New Fossil Locality in the Middle Miocene of Lava from the Chinji Formation of the Lower Siwaliks, Pakistan

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Abstract. – The middle Miocene locality in the fluvial deposits was discovered in the south-eastern part of Lava village (Chakwal, northern Pakistan). The mammalian assemblage originating from this locality is described. The faunal association consists of rhinocerotids Gaindatherium browni and Brachypotherium fatehjangense, a suid Listriodon pentapotamiae, a caprine Kubanotragus sp., a bovid Helicoportax cf. tragelaphoides, a tragulid Dorcatherium, a giraffid Giraffokeryx punjabiensis and a proboscidean Deinotherium cf. pentapotamiae. The assemblage indicates the locality is middle Miocene in age (ca. 14–11 Ma) and it displays regional characteristics of the Chinji Formation of the Lower Siwaliks, Pakistan.

Key Words: Lava, Middle Miocene, Chinji Formation, Lower Siwaliks, vertebrates.

INTRODUCTION

A fossil locality has been found near Lava village which is 14 km east of Rawalpindi - Mianwali highway. The fossil site is 11 km south east of the village Lava, district Chakwal (Punjab, Pakistan) and east of Dera Rehmatay Aali along the road opposite to Kas Badri from which we obtained fossils in a very dense concentration over a small area (Fig. 1). The fossils are fragmentary mostly postcranial than the cranial ones. The weathering cracks, abrasion marks and bite marks are frequently noted on the specimens. The site is highly fossiliferous and seems to be exposed since long time. Owing to the long exposure fragmentary bones and enamels are present all over the site. Nearly every sandstone has some embedded vertebrate remains. The locality is characterized by sandstone and reddish shale which is characteristic of Chinji Formation of the Siwaliks (Fig. 1). The Formation consists primarily of grey, sandy to muddy fluvial deposits (Barry et al., 2002).

The section consists of shales, siltstones and sandstones. The fluvial sediments display large lateral and vertical variations in their degree of cementation. A few cheek teeth fragments, some undeterminable tooth splinters and some fragmentary postcranial bones are found in the section. This paper presents the study of some new vertebrate fossil material from the discovered locality of the village Lava collected in 2007 – 2009 by the ‘team’ formed by the Zoology Department of Punjab University, Lahore and the Zoology Department of GC University, Faisalabad, Punjab, Pakistan.

The specimens were catalogued and given a number comprising year of collection and a serial catalogue number (e.g. 07/104). Various measurements of the studied specimens in millimeters were taken with the help of metric vernier caliper. Tooth length and width were measured at occlusal level. Heights were measured on the mesostyle of the upper molar, the metastylid of the lower molar and the protoconid of the lower premolar. The upper case letter denotes upper dentition and the lower case letter denotes lower dentition. Measurements given for teeth are occlusal length and occlusal width. All the described fossils are housed in the Palaeontological Collection of the Punjab University, Lahore (PUPC) and the Palaeontological Collection of GC University, Faisalabad (PC-GCUF).
Abbreviations
PUPC, Punjab University Paleontological Collection; PC-GCUF, Palaeontological Collection of GC University, Faisalabad; C, canine; d, deciduous; H, height; I, incisor; L, largest length; l, left; M, molar; Ma, million years; MN, Mein Zones; P, premolar; r, right; W, width.

SYSTEMATIC ACCOUNT
Order Perissodactyla Owen, 1848
Family Rhinocerotidae Gray, 1825
Subfamily Rhinocerotinae Gray, 1821
Tribe Rhinocerotini Gray, 1821
Subtribe Rhinocerotina Owen, 1845
Genus GAINDATHERIUM Colbert, 1934

Gaindatherium browni Colbert, 1934

Referred material
PUPC 07/101 – rM1; PUPC 07/102 – rM2.

Description
PUPC 02/101 is a well preserved first molar and slightly worn (Fig. 4A). PUPC 02/102 is complete, newly erupted and excellently preserved second molar (Fig. 4B). The median valley is filled with matrix in the second molar. The enamel is rugose and the traces of the cement are present all around the molars. The anterior cingulum is well developed and serrated. The posterior cingulum is limited around the postfossette. There is no cingulum at the lingual and buccal face of the tooth. The postfossette is deep and funnel shaped. The median valley is wide open and the protocone and the hypocone are far apart from each other. There is no trace of antecrochet or crista. However a delicate crochet extends into the median valley from the apex of the metaloph. A weakly developed mesostyle is present. The parastyle and the paracone fold are well developed and prominent. The metastyle is also well developed and the metacone rib is also weakly developed. The protoloph and the metaloph are oriented obliquely to the ectoloph. The concave ectoloph is present behind the paracone fold. A convexity corresponding to the mesostyle is also present. The comparative measurements of all the specimens are provided in Table I.

