresenta la prima segnalazione della presenza della specie *Potamochoerus theobaldi* nei depositi delle Siwaliks dell'India.

Introduction

The genus *Potamochoerus* was named by Gray in 1854. It is represented by two living species, *P. porcus* (Red River Hog) and *P. larvatus* (the Bush Pig), which currently inhabit sub-Saharan Africa (Vercammen et al. 1993). The fossils of the genus are known from Africa (Harris & White 1979; Cooke & Wilkinson 1978; White & Harris 1977; Kullmer 2008; Bishop 2011), Europe (Arribas & Garrido 2008) and Asia (Pilgrim 1926; Colbert 1935; Li 1963; Han 1987; Gaur 1987b; Qi et al. 1999). The oldest record of the genus is probably from the Late Miocene to Early Pliocene Siwalik deposits of the Indian Subcontinent (Gaur 1987a). In Africa, the fossil *Potamocherus* is represented by *P. afarensis* (Bishop 2011). *Potamochoerus afarensis* was first described as *Kolpochoerus afarensis* by Cooke (1978). It was subsequently considered as better belonging to genus *Potamochoerus* (Bishop 2011), although recently both Pickford (2012) and Haile-Selassie & Simpson (2012) point out that *Kolpochoerus afarensis* has been consistently but wrongly attributed to *Potamochoerus*. Opinions differ as to when *Potamochoerus* arrived in Africa. According to Bishop (2011), *Potamochoerus* or its ancestors presumably arrived in Africa from Eurasia some time before 4.5 million years. Pickford (2012, p.17), however, believes that *Potamochoerus* colonized Africa sometime later, during Early Pleistocene. Until recently, there was no record of *Potamochoerus* from Europe. However, very recently Arribas & Garrido (2008) reported a new species, *Potamochoerus magnus*,

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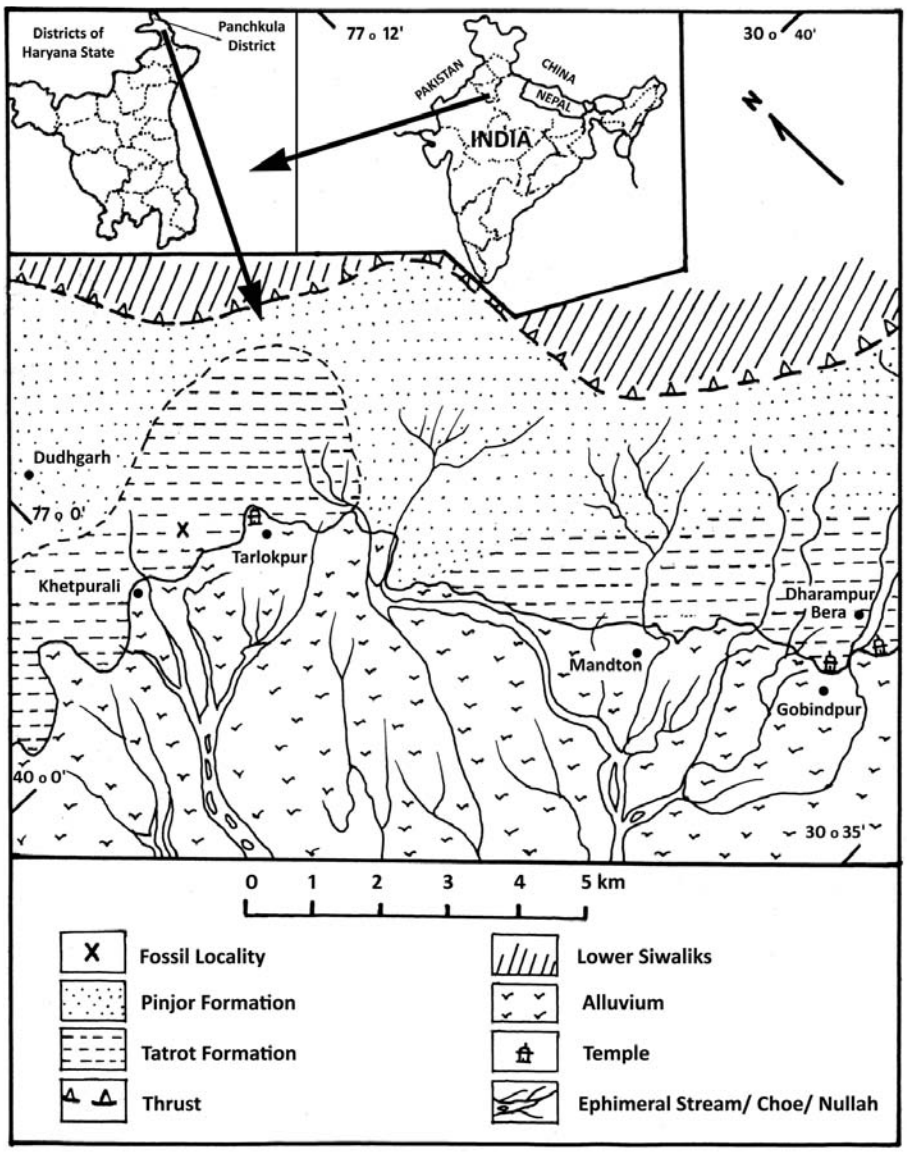

