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The striking similarity among the molars of *Listriodon* and *Deinotherium* from the lower Siwaliks of Pakistan

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Abstract

The fossil teeth of *Listriodon pentapotamiae* and *Deinotherium pentapotamiae* have been collected from Dhok Bun Ameer Khatoon, Chinji and Lava; district Chakwal, Punjab, Pakistan. These sites belong to Lower Siwaliks, Chinji Formation. The specimens include upper molars of *Listriodon* and an isolated upper molar of *Deinotherium which was discovered* from the locality of Dhok Bun Ameer Khatoon for the very first time, but not unknown from the Chinji Formation. The type of the teeth and the habit of feeding are interlinked. The striking similarity has been observed among the molars of *Listriodon* and *Deinotherium*.

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Introduction

Dhok Bun Ameer Khatoon is a village of Chakwal district; Punjab, Pakistan and a rich location of Miocene deposits of Lower Siwaliks (Fig. 1). The geographic coordinates of the village are 32°47' 26.4" N, 72° 55' 35.7" E. The fossil fauna of Miocene age of Dhok Bun Ameer Khatoon is quite rich and diverse and keeps in it a complete sequence of faunal assemblage of the Siwaliks. The locality is characterized by colored shale, containing some amount of unweathered igneous minerals, notable feldspar.

The representative fauna of the locality comprises of Artiodactyla (suids, tragulids, giraffids, cervids and bovids) and Perissodactyla (rhinocerose). Crocodilian elements and isolated teeth of *Deinotherium* have also been found from here. Several mammalian groups have been found here like carnivores, artiodactyles, perissodactyles, and several others. Physical and ecological characteristics of the habitat of an animal strongly influence the dietary habits of that animal (Kingston and Harrison, 2007). Most of the Miocene period in Asia (Northern Pakistan, Siwalik sequence) is represented by warm tropical, subtropical forest zones. During that period in Asia; the fauna and flora of Chinji and Dhok Pathan from late Middle Miocene to early Late Miocene was equivalent to the Europe flora and fauna (Bernor, 1984; Barry *et al.,* 1985).

The Late Miocene (9.6-9.2Ma) environment of the Western and Eastern Europe is represented by closed habitats, forested conditions temperate forests dominated by deciduous angiosperms and conifers (Agusti *et al.,* 1999, Fortelius *et al.,* 1996, 2002, 2003a, 2003b) and in central Eurasia dry sclerophyllous forests and woodlands (Palamarev, 1987; Axelrod, 1975; Kovar-Eder *et al.,* 1996, 2006; Suc *et al.,* 1999; Collinson and Hooker, 2003; Kovar-Eder, 2003; Ioakim *et al.,* 2005). The rainy humid environment was responsible for the persistence of the forested environment in Africa.

Wooded conditions may point towards the browsing nature of the mammalian fauna of that age that includes deinotheres and listriodonts (Agusti *et al.,* 1999).

Harris (1975) has discussed the dietary preferences of deinotheres considering their mode of feeding and the type of food they fed on. Deinotheres are considered to be "shearing browsers" with anterior teeth for the purpose of crushing the food and the second and third molars to grind the non-gritty soft vegetation, using lower down turned incisors to strip the bark off (Athanassiou, 2004).

They had strong tusks placed in the end of the mandible, curving downward and backward. For browsing on leaves and tough vegetation they have bi-loph molars. They used to process their food prior to digestion with the help of bi-lophodont brachydont teeth (Cerling *et al.,* 1999). They were browsers, feeding on C3 diet from Early Miocene through the Early Pleistocene (Cerling *et al.,* 1999, Agustí *et al.,* 1999). The browsing habit of deinotheres on C3 plants has been confirmed by molar δ13C enamel values (Cerling *et al.,* 1999, Schoeninger *et al.,* 2003, Kingston and Harrison, 2007). The values of the Carbon, Oxygen isotopic contents exclude any possibility of the use of C4 diet (Cerling *et al.,* 1999).

Listriodon inhabited the whole of Eurasia to the Iberian Peninsula and eastern and central Europe (Made 1996). They were lophodont, browsing on vegetation. Considering the lophodont dentition of Listriodon, Leinders (1978) argued that they were herbivores also concluded by Hunter and Fortelius (1994) considering their dental micro wear.

