Early Pliocene Cervids (Artiodactyla-Mammalia) from the Siwaliks of Pakistan

Pakistan’in Siwaliks bölgesindeki Erken Pliyosen Cervidleri (Artiodactyla-Mammalia)

Abdul GHAFFAR 1, *Muhammad Akbar KHAN2, Muhammad AKHTAR3
1Department of Meteorology, COMSATS Institute of Information Technology (CIIT), Islamabad, PAKISTAN
2Department of Zoology, GC University, Faisalabad, PAKISTAN
3Department of Zoology, University of the Punjab, Quaid-i-Azam Campus, Lahore, PAKISTAN

ABSTRACT

In this study, Cervid material from different sites of the two well known fossil localities of Pakistan (i) Dhok Pathan (Chakwal district) and (ii) Hasnot (Jhelum district) is identified, described and discussed. The material represents four cervid species Rucervus cf. simplicidens, Cervus cf. triplidens, C. cf. sivalensis and C. cf. rewati. The fossil remains described here reveal the evidences of Early Pliocene cervids from the Siwaliks continental deposits.

Key Words: Cervus, Dhok Pathan, Early Pliocene, Hasnot, Rucervus, Siwaliks.

ÖZ

Bu çalışmada, Pakistan’in (i) Dhok Pathan (Chakwal bölgesinde) ve (ii) Hasnot (Jhelum bölgesinde) adlı ve iyi bilinen iki fosil alanında derlenen Cervid malzemesi ayırtlanmış, tanımlanmış ve tartışılmıştır. Bu malzeme; Rucervus cf. simplicidens, Cervus cf. triplidens, C. cf. sivalensis ve C. cf. rewati omak üzere dört cervid türünü temsil etmektedir. Bu çalışmada tanımlanan fosil kalıntılar, Siwaliks kıtasal çökellerinde gelmiş Erken Pliyosen cervidlerinin varlığını göstermektedir.

Anahtar Kelimeler: Cervus, Dhok Pathan, Erken Pliyosen, Hasnot, Rucervus, Siwaliks.
INTRODUCTION

The cervids are characterized by the presence of antlers and prominent lacrimal depressions anterior to the eyes that are occupied by the pre-orbital glands in the living animals (Gentry et al., 1999; Gentry, 2000). They appeared in the Siwalik sequence of Indo-Pakistan during Plio–Pleistocene times (Barry and Flynn, 1989; Barry et al., 2002; 1982; Van Der Made, 1999) and remained poorly known. Several cervid species are identified in the Neogene of the Siwaliks (Lydekker, 1876, 1884; Brown, 1926; Matthew, 1929; Colbert, 1935; Azzaroli, 1954). The number of species, taxonomy and validity, as well as the stratigraphic range of these species in the Siwaliks have already been considered as exaggerated (Arif et al., 1991a; Arif and Raza, 1991; Akhtar et al., 1999) and needs precise paleobiogeographic and biochronologic studies. The aim of this paper is the description of new fossil remains of poorly known cervids from the Early Pliocene (upper Dhok Pathan Formation) of the Siwaliks of Pakistan. Regional differentiation of ruminants became more intense during the latest Miocene-Pliocene; therefore their territories were expanded from those of their evolutionary origins during the time in question (Fortelius et al., 2002; Gentry, 1970).

The recovered fossils material came from the localities of the Dhok Pathan (Lat. 33° 33′ 32.09 N: Long. 73° 9′ 24.56 E) and the Hasnot (Lat. 32° 49′ 27.89 N: Long. 73° 07′ 52.68 E). The Dhok Pathan fossil site (Figure 1) is situated at 65 km NE from the Chakwal city and is considered as extremely rich in fossils (Barry et al., 2002). The Hasnot village is situated at about 54 km west of

Figure 1. Map of Pakistan (inset) with an enlargement of the studied areas of the Hasnot, from Jhelum and the Dhok Pathan from Chakwal, Punjab, Pakistan.

Şekil 1. Pakistan haritası ile Chakwal, Punjab’i’ taki Dhok Patham ve Jehlum’da’ nı Hasnot (Pakistan) çalışma alanlarının büyültümüş haritaları.
the Jhelum city in the Potwar Plateau of northern Pakistan (see Figure 1), surrounded by extensive Neogene freshwater sedimentary rocks. These two fossil sites represent lateral facies associations within the fine grained fossil-bearing floodplain deposits that are characteristic of fluvial depositional environment (Barry et al., 2002; Barry and Flynn, 1989; Wills and Behrensmeyer, 1995; Behrensmeyer et al., 1995).