Fig. 1 - Generalised locality map of the area.

from the Early Pleistocene of Spain (earliest Late Villafranchian, cfr. Rook & Martínez-Navarro 2010). Another species, *P. chinhsienensis*, was reported by Li (1963) from Chinhsien, Shansi District of China presumably from Early Pleistocene deposits. Han (1987) described a new species, *Potamochoerus nodosarius*, from Early Pleistocene deposits of Liucheng cave, China. Qi et al. (1999) recorded *Potamochoerus* sp. from Zouzhen Pleistocene deposits of Taiwan.

In the Indian Siwaliks, *Potamochoerus* is represented by two species, *P. palaeindicus* and *P. theobaldi*, both of which were created on the basis of mandibular fragments by Pilgrim (1926). Colbert (1935) reported a maxillary fragment (A.M. 19878) with P^3-M^2 of *P. palaeindicus* from the Upper Siwaliks. Until this report, no published record of maxillary dentition of *P. theobaldi* was available from India. The present specimen PUA/SK-07/94, a right maxillary fragment with P^4-M^2 was collected *in situ* from a pinkish mudstone layer of the Tatrot Formation exposed northeast of Khetpurali Village (Figs 1, 2). This report represents the first record of maxillary dentition of *P. theobaldi* from the Indian Siwaliks, and a new addition to our knowledge of this extinct *Potamochoerus* species.

No radiometric dates are available for the Tatrot Formation of India. Magnetostratigraphic investigations conducted by Azzaroli & Napoleone (1982) and Tandon et al. (1984) in the Upper Siwaliks near Suketi and east of Chandigarh, respectively, placed the Tatrot/Pinjor boundary at the Gauss/Matuyama transition at about 2.5 Ma. Azzaroli & Napoleone (1982) placed the lower limit of the Tatrot Formation of the Suketi area at 3.15 Ma. However, studies in the Pakistan Siwaliks by Johnson et al. (1982) placed the Dhok Pathan/ Tatrot boundary at 5.1 Ma. A radiometric age of 2.53 Ma was assigned by Johnson et al. (1982) to the volcanic tuff layer in the Kotal Kund and Jalalpur Upper Siwalik section of Pakistan, which helped to mark the boundary