Micro wear analysis has also indicated that *Listriodon* had a rather uniform diet which indicates a specialization in the browsing of vegetation. Maglio (1973) has described bunolphodonty associated with grinding-shearing mastication and browsing on foliages and fruits or both in herbivores. Pickford and Morales (2003) are of the view that *Listriodon* were browsers. Lengthening of distal limb segments may be interpreted as the adaptation for open habitats (Agustí *et al.,* 1999). In this article we have discussed their same feeding habitat having same pattern in structure while they have greater difference in teeth size.

This research work specifies tooth similarities in two extinct species of *Listriodon* and *Deinotherium* and the main aim was to update the fossil fauna form the lower Siwaliks of Pakistan, but there are many other species form the Potohar plateau of Pakistan which needed to be described on similarity bases to build a chain of links.

Materials and methods

Collection way and material

The primary mean was the surface collection of the *Dorcatherium* remains. Secondly excavation was conducted very carefully at dense concentrations of fossil bones were happen in sandstones by using the chisels, geological hammers, fine needles, hand lenses and brushes. Cotton was use to wrap each specimen for protection during transportation. In laboratory samples were studied for morphological and taxonomic analysis.

Cleaning of fossils

Surplus siliceous solid and dust particles were removed with the help of fine needles and brushes to prepare the specimens for observation. The specimens were carefully washed and cleaned in the Palaeontology laboratory of Zoology Department, GC University, Faisalabad.

Morphological analysis cataloguing and photography

To avoid ambiguity and to study very small morphological characteristics a hand lens was used. Vernier calliper was used to take the measurements in millimetre (mm).

The terminology and measurement of the teeth follow Gentry and Hooker (1988) and Gentry *et al.,* 1999. The catalogue number was assigned as PC-GCUF which represent the collection year (numerator) and serial number (denominator) of that year (e.g. 2012/06). A digital camera (Canon EOS 1100 D) was used to take photograph of specimens and amended hard copies were prepared by using a soft wear (adobe Photoshop).

Results

Systematic Palaeontology

Order: Artiodactyla Owen 1848

Suborder: Suiformes Jaeckel 1911

Superfamily: Suoidea Gray 1821, Cope 1887

Family: Suidae Gray 1821

Subfamily: Listriodontinae Simpson 1945

Genus: *Listriodon* Von Meyer 1846

Type species

Listriodon splendens Von Meyer 1846

Distribution

Listriodon is well known genus of Ngorora formation of Africa, basal middle Miocene deposits of Europe and Chinji formation Siwaliks. (Pilgrim, 1926; Pickford and Morals, 2003; Khan *et al.,* 2005).

Generic Diagnosis

These are small lophodont molars having sharp cutting ends with prefect crests. Many species of this genus having different sized talonid and symphysis (Colbert, 1935).

Listriodon pentapotamiae Falconer *1868*

Type specimen

GSI B 107, a complete right M^2 and fragment of right M^3. Also right and left P^4.

Locality

Khushalghar below Attock, Punjab (Colbert, 1935).

Stratigraphic Range

Lower and middle Siwaliks (Colbert, 1935).

Diagnosis

Sample have resemblance with *Listriodon splendens* of Europe, where as having a solid cingulum in P4, larger talonid on M3 and having shorter and more slender symphysis as compare to European *Listriodon splendens* .

Material

PUPC 94/64, a right upper first molar

Locality

Lava, District Chakwal, Punjab, Pakistan

Stratigraphic range

Lower Siwalik (Chinji formation).

Description

PUPC 94/64 (Fig. 2)

It is a right upper second molar. It is a well preserved shiny rugose tooth with unworn enamel. All the four cones are on the same level of height and intact. The protocone and paracone, and the metacone and hypocone join with each other to form V- shaped lophs deepening in the middle and rising on the sides. The width of the cones is almost equal. A pronounced cingulum frills the anterior as well as posterior faces of the tooth. V-shaped depression is present on the posterior faces of the mesial and the distal lophs of the tooth. The median valley between the lophs is deeper labially while a median ridge slightly elevates from the base more towards the buccal edge.

Order: Proboscidea, Illiger 1811
Suborder: Deinotherioidea, Osborn 1921
Family: Deinotheriidae, Bonaparte 1845
Genus: *Deinotherium,* Kaup 1829

Type Species

Deinotherium giganteum, Kaup 1829

Distribution

The genus appeared in Africa during Lower Miocene (Andrews, 1911). Europe (Kaup, 1829) and South Asia (Pilgrim, 1910). It was on its peak during Lower Pliocene of Europe (Eichwald, 1835). The genus was not found after the Middle Pleistocene and the last surviving form is said to be *Deinotherium hopwoodi* from Olduvai, Tanganyika (Osborn, 1936). The recent most finding from South Asia is in Dhok Pathan region of the Middle Siwalik (Falconer, 1845). Stefanescu (1892) found the specimens from Middle Pliocene of Roumania, Europe.

