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New materials of Choerolophodon (Proboscidea) from Dhok Pathan Formation of Siwaliks, Pakistan (Postprint)

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Full Text

Preamble

New materials of Choerolophodon (Proboscidea) from Dhok Pathan Formation of Siwaliks, Pakistan

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Abstract

Choerolophodon corrugatus is the only species of the genus *Choerolophodon* found in the Siwalik Group. Its first appearance is in the Kamlial Formation (Middle Miocene) of the Lower Siwalik Subgroup and it is most abundant in the Dhok Pathan Formation of the Middle Siwalik Subgroup (Late Miocene to Early Pliocene). New remains of *Choerolophodon corrugatus* have been recovered from the Dhok Pathan type locality and its adjacent areas. The specimens include tusks, mandible and maxillary fragments, and deciduous premolars and permanent molars. The Siwalik species shows great affinity with the European species *Ch. pentelici* in dentition and differs in the cranial and mandibular characteristics.

Keywords: Siwalik Group, Dhok Pathan Formation, Miocene, Pliocene, *Choerolophodon*

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1 Introduction

Choerolophodon was mainly present in the Miocene of Africa, Eastern Europe, and Eastern, Western and Southern Asia (Gaziry, 1976, 1987; Tobien, 1980; Tassy, 1983, 1986; Pickford, 2004, 2005; Shoshani and Tassy, 2005; Wang and Deng, 2011). The genus *Choerolophodon* was established by Schlesinger (1917) and the subfamily Choerolophodontinae was erected by Gaziry (1976). Later, the subfamily status was raised to the family level by Gheerbrant and Tassy (2009). Previously, this difference was also noted by Tassy (1988, 1996a) in his cladistic analysis studies. In these analyses, the genus *Choerolophodon* appeared to be a sister group of amebelodons, gomphotheres, stegodontids and elephantids (Tassy, 1988: figs. 1, 3b, 4a, b) and this is consistent with node 8 (unnamed) of Tassy (1996a), which is partly comprised of Tobien' s (1973) "bunodont group." In this, *Choerolophodon* and all other clades of more basal taxa (Mammutidae to Anthracobune) have the plesiomorphic condition of nasal fossa which is narrow and does not extend laterally beyond the width of the rostrum (Tassy, 1996a).

The low and long skull with extended bony palate and retracted orbits render *Choerolophodon* extremely divergent among elephantoids. The mammutids, choerolophodons, and amebelodons are considered as earlier offshoots of Elephantoidea. Gomphotheriidae, Stegodontidae, and Elephantidae are characterized by higher cranial vault (Tassy, 1996b).

The *Choerolophodon* remains described in this paper have been discovered from the Dhok Pathan type locality (stratotype of Dhok Pathan Formation) and its adjacent areas (Fig. 1 [Figure 1: see original paper]). The Dhok Pathan type

locality is well studied and its lithology, biostratigraphy, magnetostratigraphy and paleoecology have been discussed in detail by Pilbeam et al. (1977, 1980) and Barry et al. (1982, 2002, 2013). The upper Dhok Pathan Formation is 5.1 Ma in the lower part of "chron" (Tatrot stratotype). The boundary between Nagri/Dhok Pathan is present in Khaur, 7.9 Ma in the upper part of "chron" (Barry et al., 1982, 2002). We present here in situ fossils from the Middle Siwalik Subgroup of Pakistan and provide evidence of the presence of *Choerolophodon corrugatus* in Pakistan. The article will enhance our understanding of the proboscideans in the Siwalik Group of Pakistan.

The specimens have been prepared and displayed in Dr. Abu Bakr Fossil Display and Research Center, Department of Zoology, University of the Punjab, Lahore, Pakistan. The dental nomenclature and measurements follow Tassy (1983, 1996c, 2013). The collected site of each specimen is given in parenthesis under the heading "New material."

Fig. 1 Map of the stratotype of Dhok Pathan Formation and its adjacent areas showing the fossiliferous sites yielding *Choerolophodon corrugatus* in the Potwar Plateau, Punjab, Pakistan.