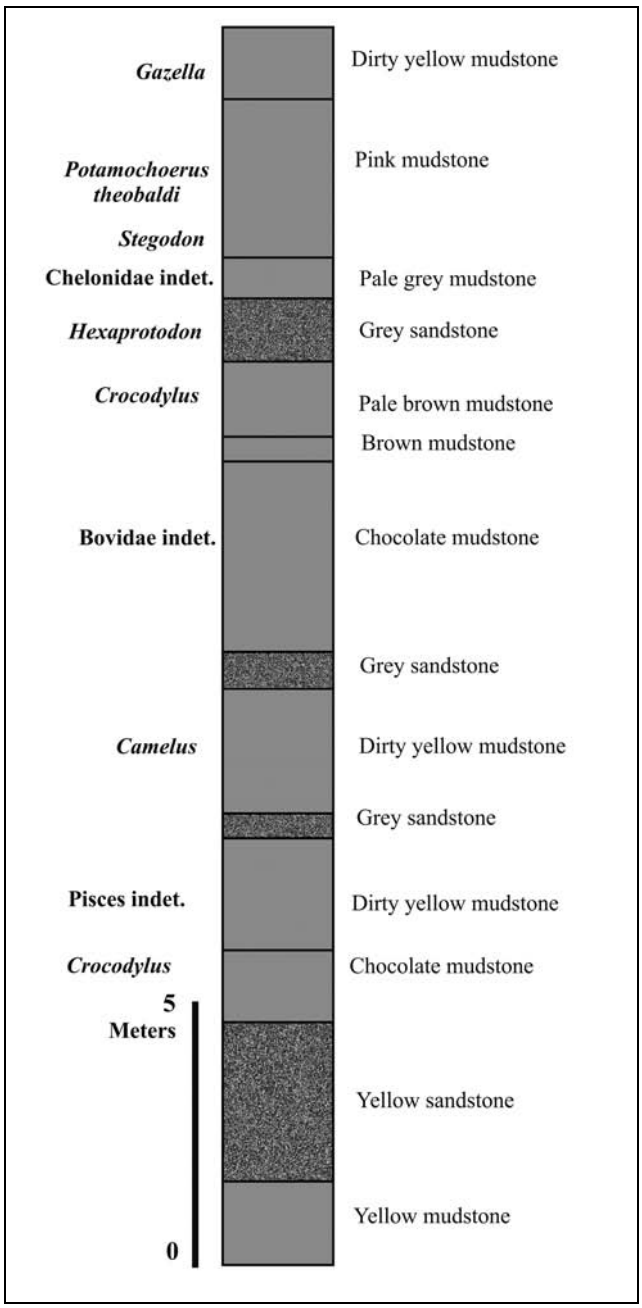

Fig. 2 - Local stratigraphic section of the Tatrot Formation of the area.

between Gauss and Matuyama magnetic chrons that are considered to mark the transition between Tatrot and Pinjor (Opdyke et al. 1979; Azzaroli & Napoleone 1982). The present specimen was recovered from slightly above the base of the Tatrot Formation. It was found associated with several Pliocene mammalian taxa, which include *Stegodon insignis, Hexaprotodon sivalensis, Camelus sivalensis, Gazella* sp., and yet to be identified Bovini (Fig. 2). On the basis of the associated fauna and its recovery from slightly above the base of the Tatrot Formation, the specimen may be provisionally assigned an age of between 4 and 5 million years. According to Gaur (1987a), the mammalian faunal assemblage of the Tatrot Formation of the Upper Siwaliks in the area is suggestive of an Early Pliocene age.

Systematic Palaeontology

Order **Artiodactyla** Owen, 1841
Family Suidae Gray, 1821
Subfamily Suinae Gray, 1821
Genus *Potamochoerus* Gray, 1854

Potamochoerus theobaldi Pilgrim, 1926

Holotype: G.S.I. No. B 11, a right mandibular ramus.
Type Locality: Kangra District, North India.
Type Horizon: Upper Siwaliks, Pinjor Formation.
Additional Material: PUA/SK-07/94, a right maxillary fragment with P^4-M^2.
Locality: About 1 km northeast of Khetpurali Village, Block Raipur Rani, District Panchkula, Haryana State, India.
Horizon: Upper Siwaliks, Tatrot Formation.

Description. The specimen consists of a right maxillary fragment with P^4- M^2 (Fig. 3). Only a small part of the hard palate can be seen on the lingual side. On the buccal side the alveolar process is eroded thereby exposing the roots of P^4 and M^2. The maxillary fragment is broken immediately anterior to P^4 and distal to M^2.