Table I.- Comparative measurements (cm) of the cheek teeth of G. browni.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>G. browni</th>
<th>G. browni</th>
<th>G. browni</th>
<th>G. vidali</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>present</td>
<td>Heissig</td>
<td>Colbert</td>
<td>Heissig</td>
</tr>
<tr>
<td></td>
<td>collection</td>
<td>(1972)</td>
<td>(1934)</td>
<td>(1972)</td>
</tr>
<tr>
<td>PUPC</td>
<td>L</td>
<td>44.5</td>
<td>43.0</td>
<td>40.0</td>
</tr>
<tr>
<td>07/101 –</td>
<td>W</td>
<td>51.0</td>
<td>53.0</td>
<td>51.0</td>
</tr>
<tr>
<td>rM1</td>
<td>H</td>
<td>45.0</td>
<td>46.0</td>
<td>X</td>
</tr>
<tr>
<td>PUPC</td>
<td>L</td>
<td>45.4</td>
<td>46.0</td>
<td>42.0</td>
</tr>
<tr>
<td>07/102 –</td>
<td>W</td>
<td>50.5</td>
<td>52.0</td>
<td>52.0</td>
</tr>
<tr>
<td>rM2</td>
<td>H</td>
<td>42.0</td>
<td>42.0</td>
<td>-</td>
</tr>
</tbody>
</table>

Discussion
Colbert (1934) described genus Gaindatherium with G. browni from the Chinji locality.
Formation of the Lower Siwaliks. Heissig (1972) worked on the Siwalik rhinoceros and described two successive species of Gaimdatherium G. browni and G. vidali from the Chinji Formation and from the Nagri Formation of the Siwaliks, respectively. The upper molars show the features of the diagnosis; a simple crochet which is strongly angled against the metaloph, the paracone is narrow and backward, not clearly demarcated, and the parastyle and parastyle folds are strongly developed. Features of the molars, like presence of a stronger anterior cingulum and a protocone fold, presence of a strong metacone rib, are the characteristics of the G. browni. The inner cingulum in G. vidali is weaker than G. browni. The paracone and the metacone are also weakly demarcated. The dimensions of the present material are closer to G. browni and it differs from G. vidali in crown morphology and size (Table I, Fig. 2).

![Fig. 2. Size variation of G. browni and G. vidali.](image)

Subtribe Teleoceratina Hay, 1902
Genus BRACHYPOTHERIUM Roger, 1904

Brachypotherium fatehjangense Pilgrim, 1910

Referred material

Description
PUPC 07/104 is broken on the posterior side and fairly identical to the second premolar. It displays a reduced paraconid and open posterior valley. The anterior cingulum is low and asymmetrical. Its height is important on the posterior side and decreases anteriorly (Fig. 4C).

PUPC 07/105 and PUPC 07/109 are partially broken right upper second premolars (Fig. 4D,E).

The premolars are characterized by the open median valley, antecrochet is moderately present, ectoloph is broken and the metaloph is complete. The premolars are in late wear. The cingulum and crista are absent. The crochet is prominently present. The protocone is slightly extended. The posterior fossette is also present.

PUPC 07/106 is in middle wear with broken ectoloph (Fig. 4F). The protocone is slightly extended as compared to the hypocone. The metaloph is incomplete and the protoloph has broken away. The protocone is a strong lingual-anterior pillar, well separated from the hypocone pillar due to the presence of a medisinus. The crista and the crochet are absent. The parastyle has broken off.