Lithostratigraphically, the sediments belong to the upper Dhok Pathan Formation (Middle Siwaliks equivalent to European Early Ruscinian), which is characterized by sandstones with alternate clays orange brown in color and scattered conglomerates in the lower part and conglomerate with sandstone and clays in the upper part (Pilbeam et al., 1977; Johnson et al., 1982; Barry et al., 1982; Cheema et al., 1977). This formation has widespread distribution in Chakwal and Jhelum districts (study areas). The upper Dhok Pathan Formation is remarkable for its rich hipparionine assemblages and numerous artiodactyls. These faunas indicate an Early to Middle Pliocene age. According to Dickinson et al. (2002), an unconformity is present close to the Miocene – Pliocene boundary. This unconformity is angular (generally $<1$–$5^\circ$ angularity) with the underlying Miocene units having been deformed and eroded prior to the deposition of the Pliocene succession. The Miocene-Pliocene boundary therefore represents an interval of significant regional uplift in the Siwalik continental deposits.

The fossils described in this study, are housed at Abu Bakr Fossil Display and Research Centre, University of the Punjab, Lahore, Pakistan and were collected from the Early Pliocene of Dhok Pathan Formation (5.3 – 3.5Ma) (Barry et al., 1980, 1982, 1985, 2002, 2005; Pilbeam et al., 1977). The material thus described here extends the range of this family to Early Pliocene (Middle Siwaliks) instead of Late Pliocene-Pleistocene (Upper Siwaliks).

**ORIGIN OF THE CERVIDS**

Cervids appeared in Oligocene with small sized forms lacking antlers. Early small cervids, e.g., *Eumeryx* and *Iberomeryx*, appeared in the Late Oligocene sediments of Central Asia from where they dispersed to Europe and North America, most probably in the Early Miocene (Savage and Russel, 1983; Romer, 1974). With the origin of antlered cervids (*Procervulus*) in the late Early Miocene (MN3), a second radiation within the Ruminantia started and these ruminants became a major component in fossil faunas. Early to Middle Miocene cervids show great dental and skeletal similarities to their moschid ancestors. The dentition of these early cervids is generally comparable with those of Moschidae with a most advanced brachydont cervoid dentition (Gentry et al., 1999). The most outstanding and typifying character among cervids except *Hydropotes* is the possession of antlers in males (Janis and Scott, 1987). The double lacrimal aperture, a lacrimal pit and anterior vacuity "pre-maxillary fossa" are also present in Moschidae and Palaeomerycidae.

It is supposed that red deer (*Cervus elaphus*) originated in Asia and migrated to Europe. This can be seen by close similarity in dentition of conserved moschids ruminants as *Dremotherium*, which is considered a sister group of cervids having common ancestor in Asia (Ginsburg et al., 1994). At the same time in North America the Antilocapridae ancestors of the pronghorn appeared, probably arising in the same radiation (Azanza and Ginsburg, 1997). The earliest antlered deer *Dicrocerus* and *Heteroprox* appeared in the Late Orianian in MN5 (Mammalian Neogene biostratigraphic divisions, about 17 Ma), and *Euprox* appeared in the succeeding Early Astaracian in MN6 (about 16 Ma) (Gentry, 1994). Azanza (1993) already classified *Euprox* to Muntiacinae, a subfamily which has been considered as the primitive stem-group of all other cervids and to be a monophyletic clade (Pitra et al., 2004).

The second fossil calibrated node is the Muntiacinae–Cervinae split. The oldest fossil remains assignable to this node appear in the Late Miocene deposits (7 Ma) of Lufeng, China. According to Pitra et al. (2004), the evolutionary radiations of Old World deer occurred at the Miocene/Pliocene transition. Molecular phylogenetics based on mitochondrial DNA, nuclear DNA or amino acid sequence comparisons
have contributed considerably to resolve evolutionary relationships at family level but these studies did not fully resolve the phylogeny of the Cervinae because they lacked many of the extant Old World deer species. Petronio et al. (2007) named the Late Miocene Pliocervini, Cervavitus novorossiae (Khomenko, 1913), as the most primitive member of the Cervinae and also identified Early/Middle Pliocene Cervus magnus Zdansky, 1925 from Eurasia. Pliocervines were recorded by Vislobokova, (2005) in MN11 of Greece, Iran and Afghanistan. Similarly Şen et al. (1997) also described the Late Miocene ploicervine (cf. Cervavitus novorossiae) from Khurdka-bul basin of Afghanistan. Tribe Pliocervini in fact represents an important evolutionary passage between the Middle Miocene Dicrocerini and Plio-Pleistocene Cervini (Bubenik, 1990). The genera and species belonging to ploicervines show a wide geographical distribution covering most of the Eurasia except arctic zones and Indian subcontinent (Petronio et al., 2007).