Abbreviations: DhP, Dhok Pathan; PUPC, Punjab University Palaeontological Collection, Zoology Department, University of the Punjab, Lahore, Pakistan; GSP, Geological Survey of Pakistan; IM, Indian Museum.

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2 Systematic Paleontology

Order Proboscidea Illiger, 1811
Family Choerolophodontidae Gheerbrant and Tassy, 2009
Genus *Choerolophodon* Schlesinger, 1917
Choerolophodon corrugatus (Pilgrim, 1913)

Holotype: A 98 = W 3/16, IM, Calcutta, figured by Lydekker (1880: pl. 35, fig. 4 [Figure 4: see original paper], pl. 36, fig. l) and Osborn (1936: 658, fig. 626 [Figure 626: see original paper]). Mandible fragment with symphysis and the right horizontal branch with broken m2 and m3.

Type locality: Hasnot, without stratigraphic precision (Lydekker, 1885).

Diagnosis: Large size, high face, orbits located slightly posterior to the last functional cheek tooth, base (perinasal area) of the skull redressed, mandible ramus high, height of the horizontal branch increasing anterior to the dental series, mandibular symphysis bent downwardly, cheek teeth a little wider than in *Choerolophodon pentelici* (Tassy, 1983).

Stratigraphic range: Kamlial Formation to Dhok Pathan Formation, Lower Siwaliks to Middle Siwaliks (18.3–3.5 Ma, Pilgrim, 1913; Osborn, 1929, 1936; Tassy, 1983) and may be Tatrot Formation, Upper Siwaliks (3.5–3.3 Ma, Tassy,

1983). This time corresponds to European Land Mammal Zone, MN 3 to MN 16.

New material (the fossiliferous sites are in parenthesis): PUPC 14/01, partial left juvenile tusk (DhP2); PUPC 14/02, partial left adult tusk (DhP5); PUPC 87/332, partial right DP2 (DhP7); PUPC 96/30, right DP3 (DhP4); PUPC 14/39, right maxillary fragment with M2 and first loph of M3 (DhP1); PUPC 96/21, left dp3 (DhP3); PUPC 96/15, partially erupting left dp3 (DhP6); PUPC 15/229, right mandible fragment with dp3 (DhP8); PUPC 14/17, partial left dp4 (DhP9); PUPC 14/04, left mandible fragment with partial m2 and anterior roots of m3 (DhP3); PUPC 14/14, left m2 and anterior part of m3 (DhP10); PUPC 14/05, right mandible fragment with m2–3 (DhP10).

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3 Description

Tusk: The tusk PUPC 14/01 is broken near the base and covered by enamel throughout its surface (Fig. 2B [Figure 2: see original paper]). At certain places, the enamel has been removed owing to weathering and erosion. The presence of enamel and small pulp cavity at the apex indicates a young individual. The pulp cavity is not much wide. The cross section is slightly oval at the base and completely oval at the tip. The dentine is smooth and arranged in incipient circles.

The anterior most part of the tusk is missing in PUPC 14/02 (Fig. 2A). The preserved tip has a very small pulp cavity and the enamel is in minute quantity, indicating it belongs to an adult individual. The tusk is concave dorso-anteriorly and concave latero-ventrally. The cross section is regularly oval, and the tooth gradually tapers towards the apex. The dentine is finely grooved and smooth. The ventral side of the tusk is more wrinkled.

Upper cheek teeth: The DP2 is bilophodont and triangular (Fig. 2C). The main cusps have well-developed mesoconelets. The main pretrite cusp of the first loph has thick posterior pretrite central conule whereas that of the second loph has well developed anterior pretrite central conule. The antero-posterior cingulum is present. A small valley is present between the two lophs which is wide labially. Abundant cement is deposited at the base of the tooth.