Discussion
A reduced paraconid in the second lower premolar is an autapomorphy of Brachypotherium (Antoine, 2002). The morphological features are consistent with B. fatehjangense, known from the early Miocene to the late Miocene in South Asia (Heissig, 1972; Antoine and Welcomme, 2000; Welcomme et al., 2001). An open posterior valley, low and asymmetrical anterior cingulum, the posterior cingulum extends until the posterior groove of the ectolophid are the characteristics correspond to B. fatehjangense. All these characters are observed in the studied material, which clearly identify it to B. fatehjangense. Morpho-metrically, the specimen resembles with specimens originating from the middle Miocene Chinji Formation of the Lower Siwaliks of Pakistan and Myanmar (Table II).
tooth is almost straight. The distal edge of the tooth forms a second cutting edge at right angle to the first one. The incisor is mesio-distally compressed posteriorly. There is a prominent centrally placed lingual pillar. The distal edge protrudes slightly forming a shallow scoop like basin between the central pillar and distal edge of the crown.

PC-GCUF 09/27 is a lower canine with a long permanently growing single root (Fig. 4H). The canine emerges almost horizontally and sweeps outwards and eventually backwards with scrofic cross section. The canine root is long and circular. The enamel is present on the lingual and labial surfaces but it does not extend onto the root. There is a prominent wear facet anteriorly caused by abrasion against the upper canine.

PUPC 07/111 is four cusped lophodont tooth (Fig. 4I). The tooth is molarized with well developed anterior and posterior cingula. The premolar has prominent innenhugel which is closely fused to the main cusp and rectangular occlusal outline. Anteriorly the anterior crested of the main cusped is swollen and descends rapidly towards a well developed but low cingulum. Distally there is a prominent talonid joined lingually and labially by a swollen cingulum. The distal accessory cusplet is two thirds height of the crown. The distal cingulum fades into the labial and lingual surfaces of the crown.

**Discussion**

The lower incisor shows the typical morphology of listrodonts with stepped edge. The long permanently growing root is present in a male lower canine of *L. pentapotamiae* (Pickford, 1988).
Suborder Ruminantia Scopoli, 1777
Family Tragulidae Milne-Edwards, 1864
Genus DORCATHERIUM Kaup, 1833
Dorcatherium sp.

Referred material
PUPC 07/112 – p4.

Description
The premolar is triangular in lateral view and increase in length from front to back. The tooth is somewhat elongated (Fig. 6A). The premolar has a strong protoconid linked by a straight longitudinal crest to a small, mesio-lingually centrally located paraconid. The protoconid crest is slightly curved lingually, and joins the more lingually situated paraconid. The hypoconid is situated at the rear of the tooth. The hypoconid is weaker and lower than the protoconid. The posterior side of the hypoconid forming a well marked transverse spur delimits a small, lingually open rounded basin. A very tiny transverse entostylid present at the posterior edge of the crown.

Discussion
The morphology and the orientation of the occlusal outline of the fourth premolar are close to Dorcatherium and differ from those of bovids (Farooq et al., 2008). The size index of the premolar is close to Dorcatherium majus (Table IV). Unfortunately, a mandibular ramus with molars missed on the way from Lava locality to village Lava. The lower molars had well developed Dorcatherium folds. The molars were rectangular in shape and bunoselodont. Enamel slightly wrinkled. The morphology of the teeth suggests that they belonged to the Dorcatherium. The lack of material does not allow us to assign species for the remains.

Table IV.- Comparative dental measurements (mm) of fourth lower premolars in Dorcatherium. Comparative material is taken from Farooq et al. (2008). * studied specimen.

<table>
<thead>
<tr>
<th>p4</th>
<th>PUPC 86/2</th>
<th>PUPC 86/5</th>
<th>AMNH 19524</th>
<th>GSI B593</th>
<th>* PUPC 07/112</th>
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<tr>
<td>L</td>
<td>13.3</td>
<td>13.1</td>
<td>14.5</td>
<td>17.3</td>
<td>16.0</td>
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<td>6.0</td>
<td>5.7</td>
<td>5.0</td>
<td>6.2</td>
<td>6.3</td>
</tr>
</tbody>
</table>

Family Bovidae Gray, 1821
Tribe Boselaphini Knottnerus-Meyer, 1907
Genus HELICOPORTAX Pilgrim, 1937

Helicoportax cf. tragelaphoides

Referred material
PUPC 07/114 – M1; PUPC 09/55 – lp3-m1.

Description
The molar is quadrate. The median ribs are present and the posterior median rib is weaker than the anterior one. The entostyle like basal tubercle is present. The enamel is rugose and has prominent striae (Fig. 6B). The molar has pronounced neck at the base of the crown. The molar has divergent styles and strong buccal folds. The lower molars are narrow crowned and also hypsodont (Fig. 6C). They have pronounced neck at the base like upper dentition. These are in early wear. The p3 is long with separated parastylid-paraconid and entoconid-entostylid. The p4 is also long with an anteroposteriorly expanded metaconid and open lingual valleys. The tooth is pretty molariform. The lower molar has weak lingual ribs and anterior transverse flange. The median basal pillar is present.