Generic Diagnosis

Low and flat cranium, anteriorly downturned lower jaw with backwardly directed tusks. Upper tusks absent. Grinding teeth with sharp ridge plates. Premolars only deciduous. All grinders in use at the same time. Brachydont dentition.

Deinotherium pentapotamiae (Lydekker, 1829)

Type Species

Deinotheriun giganteum, Kaup 1829

Type Specimen

A right P^3 and right M^1

Locality

Khushalghar, near Attock, Punjab, Pakistan, (Lydekker, 1876).

Stratigraphic Range

Lower Siwaliks

Diagnosis

Smaller than *D. indicum*, Second upper molar squarish with no transverse elongation. Entrance of transverse valleys not blocked by cingular tubercles. Laterally compressed mandibular ramii.

Known Distribution

The species is found only in Pakistan. The oldest geological record is stated from Bugti Hills of Lower Miocene age (Eames, 1950b). Lydekker (1880) found it in Lakki Hills; Palmer (1924), Huma (2003) and present authors in Chinji.

Material

PUPC 08/118 a right upper second molar.

Locality

Dhok Bun Ameer Khatoon, District Chakwal, Punjab, Pakistan.

Horizon

Lower Siwalik (Chinji Formtion)

Description

PUPC 08/118 (Fig. 2): It is heavily worn and well preserved. It is a biloph molar with a shiny quadrate crown. The grinding surfaces have gone with much exposed dentine on the ridge plates. The wear facets are visible only on the extremities of the lophs with no tapering of the surfaces.

The enamel is thick with 3 mm thickness (Table 1). The proximal loph is wider than the distal one. The posterior loph is concave and forms a sigma curve. A prominent parastyle marks the distal face of the tooth. The transverse valley has gone due to the attritions but shows a sharp slope on the lingual side with a little ridge of the crown.

On the buccal side it shows a depression bounded by the crown of the tooth. Cingulum can be seen on the anterior and posterior faces of the molar but not present on lateral sides. Metaloph has broken post-mortem. Pressure mark is present on the anterior as well as posterior faces of the tooth. Talon ridge is absent on either side of the molar.

Material

PUPC 97/36 (Fig. 2) a left M^3

Locality

Chinji, district Chakwal, the Punjab Province, Pakistan

Horizon

Lower Siwaliks

Description

The specimen under study (PUPC 97/36) is an isolated left third molar of upper jaw. It is well preserved and bilophodont tooth.

It is in an early stage of wear. It is approximately squarish in shape having and anteroposterior length of 73 mm and a transverse width of 65 mm. It has a talon ridge anteriorly as well as posteriorly which along with anterior sloping of the grinding surface of the ridge plates determine it's belonging to the left side of the upper jaw.

It is certainly a last true molar as the second ridge-plates is less wide than the first one and there is no pressure mark at the posterior face of the tooth.

The first ridge plate is less arched than the succeeding one. The first ridge-plate is thick anteroposteriorly at outer and the inner extremities but is narrow in the middle.

The inner sides of both the ridge-plates are more worn and show the expose dentine. From the inner summit of the first ridge-plate on oblique but weak ridge extends posteriorly and outwardly. This ridge is more prominent in second ridge-plate.

Table 1. Comparative Measurements (in mm) of molar teeth ($M_{1\text{-}3}$) referred to *L. pentapotamiae* and *D. pentapotamiae*.