Upper fourth premolar. The premolar is sub-triangular in outline. Except for traces of wear on the anterior-buccal angle, the premolar is unworn. The paracone is distinctly larger than the lingual protocone, which is slightly broken at its apex. The metacone is unworn. The anterior cingulum is less developed than the posterior cingulum, which is also more beaded. The central longitudinal valley is relatively open and simple and not crowded with conules as is in the case of *Sus* and *Hippohyus*. The anterior sagittal cusplet is very close to the paracone. The posterior sagittal cusplet is very small and is indistinctly connected to the distal cingulum. The anterior border near its buccal corner shows an interstitial pressure facet. The premolar shows several cracks, probably caused by weathering before burial. The crown lacks the hypsodonty seen in *Hippohyus, Tetraconodon* and *Sivachoerus*. The premolar does not show the enlargement that is so typical of *Tetraconodon* and *Sivachoerus*. The premolar also lacks the rugosity of enamel as seen in *Conohyus* and *Sivachoerus.*

Upper first molar. The molar is low-crowned and more or less squarish in outline. The anterior cingulum is comparatively better developed than the posterior cingulum. Faint cingular developments can also be noticed on the lingual side at the base of hypocone. The median transverse valley of the molar is occupied by a

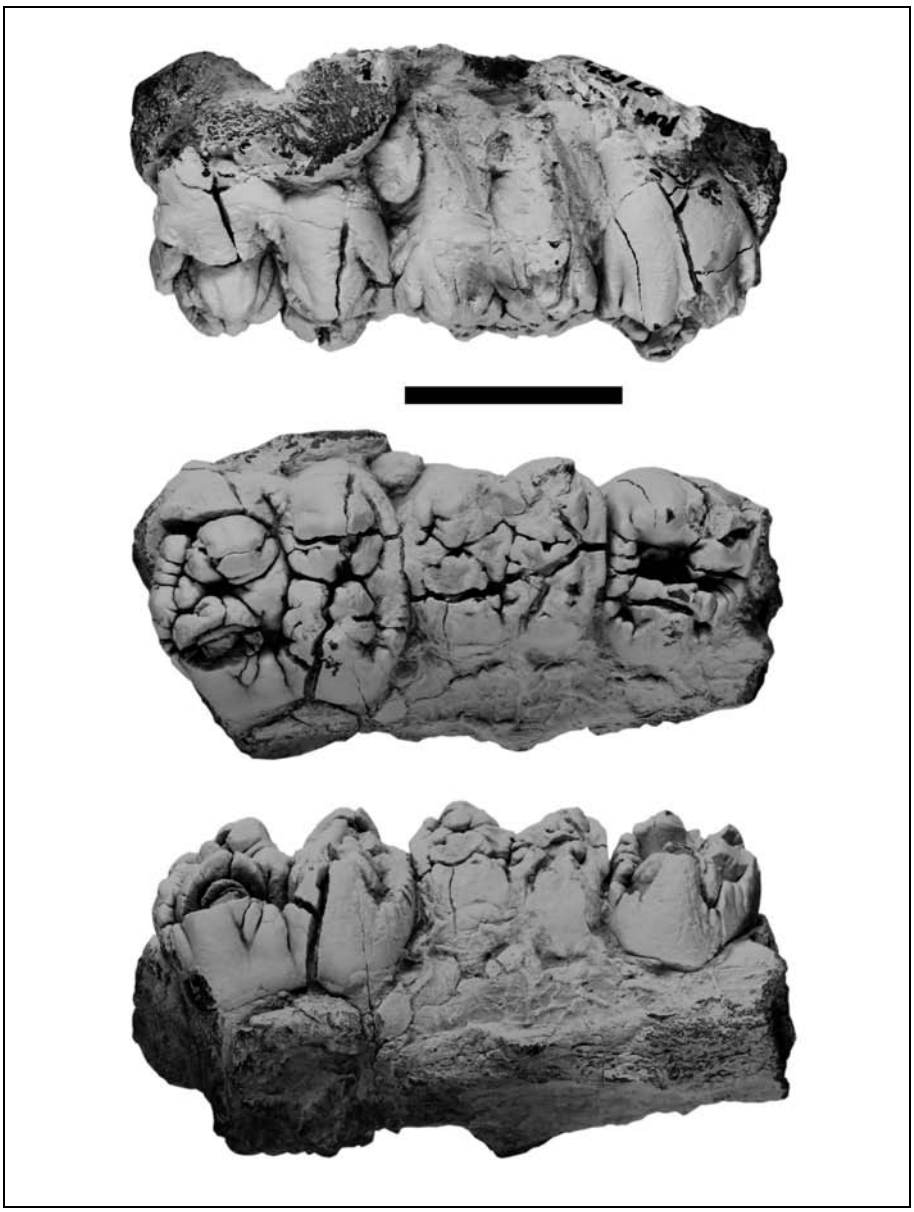

Fig. 3 - PUA/SK- 07/94, right maxillary fragment of *Potamochoerus theobaldi* with P^4-M^2. a: lingual, b: occlusal, and c) buccal views (please note that Fig. 3c is reversed). Bar scale represents 2 cm.

median accessory cusp. The first molar is only faintly touched by wear. The tooth shows several matrix-filled pre-burial cracks.

Upper second molar. The second molar is distinctly larger than the first molar and is squarish in outline. The hypocone is partly broken on the lingual side. Anterior and posterior cingula are well developed. The posterior cingulum is more beaded than the anterior one. Between the metacone and the hypocone there is a distinct median accessory cuspule in the median valley. As is the case of P^4 and M^1, the M^2 also displays cracks on its crown, probably caused by pre-burial weathering.