Discussion
The specimens with pronounced neck, weak median ribs, divergent styles and open second lingual valley are represented by one species. The specimens are differentiated from the other bovids of Lava by the pronounced neck. The crown pronounced neck was present in Selenoportax and Helicoportax (Pilgrim, 1937, 1939). The Selenoportax was a large sized Siwalik boselaphine
of the upper Miocene (Khan et al., 2007; Khan, 2008). The Lava specimens is smaller than the Selenoportax and correspond very well with it dental morphology and size to Helicoportax. The preserved specimens were not well enough to allow identifying of a species exactly. Nevertheless, the metrical values of the specimens are close to H. tragelaphoides and Helicoportax cf. tragelaphoides is assigned for the specimens (Table V, Fig. 5).
Table V.- Comparative dental measurements (mm) of *Helicoportax*. Comparative material is taken from Pilgrim (1937, 1939). * studied specimens.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Specimen</th>
<th>Length</th>
<th>Width</th>
</tr>
</thead>
<tbody>
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<td>H. sp</td>
<td>*PUPC 07/114 – M1</td>
<td>17</td>
<td>17</td>
</tr>
<tr>
<td>H. cf. tragelaphoides</td>
<td>GSI 822-M1</td>
<td>15</td>
<td>15.5</td>
</tr>
<tr>
<td>H. tragelaphoides</td>
<td>AMNH 29909 – M1</td>
<td>17</td>
<td>17</td>
</tr>
<tr>
<td>H. tragelaphoides</td>
<td>AMNH 29945 – M1</td>
<td>15</td>
<td>15</td>
</tr>
<tr>
<td>H. praecox</td>
<td>AMNH 19476 – M1</td>
<td>12.5</td>
<td>15.5</td>
</tr>
<tr>
<td>H. praecox</td>
<td>AMNH 19998 – M1</td>
<td>13</td>
<td>13</td>
</tr>
<tr>
<td>H. praecox</td>
<td>AMNH 29867 – M1</td>
<td>13</td>
<td>13</td>
</tr>
<tr>
<td>H. sp</td>
<td>*PUPC 09/55 – p3</td>
<td>15</td>
<td>7</td>
</tr>
<tr>
<td>H. sp</td>
<td>*PUPC 09/55 – p4</td>
<td>13</td>
<td>8</td>
</tr>
<tr>
<td>H. sp</td>
<td>*PUPC 09/55 – m1</td>
<td>14</td>
<td>10</td>
</tr>
<tr>
<td>H. praecox</td>
<td>AMNH 29858 – p3</td>
<td>9.5</td>
<td>6.5</td>
</tr>
<tr>
<td>H. praecox</td>
<td>AMNH 29855 – m1</td>
<td>13.5</td>
<td>8.5</td>
</tr>
<tr>
<td>H. cf. tragelaphoides</td>
<td>GSI 821-m1</td>
<td>13</td>
<td>9</td>
</tr>
<tr>
<td>H. cf. tragelaphoides</td>
<td>GSI 821-p3</td>
<td>13</td>
<td>11</td>
</tr>
</tbody>
</table>

Fig. 5. Size variation in the Siwalik *Helicoportax* (*H. tragelaphoides* and *H. praecox*).  

Subfamily Caprinae Gray, 1821  
Genus *KUBANOTRAGUS* GABUNIA, 1973  
*Kubanotragus* sp.

**Referred material**  
PUPC 07/115 – rp3; PUPC 07/116 – rp4; PUPC 07/117 – rM1; PUPC 09/59 – lm1; PUPC 07/118 – lm3; PUPC 09/56 – lm3; PUPC 09/57 – lm3.