Number	Nature	Position	Length	Width	Height	W/L index	H/Windex
		(L)	(W)	(H)			
PUPC 08/09	molar	M_1	17	13	-	76.4	-
AMNH 19519	molar	M_1	16	12	-	75	-
AMNH 19475	molar	M_1	17	13.5	-	77	-
PUPC 08/09	molar	M_2	22	16	-	72.7	-
AMNH 19519	molar	M_2	19	16	-	84	-
AMNH 19624	molar	M_2	23	18	-	78	-
AMNH 19432	molar	M_2	21	15	-	72	-
PUPC 08/09	molar	M_3	28	16	-	58	-
AMNH 19519	molar	M_3	27.5	18	-	65	-
AMNH 19432	molar	M_3	28	16	-	58	-
AMNH 19625	molar	M_3	28	16	-	58	-
PUPC 08/118	molar	M_2	73	78.85	48.40	108.01	61.38
PUPC 97/36	molar	M^3	73	65	36	89.04	55.38
PUPC 94/64	molar	M^2	18.8	17.5	12.5	93.08	41.43

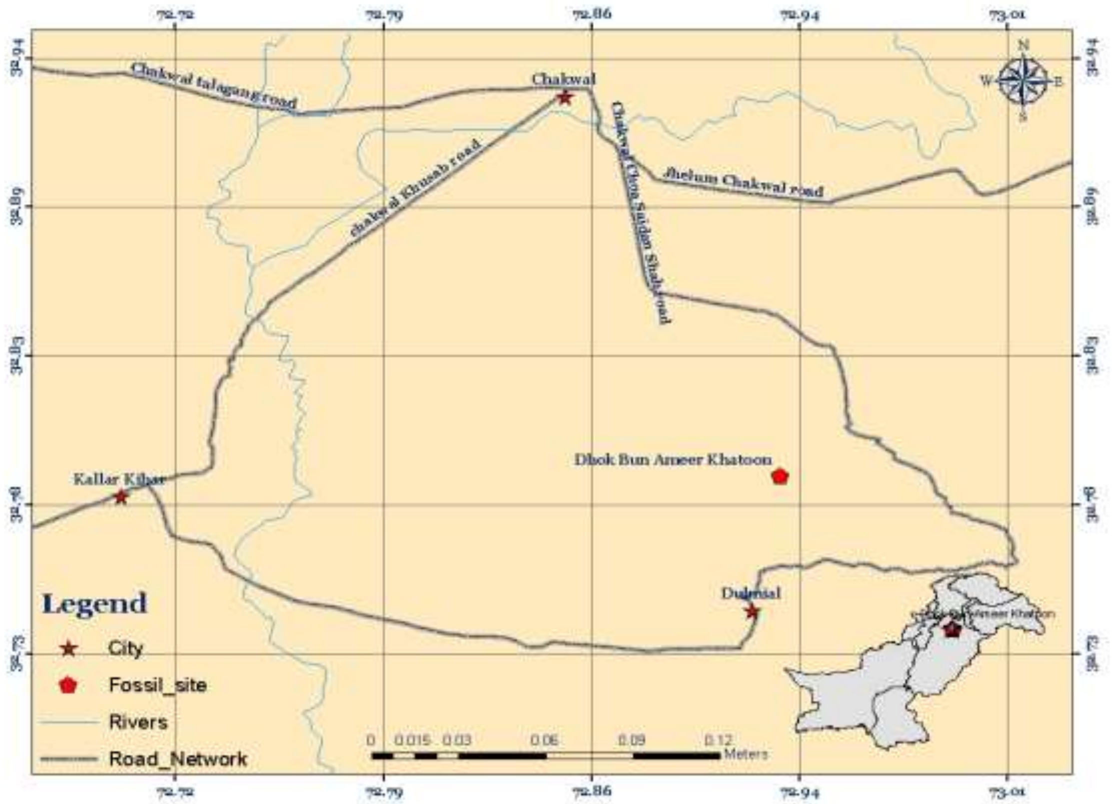

Fig. 1. Map of site (Dhok Bun Ameer Khatoon) from where the fossils were collected.

Fig. 2. *Listriodon pentapotamiae*, PUPC 94/64, right upper second molar (1 A-C); *Deinotherium pentapotamiae*, PUPC 08/118, an isolated right upper M^2 (2 A-C); PUPC 97/36, an isolated left M^3 (3); A- buccal view, B- occlusal view, C- lingual view. Scale bar 10 mm.

Discussion

In Pakistan and India three species of the genus *Deinotherium* are known i.e.

D. pentapotamiae Lydekker

D. orlovii Sahni and Tripathi

D. indicum Falconer

The material under study cannot be referred to the specie *D. indicum* because of the small anteroposterior length of the molars which are relatively much larger in *D. indicum* and absence of cingular tubercles at the extremities of transverse valley which is present in *D. indicum* (Sahni and Tripathi, 1957). The specimen under study (PUPC 97/36) is also differentiated from those of *D. orlovii* which shows additional tubercles (Sahni and Tripathi, 1957).