Comparisons. Several genera of Suidae, namely *Hyotherium*, *Sivachoerus, Tetraconodon, Hippopotamodon*, *Propotamochoerus, Hippohyus, Sus* and *Potamochoerus* are known from the Upper Siwaliks deposits of India. The specimen under discussion differs from *Hyotherium* due to the presence of accessory cusplets in the sagittal valley. The present maxillary fragment differs from *Sivachoerus* and *Tetraconodon* due to the smaller size of its premolar, compared to the size of the molars. *Tetraconodon* and *Sivachoerus* are characterized by their enlarged premolars, as compared to the size of the molars. The lack of enamel wrinkling on P^4 in the present specimen further distinguishes it from that of *Tetraconodon*, *Conohyus* and *Sivachoerus*. The more complex structure and deeply cleft outer crest of the P^4 in this specimen also separate it from the above genera. The P^4 in the present specimen is simple with a relatively open longitudinal valley and in this aspect it differs from *Sus*, *Sivachoerus* and *Hippohyus* in which the P^4 is more complex with more cusps. It further differs from *Hippohyus* in being much less hypsodont and in the absence of the characteristic complex enamel pattern on molars.

Pickford (1988) carried out a comprehensive revision of the Miocene Suidae of the Indian Subcontinent, including those from the Siwaliks. In the revision he resurrected the genus *Hippopotamodon* that was originally created by Lydekker in 1877. Pickford (1988) argued that Pilgrim (1925, 1926) was incorrect in creating a new genus *Dicoryphochoerus* since the genus *Hippopotamodon* was already available and had priority. Several specimens identified as *Dicoryphochoerus titan* and *Dicoryphochoerus robustus* along with several other specimens belonging to *Sus titan, Sus giganteus, Potamochoerus titan*, were synonymized under *Hippopotamodon sivalense*. While revising Miocene suids Pickford (1988) considered the genus *Dicoryphochoerus* to be a junior synonym of *Propotamochoerus* and synonymized several species of *Dicoryphochoerus* (*D. vagus, D. durandi, D. vinayaki* and *D. haydeni*) under *Propotamochoerus hysudricus.* Pickford (1988) considered *Propotamochoerus* to have been derived from *Hyotherium* sometime around 11 Ma. *Propotamochoerus* is largely restricted to the Middle Siwaliks of the Indian Sub-continent, while the present specimen is from the Tatrot Formation of Upper Siwaliks.