**Description**  
The material consists of isolated teeth. The p3 has the paraconid well separated from the parastylid (Fig. 6E). The premolar is in early wear, brachydont, rugose and molarized. The metaconid extend forwards meeting the base of the paraconid. The crest joins to the metaconid and incorporates the entoconid. The entoconid is independent from the metaconid in early wear. A well developed furrow separates the hypoconid from the strong protoconid on the buccal side. The p4 is highly molariform (Fig. 6F). The metaconid is expanded lingually. The parastrylid is thinner than in p3. The anterior lobe is large and closed lingually. The protoconid is connected to the hypoconid and tends to fuse with the entoconid lingually. The trigonid is distinguished by a furrow. The first molar is partially broken, simple with finely rippled enamel. The ectostylid and anterior fold are very weak but a well developed metastylid is present. The upper molar has well developed styles and ribs but it has a weakly develop entostyle. The protocone is angular and slightly constricted lingually (Fig. 6G). A cingulum is weakly developed. The hypoconulid of the third molar is elliptical forming a complete loop (Fig. 6H).
Discussion

The large sized brachydont teeth with sculpture enamel make their inclusion to giraffids (Colbert, 1935). The Siwalik giraffids are divided into two groups, one comprises the large forms of the upper Miocene and the other one comprises the small forms of the middle Miocene (Akhtar and Sarwar, 1987). The small sized Siwalik forms are
**Table VI.- Comparative dental measurements (mm) of** \(G.\) *punjabiensis.* *studied specimens.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Specimen</th>
<th>Length</th>
<th>Width</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>G. punjabiensis</em></td>
<td>PUPC 07/115 – p3</td>
<td>25</td>
<td>14</td>
</tr>
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<td><em>G. punjabiensis</em></td>
<td>PUPC 07/116 – p4</td>
<td>23.6</td>
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<td>PUPC 07/117 – M1</td>
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<td>28</td>
</tr>
<tr>
<td><em>G. punjabiensis</em></td>
<td>PUPC 07/118 – m3</td>
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</tr>
<tr>
<td><em>G. punjabiensis</em></td>
<td>PUPC 09/56 – m3</td>
<td>26</td>
<td>cf. 13</td>
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<tr>
<td><em>G. punjabiensis</em></td>
<td>PUPC 09/57 – m3</td>
<td>36</td>
<td>17</td>
</tr>
<tr>
<td><em>G. cf. punjabiensis</em> (Geraads et al., 1995)</td>
<td>m3</td>
<td>34</td>
<td>17</td>
</tr>
<tr>
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<td>p4</td>
<td>22.5</td>
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<tr>
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<tr>
<td><em>G. punjabiensis</em> (Bhatti, 2005)</td>
<td>PUPC 02/12 – m3</td>
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<td><em>G. punjabiensis</em> (Bhatti, 2005)</td>
<td>PUPC 02/19 – m3</td>
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<td>PUPC 02/06 – p4</td>
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<td><em>G. punjabiensis</em> (Colbert, 1935)</td>
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<td><em>G. punjabiensis</em> (Colbert, 1935)</td>
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<td>12</td>
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<td>AMNH 19587 – m3</td>
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<td><em>G. punjabiensis</em> (Colbert, 1935)</td>
<td>AMNH 19472 – M1</td>
<td>23</td>
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**Order Proboscidea Illiger, 1811**  
**Family Deinotheriidae Bonaparte, 1845**  
**Genus DEINOTHERIUM Kaup, 1829**

**Deinotherium cf. pentapotamiae**

**Referred material**  
PC-GCUF 09/29 – m1 (length, 26; width I ridge plate, 17; width II ridge plate 20).

**Description**  
The tooth is complete, isolated, unworn, brachydont and excellently preserved. The tooth is bilophodont with the contact facets (Fig. 6I). The crown of the tooth is elongated antero-posteriorly. The tubercles are present anterior to the first ridge plate. The posterior ridge plate is larger transversely than the anterior one. The ridge plates are concave anteriorly and convex posteriorly. The transverse valley between the first and the second ridge plate does not have any cingular tubercle. The cingulum surrounds the tooth anteriorly, buccally and posteriorly but it is prominent posteriorly where it forms a talon ridge enclosing a shallow valley.

**Discussion**  
The tooth is bilophodont, typically the family Deinotheriidae. The true molar in Deinotherium, is always bilophodont (Sarwar, 1977). Three species of Deinotherium *D. pentapotamiae, D. orlovii* and *D. indicum* are recognized in the Siwaliks (Sarwar, 1977). *D. orlovii* and *D. indicum* are comparatively larger than *D. pentapotamiae*. The studied molar is
small in size and can be assigned *D. pentapotamiae*. Nevertheless, differences in the dentition are present but are generally of minor nature, which renders specific identification. Therefore, the specific identification upon isolated teeth is a matter of some uncertainty.