From Early to Middle Pliocene, the first forms surely referable to the subfamily Cervinae were found in central and western Asia. These forms are referable to genera Rucervus Hadgson, 1838, Cervus Linnaeus, 1758, Axis Smith and Pedgeon, 1827, Rusa Smith and Pedgeon, 1827, Elaphurus Milne-Edwards, 1866 and Pseudaxis Gray, 1872. The form, which can be considered closest one to the ancestor of Rucervus, is Early-Middle Pliocene C. magnus (Geist, 1971). All the cervid forms phylogenically linked with red deer or with its ancestors must be referred to the genus Cervus. The most archaic remains referred to the genus Cervus were previously attributed to Early-Middle Pliocene Pseudaxis. Cervus magnus is the most ancient species belonging to the genus Cervus. Cervus warthae Czyzewska, 1968 and C. perrieri Croizet and Jobert, 1828 represent two primitive European forms of the genus Cervus evolved from an Asian species phylogenically linked with C. magnus. Cervus grayi Zdansky, 1925 is very common in the Asian faunal assemblages; it occurs during late Early Pleistocene but much evolved than C. magnus. Overall morphological characteristics of this species are very similar to living Sika deer, C. nippon Temminck, 1838. The red deer (C. elaphus) is however the best known species of the genus Cervus. It occurs in Europe (Italy) in the early Middle Galarian faunal association and it soon became one of the most common elements. Red deer is divided into four distinct and monophyletic sub specific groups. The first group includes six subspecies from Europe (C. e. hippelaphus, C. e. corsicanus, C. e. atlanticus, C. e. hispanicus), one from Caucasia, Turkey and Iran (C. e. maral) and two from middle Asia (C. e. bactrianus, C. e. yarkandensis) and four from Indochina (C. e. wallichi, C. e. macneilli, C. e. kansuensis and C. e. xanthopygus) (Di Stefano and Petronio, 2003; Pitra et al., 2004).

According to Di Stefano and Petrinio (2003), some medium-sized cervids belonging to the genera Axis and Rusa spread into continental and Mediterranean Europe. The genus Axis is prevalent in the southern areas and in the Italian peninsula while the genus Rusa is found throughout the habitats of the northern areas. There are great similarities between the representatives of the genus Rusa and Plio-Pleistocene cervines from the central and northern Europe referred to genus Pseudodama but the cervids from Italy referred to this genus are now referred to the genus Axis and the genus Axis is widely distributed in central southern Asia from Indochina to Iran.

The cervids follow two main migration pathways from central Asia to Europe, from Pliocene to Pleistocene. The main pathway followed by the representatives of genera Rusa and Cervus may be drawn north of the Alpine-Himalayan range, through Russia, above the Caspian Sea and the Black Sea. This pathway has been active since Oligocene and starting from the Miocene it was the main pathway for the migration of almost all Asian mammals to Europe. The second pathway was active from Pliocene to the Early Pleistocene and followed a corridor between the Elbourz range, Caucasus and Carpathian range at north and the almost continuous range of Taurus-Zagros-Belouchi at south. Some mammals like Axis, Bos galerianus and Elephas namadicus-antiguus migrated to Europe through this pathway (Di Stefano and Petronio, 2003).
The Siwalik cervids were only known until now from deposits credited to the Tatrot Formation, suggesting Late Pliocene/Early Pleistocene age, probably no older than 3.4 Ma (Barry et al., 2002). If indeed the new material is correctly attributed to the cervids, they might suggest a longer chronological range, as they migrate from the Early Pliocene deposits of the Dhok Pathan Formation of the Middle Siwaliks, dated approximately between 7-3.4 My. The presence of the cervids in the Early Pliocene of the Siwaliks is not surprising. During the end of the Miocene and the Early Pliocene, there was a land connection between Indian Subcontinent and Europe (Hsü et al., 1977). Indications of similar biotopes occurred in south east Europe and Pakistan in the Early Pliocene suggest close affinity of the faunas (Van der Made, 1999). In this case, the cervids record in Pakistan would span from the Early Pliocene up to the Late Pleistocene, modifying previous concepts.

MATERIALS AND METHODS

The described specimens were collected from the sediments of the Dhok Pathan and the Hasnot (Dhok Pathan Formation), Punjab, Pakistan. The collections were carried out by authors during the field trips that took place from 1998 to 2005. In addition some of the specimens used in this study already belonged to the collections of the Abu Bakr Fossil Display and Research Centre, University of the Punjab, Lahore, Pakistan, and had been collected in the past from the above-mentioned localities (Dhok Pathan and Hasnot).