The P^4 and molars in the present specimen are considerably smaller than that of *Hippopotamodon sivalense* and its P^4 lacks a large posterior accessory cusp (nearly as large as two main buccal cusps) that characterizes *Hippopotamodon*. The presence of well-developed cingulum on the molars distinguishes the present specimen from *Propotamochoerus.* The posterior sagittal cusplet in P^4 of PUA/SK-07/94 specimen is very weak and is faintly connected to the distal cingulum. In *Propotamochoerus hysudricus* both the sagittal accessory cusplets arise from ridges that develop on the lingual aspect of the two main labial cusps (Pickford 1988, p. 63).

Very recently, Pickford (2012) has elevated *Dasychoerus* to the status of a full-fledged genus and classified the Warty Pigs *Sus verrucosus* and *Sus celebensis* under it, keeping *D. verrucosus* as type species. *Dasychoerus* is a genus originally proposed by Gray (1873) for warty pigs, which he considered different from wild boar (*Sus scrofa*). However, subsequent workers did not agree with Gray's contention. Berdondini (1992), while describing fossil suids from Early Villafranchian of Italy and Pliocene Shanxi Province of China, recognized a close relationship between *Sus minor* and *Sus strozzii* and the living taxa *Sus verrucosus* and *Sus celebensis* of Southeast Asia. She resurrected *Dasychoerus* as a subgenus for these *Sus* species not only to indicate their mutual relationship but also to stress their distinctiveness from the extant *Sus scrofa.* The Plio-Pleistocene and the recent Indonesian suids (*Sus barbatus, Sus macrognathus, Sus brachygnathus, Sus timorensis, Sus celebensis*) were reviewed by Hardjasasmita (1987) who noted the distinctiveness of these species from *Sus scrofa* (wild boar) and *Sus huereni*, particularly with reference to the cross-section of canines and the presence of stronger stylus/stylids on upper/lower second and third premolars. These Indonesian *Sus* species were assigned by Pickford (2012) to *Dasychoerus*, thus reinforcing their distinctiveness from *Sus scrofa*. The occurrence of *Dasychoerus arvernensis* in the Plio-Pleistocene Siwalik deposits of India has been pointed out by Pickford (2012) who considered "*Sus" hysudricus* type series specimens (housed in the Natural History Museum in London) as its junior synonym. The Khetpurali specimen (PUA/SK-07/94) is larger than *Dasychoerus arvernensis* and *D. natrunensis*. Since the present specimen does not preserve P^2 and P^3, it is not possible to comment on the nature of stylus and stylids in comparison to the Indonesian *Dasychoerus* species reviewed by Hardjasasmita (1987). However, PUA/SK-07/94 specimen is larger than *D. brachygnathus* and the median buccal valley of its M^1 is shallower than that of *D. brachygnathus*. The M^2 is more elongated in *D. brachygnathus* with a stronger talon when compared to PUA/SK-07/94, in which it is nearly squarish with less developed talon. The Khetpurali specimen can also be differentiated from *D. macrognathus* from Indonesia due to its roughly triangular P^4 and the absence of an antero-posterior fold on its lingual side. The P^4 in *D. macrognathus* is squarish and it shows an antero-posterior fold on its lingual side (Hardjasasmita 1987, Plate 4-E, p. 24).

In the morphology of its P^4 and molars PUA/SK-07/94 shows similarities with *Potamochoerus*. It differs from the earliest Pleistocene Spanish species *P. magnus* due to its considerably smaller size. It differs from *K. afarensis* (also known as *Potamochoerus afarensis*) from Africa by the distinctly greater bucco-lingual diameter of its first molar. The genus *Potamochoerus* is represented in the Indian Siwaliks by two species, namely *P. palaeindicus* and *P. theobaldi*, both of which were erected on the basis of mandibular fragments by Pilgrim (1926). Subsequently, Colbert (1935) reported a maxillary fragment (AM 19878) with P^3-M^2 of *P. palaeindicus* from Upper Siwaliks. The specimen herein described is smaller and shows limited morphological resemblance with the specimen of *P. palaeindicus* (AM 19878). Colbert (1935, p. 224) in the diagnosis of *P. theobaldi* states that the latter differs from *P. palaeindicus* in that *P. theobaldi* premolars are reduced in size compared to the molars. This character would be expected to occur in the maxillary dentition too, because, normally, the size of upper and lower dentition is related. The P^4 in the present specimen is smaller than that of *P. palaeindicus* and comes close in size to that of the extant species *P. porcus.*