**BIOSTRATIGRAPHY AND CONCLUSIONS**

Eight mammalian taxa have been recognized from the locality exposed in the south-eastern of village Lava, Jhelum, northern Pakistan. The fauna mainly consists of ruminants and rhinos, but the other groups are rare. The faunal list may be compared with the other middle Miocene Siwalik localities.

*Brachyopotherium fatehjangense* is a common species of the Siwalik middle Miocene (Heissig, 1972; Chavasseau *et al.*, 2006). *Gaindatherium browni* was defined in the Chinji Formation and its stratigraphic range is late middle Miocene to early upper Miocene (Heissig, 1972; Colbert, 1935). The dates of occurrence for the deinotherium taxa suggest the Kamlial and the Chinji formations (ca. 18 – 14 Ma) in the Siwaliks (Tassy, 1983; Sarwar, 1977). *Deinotherium pentapotamiae* was found in the middle Miocene of the Lower Siwaliks (Dhem, 1963; Sarwar, 1977). In the Chinji strata *Listriodon pentapotamiae* is the most common suid (Pickford, 1988). Several Lower Siwalik localities of the Chinji Formation exhibit the presence of *Listriodon pentapotamiae* and the species is widely distributed in the Middle Miocene (Pickford, 1988; Pickford and Morales, 2003). Highly lophodonts *Listriodon pentapotamiae* is abundant in the Chinji succession and deposits of the similar age elsewhere in the Potwar Plateau (Pickford and Morales, 2003).

The Palaeotraginae is documented sporadically in the Chinji Formation of the Lower Siwaliks (Colbert, 1934; Bhatti *et al.*, 2007). *Giraffokeryx punjabiensis* has already been mentioned several localities of the late Middle Miocene age (Bhatti, 2005), occupying a wide territory from Western Europe to India (Bohlin, 1926; Bosscha-Erdrink, 1977; Gentry *et al.*, 1999; NOW database 2003). The *Deinotherium pentapotamiae* and *Listriodon pentapotamiae* are characteristic markers of the Chinji Formation (14 – 11.2 Ma). *Helicoportax* is also represented of the upper Chinji Formation (Pilgrim, 1937, 1939).

The long lasting and wide spread *Listriodon pentapotamiae* in the Lava locality together with *Giraffokeryx punjabiensis, Gaindatherium browni, Brachyoptherium fatehjangense, Deinotherium pentapotamiae,* and *Dorcatherium* sp. indicates a middle Miocene age of the Lava locality. The fauna is in favor of a late Middle Miocene age because the comparison of the material with several representatives of the fauna indicates a middle Miocene age (Pilgrim, 1939, 1937; Thomas, 1984; Heissig, 1972; Pickford, 1988). The dental characters of the Lava material indicate closer affinities to the middle Miocene forms of the species, suggesting a similar age for the locality. In combination with the knowledge of the *Dorcatherium, Gaindatherium browni* and *Brachyoptherium fatehjangense* temporal distribution in the Siwaliks, it is likely that the site is middle Miocene in age. The taxa of the site indicate a time range that overlaps with the species in the Chinji Formation correspond to MN6 and MN7/8 (Heissig, 1972; Colbert, 1935; Farooq, 2006; Pickford and Morales, 2003). A similar vertebrate community is present in the Chinji succession of the Lower Siwaliks (Heissig, 1972; Pickford, 1988; Pilgrim, 1937, 1939; Colbert, 1935; Sarwar, 1977).

Ecological implications are less ambiguous. Lithofacies suggest a fluvial depositional environment. *Brachyoptherium* has often been considered a marsh and lake dweller (Geraads and Sarac, 2003). *Deinotherium* indicates a forested habitat (Kay and Heissig, 2001). *Listriodon* seems to be a browser by judging from its dentition (Pickford, 1988). The selenodonty of the ruminants (*Helicoportax, Giraffokeryx, Dorcatherium*) in the locality may be interpreted for fibrous food which may have been the swamp vegetation due to the depositional environment (Janis *et al.*, 2002). *Dorcatherium* is rather indicative of swampy-paludal habitats (Köhler, 1993; Rössner and Mörs, 2001). This association points a wooded lake margin, surrounded by a more steppe or savannah like landscape.
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