PUPC 96/30, DP3 is bilophodont and larger than DP2 (Fig. 2D). It is well-developed, having more enamel folding, i.e. ptychodont. The anterior cingulum is thick, crenulated and covers the whole anterior side latterly. The protocone is well developed and has incipient mesoconelet but the anterior and posterior central conules are prominent. The mesoconelet of the paracone is divided, resulting in triplication. The valley is narrow lingually as the hypocone is shifted anteriorly. The hypocone has prominent mesoconelet with posterior pretrite central conule. The posterior cingulum is massive with postentoconule.

The length of the right maxillary fragment PUPC 14/39 is 310 mm (Fig. 2E).

The maxillary fragment is better preserved labially and has some portion of palate at lingual side. It tapers posteriorly. The first and second lophs are slightly broken labially in M2. The first loph including the anterior cingulum is severely worn so the median sulcus is vanished. The traces of median sulcus can be seen in the second and third lophs. The valleys become narrow owing to wearing and the distinction between the anterior pretrite conules and the posterior pretrite conules is not seen. The anterior pretrite conule is prominent on the third loph. The pretrite and posttrite halves of the second and third lophs are somewhat chevroning. A small posterior cingulum is present. The walls of the lophs are plicated.

Lower cheek teeth: The enamel is highly rugose in dp3 (Fig. 2F). The anterior cingulid is thick, divided and heavily worn. The posterior cingulid is thick, forming incipient third lophid. It is heavier than the anterior cingulid and the enamel is divided. The median tubercle in the anterior valley is much reduced and connected to the protolophid and hypolophid owing to the heavy wear. The median sulcus is vanished by wear as well.

PUPC 96/15 bears a broken left dp3 with some mandible fragment (Fig. 2G). The anterior cingulid is thick. The first lophid is incipient, highly ptychodont and smaller than the second lophid. The protoconid is joined to the anterior cingulid through the paracristid. The second lophid is not fully erupted. The enamel is highly rugose and plicated.

PUPC 15/229, a right partial mandible fragment with unworn dp3 (Fig. 2H). The anterior cingulid is small and bifurcated. The protoconid is joined to the anterior cingulid through the paracristid. The metaconid is stretched antero-posteriorly. The pretrite central conule is subdivided. The first valley is small. The hypoconid is subdivided into three tubercles. The posterior cingulid is strong, heavy and subdivided.

PUPC 14/17 is deeply worn (Fig. 2I). The posttrite half of the first lophid is preserved whereas the third lophid is slightly broken labially. The tooth is trilophodont. The pretrite half and anterior cingulid are heavily worn. The anterior and posterior valleys are small.

The length of the preserved mandible fragment is 300 mm in PUPC 14/04 (Fig. 2J). The corpus is heavily damaged, broken at the base completely, and partially from the anterior side. It becomes gradually narrow towards the apex. The corpus is porous indicating a juvenile individual. The first lophid with first valley is missing whereas the second and third valleys are preserved. The second valley is blocked centrally by the central tubercles, giving look of *Afrochoerodon*. The small tubercles are present in the last valley. The molar is in middle wear.

The second and third pretrite half lophids show a perfect trefoil pattern, most prominent on the third lophid. The median sulcus is evident. The posterior pretrite central conule of the second lophid joins to the third anterior pretrite central conule. The posterior cingulid is strong and divided into two tubercles. The enamel is heavily wrinkled.

PUPC 14/14 is a complete left m2 and the anterior part of the sequential m3 (Fig. 2K). The m2 is heavily worn. The pretrite half of the first and second lophids show the trefoil structure but the pretrite of the first lophid is distorted owing to the late wear. The main pretrite cusp of the first lophid (protoconid) is merged with the mesoconelet whereas the posterior pretrite conule is almost wedged in with the main cusp of the first lophid and the anterior pretrite conule of the second lophid. The pretrite mesoconelet and the anterior central conule are fused. The posttrite mesoconelets are anteriorly positioned than the corresponding main cusps, forming a chevroning structure. The third lophid is less worn than the anterior lophids and shows the same morphology as the second lophid except the posterior posttrite central conule which is united to the posterior cingulid. The accessory conules are present in the second and third valleys of the entolophid. The enamel is smooth lingually and rugose labially.