The measurements of the specimens were taken in millimetres with the help of metric vernier calipers. The morphological and metrical characteristics of the specimens are described and their systematic determination is discussed. The catalogue number of the specimens consists of series i.e., yearly catalogue number and the serial catalogue number, so the figures of the specimen represent the collection year (numerator) and the serial number (denominator) of that year (e.g. 05/12). Lowercase letters stand for lower dentition and uppercase letters for upper dentition. The terminology of the tooth crown elements and manners of measurements follow Gentry et al. (1999). The examined specimens are distinguished from each other on the basis of morphology of the teeth and comparison with the type material for each species (Ghaffar et al., 2004; Ghaffar, 2005; Azzaroli, 1954; Arif et al., 1991a, 1991b).


SYSTEMATIC PALAEONTOLOGY

Order Artiodactyla Owen, 1848
Family Cervidae Goldfuss, 1820
Subfamily Cervinae Goldfuss, 1820
Tribe Cervini Weber, 1928
Genus *Rucervus* Hodgson, 1838

*Rucervus cf. simplicidens* (Lydekker, 1876) (Figures 2-4)

*Holotype*: GSI B204, a maxillary fragment with left M1-2.

*Occurrence*: Punjab (Colbert, 1935), Hasnot, Dhok Pathan Formation (Middle Siwaliks), Pakistan, (Pilgrim, 1910, 1913).

*Diagnosis*: Molar crowns square with small accessory pillars, and with slightly rugose enamel (Colbert, 1935).

*Referred Material*: PUPC 84/115, a left maxillary fragment with M2-3 (Dhok Pathan). PUPC 83/104, a right mandibular fragment with broken m1 and well preserved m2 (Hasnot). PUPC 87/276, a right mandibular fragment with broken p2 and well preserved p3-m1 (Dhok Pathan).

*Description*: PUPC 84/115 is in the middle wear. In PUPC 84/115, the M3 crown shed away and the roots are preserved while in the M2 the lingual cones (the protocone and hypocone) are
Figures 2-6. *Rucervus* cf. *simplicidens*: 2. PUPC 83/104, right mandibular fragment with m1-2 (occlusal view); 3. PUPC 84/115, left maxillary fragment with M2-3 (a: occlusal view, b: lingual view); 4. PUPC 87/276, right mandibular fragment with broken p2 and well preserved p3-m1 (occlusal view). *Cervus* cf. *triplidens*: 5. PUPC 69/146, left mandibular fragment with broken m1-3 (a: buccal view, b: lingual view). 6. PUPC 98/77, left and right maxillary fragments with M2-3 and, left and right mandibular fragment with m1-3 (a: occlusal view, b-c: lingual views) (Scale bar equals 10 mm).

Şekil 2-6. *Rucervus* cf. *simplicidens*: 2. PUPC 83/104, ml-2 taşıyan sağ altçene parçası (çiğneme yüzeyi görüntüsü); 3. PUPC 84/115, M2-3 taşıyan sol üstçene parçası (çiğneme yüzeyi görüntüsü, b: içten görüntü); 4. PUPC 87/276, kırilmiş p2 ile iyi korunmuş p3-m1 taşıyan sağ altçene parçası (çiğneme yüzeyi görüntüsü); *Cervus* cf. *triplidens*: 5. PUPC 69/146, kırılmış m1-3 taşıyan sol altçene parçası (a: yanak görüntü, b: içten görüntü); 6. PUPC 98/77, M2-3 taşıyan sağ ve sol üstçene parçaları ve m1-3 taşıyan sağ ve sol altçene parçaları (a: çiğneme yüzeyi görüntüsü, b-c: içten görüntüler) (Ölçek çubuğu 10 mm'dir).
well preserved and the buccal ones (paracone and metacone) are broken. The basal part of the entostyle is present (Figure 2). PUPC 83/104 is also in the middle wear (Figure 3). The teeth are brachydont with slightly rugose enamel. The ectostylid is worn in the m1 and it is unworn in the m2. In the m1 only the hypoconid and the entoconid are preserved. The entoconid of the m2 is broken lingually and the rest of the three conids are excellently preserved. The protoconid is broad while the hypoconid is elongated and V-shaped. The metastylid is strong in the m2 and missing in the m1. The entostylid is poorly developed in the m1 and the m2. The posterior median rib in the m1 and the anterior median rib in the m2 are slightly damaged at the tip.

PUPC 87/276 (Figure 4) comprises premolars and a molar. They are in middle wear. The conids are not differentiated well in premolars while they are well differentiated in the molar (m1). The p3-4 metastylics are well preserved. The ectostylid is well developed and broad at the base in the m1. The principal conids are prominent and well developed. The anterior median rib is strong while the posterior one is missing.