Measurement	*P. theobaldi* present paper PUA/SK- 07/94	*P. palaeindicus* Colbert 1935 A.M. 19878	*P. porcus* Colbert 1935 A.M. 53727	*P. magnus* Arribas & Garrido 2008 FP-2001-0251	*P. afarensis* Bishop 2011 EP1058/04	*P. chinhsienensis* Li 1963
P^4						
Max. mesio-distal diameter (L)	13.2	15.0	13.0	15.0	-	-
Max. bucco-lingual diameter (B)	16.2	17.0	15.0	18.1	-	-
Index (B/L X 100)	123.0	113.3	115.4	120.5	-	-
M^1						
Max. mesio-distal diameter (L)	16.5	19.0	19.0	18.2	16.4	16.0
Max. bucco-lingual diameter (B)	15.4	17.0	17.0	19.1	12.6	16.2
Index (B/L X 100)	94.0	89.5	89.5	105.1	76.8	101.2
M^2						
Max. mesio-distal diameter (L)	21.6	26.0	23.0	28.5	-	27.5
Max. bucco-lingual diameter (B)	19.7	23.0	22.0	24.1	-	21.5
Index (B/L X 100)	91.2	88.5	95.6	84.7	-	78.2

Tab. 1 - Comparative measurements (mm) of maxillary dentitions of some species of *Potamochoerus*.

Concluding remarks

On the base of the above comparisons, one would be tempted to create a new species because of the observed size difference, however, to avoid creating a new taxon on size alone, the present maxillary fragment is assigned to *Potamochoerus theobaldi*. Gaur (1987b) suggested that *P. palaeindicus* and *P. theobaldi* may eventually be considered as variants (probably males and females) of a single species (in *Potamochoerus*, males are slightly larger than females, cfr. Geraads 2004). However, pending recovery of more complete fossil material *P. palaeindicus* and *P. theobaldi* are herein maintained as separate species. The body mass of *P. theobaldi* is estimated to be 102 kg from the length of maxillary second molar using the equation of Fortelius (1990).

Potamochoerus probably descended sometime around the Miocene Pliocene transition from *Propotamochoerus hysudricus,* which is common in the Middle to Late Miocene Siwalik deposits of the Indian Subcontinent. Subsequently it spread to Africa and, possibly, also to Europe, given the recent report by Arribas & Garrido (2008) of the *Potamochoerus magnus* occurrence in the earliest Pleistocene of Spain. In the Indian Sub-continent, *Potamochoerus* probably became extinct during Late Pliocene or Early Pleistocene.

Not much is known about the palaeoecology of *P. theobaldi.* The living species (the African *P. porcus* and *P. larvatus*) occur in forests, forest fringes, savannahs and thick bush country of eastern, central and South Africa (Grubb 1993; Smithers 1966; Dorst & Dandelot 1970). *Potamochoerus porcus* has a diet relatively rich in C_3 vegetation but is considered to be a browser to mixed feeder (Bishop 2011). It is possible that *P. theobaldi* was adapted to a bushland and forest fringe habitat. This would be in agreement with the hypothesis of Gaur & Chopra (1984) and Gaur (1987a) who suggested a landscape dominated by bushland with some forest cover for the Tatrot Formation of Upper Siwaliks in the northeast of Chandigarh, which is very close to the present locality.

Acknowledgments. Part of this research work was carried out under the University Grants Commission Major Project Grant, F. No. 39-76/2010 (SR), awarded to Prof. Rajan Gaur. Thanks are due to the two reviewers, Dr. Raymond L. Bernor and Dr. Martin Pickford, whose comments were helpful in improving the paper.

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