The broken m3 represents an anterior cingulid, the first lophid and the second lophid.

PUPC 14/05 is a heavily weathered mandible, having total length of 620 mm with partial ascending ramus and mandibular foramen (Fig. 2L). It is gradually bulged under m2 and m3. The m2 is more worn than m3; the first lophid of m3 shows the wear. The anterior cingulid is thin and much worn. The posterior cingulid is heavy and doubled, forming an incipient fourth lophid. The pretrites halves of the first two lophids show trefoil pattern which is slightly masked at the first lophid. The enamel at the third lophid is broken lingually, exposing the posterior lingual root. The lophids are finely divided into conules. The five lophids are visible in m3. It becomes narrower progressively and ptychodont. The anterior cingulid is small, composing two small conules. In the first valley, the first posterior pretrite central conule is in contact with the anterior pretrite central conule of the second lophid.

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4 Comparison

The studied mandible is without tusk, having high ramus and strongly downward inclination of the symphysis relative to the horizontal branch. The studied teeth represent subhypsodont lophids and large mesoconelets. The lophids are chevron (V-shaped occlusally) owing to the shift of the main pretrite tubercles behind the pretrite mesoconelets. The studied tusks are different from those of *Gomphotherium*, *Platybelodon* and *Zygolophodon* in having enamel cap at tip in juveniles (instead of enamel band at lateral side) and they are upwardly curved (instead of straight/ventrally curved; Tassy, 1983; Wang et al., 2013).

The lower tusks are absent, and the mandibular symphysis is medially long in *Choerolophodon* (Schlesinger, 1917). The upper tusks are upward and slightly outwardly curved; PUPC 14/02 is without enamel, however, the enamel is present at the whole surface of PUPC 14/01, which is exceptional to genus

Choerolophodon (Tassy, 1983). Nevertheless, the cross section of the tusk is oval which favors its inclusion to *Choerolophodon*.

The extreme choerodonty and ptychodonty in upper and lower cheek teeth excludes them from the genus *Anancus*, *Stegolophodon* and *Konobelodon* (Tassy, 1983). The Chinese species *Ch. guangheensis* is different from the studied species in having weak choerodonty and ptychodonty. *Ch. corrugatus* differs from *Ch. anatolicus* in having large deciduous premolars and complicated crown with strongly expressed choerodonty and ptychodonty (Sanders, 2003). In this respect, confidently, the specimens can be assigned to the genus *Choerolophodon* and the Siwalik species *Ch. corrugatus*.

The upper tusks of *Konobelodon* sp. (*Mastodon grandincisivus*, Schlesinger, 1917), have not been reported yet from the Siwaliks. However, the known upper tusks of the related species found elsewhere (Eurasia) lack the enamel band and they are ventrally curved (Wang and Deng, 2011; Konidaris et al., 2014). A single upper tusk of *Stegolophodon praelatidens* described by Chavasseau et al. (2009) from Thailand has an external/lateral enamel band. *Paratetralophodon hasnotensis*, described by Tassy (1983), has almost straight, outwardly divergent upper tusks with no enamel band, however, it has oval cross section. The tusks of *Ch. guangheensis* from China (Wang and Deng, 2011) are less curved upward and the cross section is varied along the entire length of the tusk, becoming elliptical near its base.

Tassy (1983) has already noted the difficulty in distinguishing the isolated teeth of *Ch. pentelici* from those of *Ch. corrugatus*. However, considerable differences are present in mandibles of these species and *Ch. anatolicus*. The angulation between ascending and horizontal ramus and the angulation of the symphyseal rostrum on the mandibular corpus are strong in *Ch. corrugatus* as compared to *Ch. pentelici* and *Ch. anatolicus* (Sanders, 2003; Konidaris and Koufos, 2009; Konidaris et al., 2016; present material, PUPC 14/05).