Regarding anterio-posterior length of teeth the material under study compares very well with the know material of the species *D. pentapotamiae*. The only difference is that the specimen PUPC 97/36 is somewhat larger which could be attributed to their recovery from relatively younger beds. The small size, thin enamel and the absence of cingular tubercles differentiate the specimen DP^4 PUPC 84/95 from *D.indicum* Falconer and *D. orlovii* Sahni and Tripathi, and suggest its inclusion in the species *D. pentapotamiae*. The specimen under study is much smaller than the DP^4 of *D. indicum*. The major difference between the two is that in the *D.indicum* the last ridge plate is much smaller than the first one while in the latter they are equally wider. The genus *Deinotherium* is unique in having down curved lower tusks (Bergounioux and Crouzel, 1962; Tobien, 1988; Shoshani *et al.,* 1996; Huttunen, 2002a) and lophodont dentition. They share characteristic dentition with suids, elephants, and some metatheres (Khan *et al.,* 2005; Samiullah, 2011).

The specimen PUPC 08/118 is too small to be referred to the *D. giganteum*. Thus the species described from the sub-continent *D. pentapotamiae* Lydekker, *D. orlovii* Sahni and Tripathi, and *D. indicum* Falconer are worth to be compared. Regarding the size of the material described here, the specimen is comparatively too small to be taxonomically eligible to group it with *D. indicum*.

The absence of the tubercles at the extremities of the transverse valleys again excludes the possibility of *D. indicum* and *D. orlovii* shows additional tubercles as described by Sahni and Tripathi (1957) which are absent in our specimen. Thus the specimen qualifies to be specified as *D. pentapotamiae*. As the specimen is biloph it could be a second or third molar. The pressure marks on the anterior and posterior faces also exclude the possibility of the last molar. The absence of talon ridge, along with above mentioned features mark the positioning as M^2. The quadrate shape of the tooth and the convex crown face are deciding features that tooth belong to upper jaw. The earliest type of elephant known to us as little one larger than a pig, as misunderstood by Cuvier (1798) and of a very different forcing its head under the banks of rivers for vegetation, and roots upon which it lived. The necessity of teeth for reaching and dislodging the roots and vegetation caused the front incisor teeth to develop in time into tusks. In earliest form of elephant tusks were in the upper and lower jaws. *Deinotherium* especially developed its lower tusks, which were turned sharply downward under the lower jaw, and were doubtless used for grubbing in the earth (Morewood-Dowsett, 1939).

G. Theodorou *et al.,* 2003 has described *Deinotherium* in the listing of the herbivores of Greece. The morphology of the deinotheriid cheek teeth, which are lophodont, brachyodont and simple in shape, indicate that the deinotheres were primarily folivores, consumers of soft, non-abrasive vegetation. This feeding adaptation commonly implies a forested environment (Athanassiou, 2004). The chisel shape and transverse ridges of tooth are the common features in both groups described here only the size of the tooth is discreminating feature among them. *Deinotherium* specimen is charcaterized by the two transverse lophs separated by a transverse valley, anterior loph convex while posterior loph curving inward. In *Listriodon* the lophs are bicuspid in the upper and lower molars that are linked by a thin crest with straight facets all over the structure. On the third molar of the *Listriodon* a prominent talon ridge is present. Similarity among the tooth structure of both the groups emphasizes on the similar mode of feeding of them.

Lophodont dentition with curved cutting edges and transverse lophs are common features in both the groups. The large protocone and hypocone are separated by a narrow V-shaped transverse valley that opens on the lingual side. The protoloph and metaloph are formed by protocone and paracone, and hypocone and metacone connected by sharp, anteriorly convex crests. The protoloph and metaloph show mesially oriented small, vertical wear facets. Broad occlusal surfaces are provided by the antero-posterior expansion of the cusps and lophs.

Conclusions

The studied specimens indicates that the diet of the two distinctly separate groups of mammals might remain the same and they had to rely on the same food present in their environment. The habits of feeding and also the major diet components of both groups were similar that is responsible for the similarity of their dental morphology i.e. only difference is of size. Due to same diet adaptation there is striking similarity among the molars of *Listriodon* and *Deinotherium.*

Abbreviations

M, molar; L, maximum preserved length; mm, millimeter; W, maximum preserved width; W/L, width length ratio; GCS, Government College of Science (Institutional abbreviation).

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