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5 Discussion

Choerolophodon is best known in the Indian subcontinent, under the name of *Synconolophus*, synonymized by Tassy (1983). Hopwood (1932) had considered the synonymy of European and Indian forms with the help of *Ch. pentelici* and *Mastodon pandionis* (*Ch. corrugatus*). In fact, the teeth of *Ch. pentelici* and *Ch. corrugatus* are morphologically very close (Tassy, 1983). The latest choerolophodons are dated at around 7 Ma in Europe: *Ch. pentelici* (Gaudry and Lartet, 1856) at Upper Maragheh, Iran, and around 6.8–6.5 Ma, in Pakistan: *Ch. corrugatus* (Pilgrim, 1913) (= *Synconoloplus dhokpathanensis* Osborn, 1929) from Khaur, Dhok Pathan, and Hasnot sites (Tassy, 1983). The genus *Choerolophodon*, with only one species (i.e., *Ch. corrugatus*), is relatively abundant in the Middle Siwaliks, rarer in the Lower Siwaliks. Its persistence in the Upper Siwalik (Pliocene) is uncertain (Tassy, 1983). The oldest *Choerolophodon*

comes from the Bugti area in Pakistan, suggesting the first occurrence in Eurasia, dated between 17.0-16.0 Ma, corresponding to the end of Early Miocene (Steininger, 1999). Mothé et al. (2016: 12, fig. 5 [Figure 5: see original paper]) pushed this date even to earliest Miocene.

Taxonomical study of *Choerolophodon* from the Miocene of Pakistan has a complex history. Pilgrim (1913) named *Tetrabelodon corrugatus*, based on the specimen from Hasnot, which Lydekker (1884) figured under the name of *Mastodon pandionis*. Osborn (1936) retained this as a valid species. The holotype of *Mastodon (Trilophodon) pandionis* was named *Mastodon (Trilophodon) falconeri* (M2) by Lydekker (1880). Lydekker (1880) erected *M. latidens* (DP2) and *Mastodon* sp. (fragmentary juvenile skull and associated dp3). Pilgrim (1913) ascribed *M. hasnoti*, based on three specimens depicted by Lydekker under the name of *M. (T.) sivalensis*. Osborn (1929, 1936) erected *Synconolophus dhokpathanensis*, *Serridentinus dhokpathanensis* and *Se. hasnoti* from the Siwalik. Tassy (1983) noted that all these species are attributable to *Ch. corrugatus*.

Choerolophodon kisumuensis, *Ch. ngorora* and *Ch. chioticus* were assigned to *Afrochoerodon*, a new genus erected by Pickford (2001, 2004). Pickford (2001) noted that *Afrochoerodon* is more primitive than *Choerolophodon* in having weak choerolophodonty, cementation on teeth and presence of enamel on tusks. A European species *A. chioticus* was placed as an intermediate form between *Afrochoerodon* and *Choerolophodon* by Pickford (2001). However, Tassy et al. (2013) retained the generic position of *A. kisumuensis*, *A. ngorora* and *A. chioticus* to *Choerolophodon* and declared *Gomphotherium pygmaeus* (*Ch. pygmaeus* of Pickford, 2004) *nomen dubium*. The pre-Siwalik *Choerolophodon* species *Ch. palaeindicus* was reported from the early Miocene of the Bugti Hills, Pakistan (Lydekker, 1884). Sanders and Miller (2002) proposed the placement of *Ch. palaeindicus* in *Afrochoerodon*, suggesting the probable synonym of *A. kisumuensis* from the Middle Miocene of Maboko, Kenya. Recently, Tassy et al. (2013) ascribed the Bugti species in the name of *Ch. palaeindicus*.

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6 Conclusions

Choerolophodon corrugatus is recorded from the Dhok Pathan type locality, Chakwal, Punjab, Pakistan. The Siwalik *Ch. corrugatus* is distinguished from other *Choerolophodon* species of the world in having strong choerodonty and chevroning structures. The cheek teeth of Siwalik species show great affinity with the European species *Ch. pentelici*.

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Note: Figure translations are in progress. See original paper for figures.

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