Discussion: One of the most important questions is the differentiation of the cervid fossil material from the other related taxa of ruminants. For this purpose, the authors compared the studied specimens with the Siwalik bovids and giraffids, and the following differences are noted. In the Early Pliocene bovids, the upper molars are quadrate with strong divergent styles, the entostyle is strongly developed while the ectostylic is moderately developed. The median ribs are well developed and the enamel is rugose (Pilgrim, 1937, 1939; Khan et al., 2009). During the time in question, two small sized giraffid species (Giraffa punjabiensis and Bramatherium perimense) were present in the upper Middle Siwaliks. These two species have strong median ribs and prominent rugosity. The remaining giraffid species (Sivatherium giganteum, Indratherium majori, Hydaspitherium megacephalum, H. grande and H. magnum) during this time have greater tooth dimensions than those of the studied specimens (Colbert, 1935). The brachydonty of the studied molars with weak styles/stylids and rugosity associate them to the Siwalik cervids (C. sivalensis, C. triplidens-R. simplicidens, C. rewati) (Gentry et al., 1999; Ghaffar, 2005).

PUPC 83/104, PUPC 84/115 and PUPC 87/276 (Figures 2-4; Table1) are referred to Rucervus cf. simplicidens because the molar crowns are square and this character is more evident in the molars of PUPC 84/115 and PUPC 87/276. The entostyle is weak in the M2 of PUPC 84/115. The molars are brachydont which distinguish them from C. triplidens and C. sivalensis which have hypsodont molars. In the studied molars, the basal cingulum is absent, the median valley is deep and the enamel is slightly rugose. These characters are also noted by Colbert (1935) and Arif et al. (1991a). According to Azzaroli (1954), the skull and teeth characters (AMNH 19829) are very similar to those of living R. duvaucellii and he referred AMNH 19829 to R. simplicidens contrary to previous workers who described this specimen as C. simplicidens (Lydekker, 1876; Pilgrim, 1910; Brown, 1926; Matthew, 1929; Colbert, 1935). The studied specimens (Figures 2-4; Table 1) exhibit diagnostic features of R. simplicidens and the material is referred to R. cf. simplicidens. The material is inadequate for the exact determination.

Genus Cervus Linnaeus, 1758

Cervus cf. triplidens Lydekker, 1876

(Figures 5-6)

Holotype: GSI B204, a right maxilla with M2-3.

Occurrence: Siwaliks (Lydekker, 1876), Upper Siwaliks (Brown, 1929), Middle Siwaliks (Pilgrim, 1910, 1913) the Punjab province, India.

Diagnosis: Molars hypsodont with large accessory columns and rugose enamel (Colbert, 1935).

Referred Material: PUPC 98/77, left and right maxillary with M2-3 and, left and right mandibular ramii with m1-3 (Dhok Pathan). PUPC 69/146, a left mandibular fragment with broken m1-3 (Dhok Gall; Hasnot).

Description: PUPC 98/77 includes left and right maxillary with M2-3 and right and left
Table 1. Comparative dental measurements of the Siwalik cervids in mm (millimetres). (*The specimens studied. Referred data are taken from Colbert (1935), Arif et al. (1991a, b) and Ghaffar (2005)).

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<td></td>
<td>p4</td>
<td>p4</td>
<td>10.6</td>
<td>5.5</td>
<td>0.51</td>
</tr>
<tr>
<td>Cervus rewati</td>
<td>H-GSP 18388</td>
<td>m1</td>
<td>12.6</td>
<td>9.4</td>
<td>0.74</td>
</tr>
<tr>
<td></td>
<td>m2</td>
<td>m2</td>
<td>16.7</td>
<td>10</td>
<td>0.59</td>
</tr>
<tr>
<td></td>
<td>m3</td>
<td>m3</td>
<td>22</td>
<td>13.5</td>
<td>0.61</td>
</tr>
</tbody>
</table>
mandibular ramii with m1-3 (Figures 6a-c). They are in late wear. The entostyle is small and the principal cusps are well preserved. The styles are missing in the M3 and the median ribs are well developed. The ectostylids in the lower molars are well preserved at the base and broken at the tips. The talonid is well preserved in the m3. PUPC 69/146 is in late wear (Figure 5) and it is a partially damaged specimen. The ectostylid and metastylid in the m2-3 are well preserved. The ectostylid in the m1 is poorly developed.

Discussion: PUPC 69/146 and PUPC 98/77 (Figures 5-6; Table 1) are characterized by hypsodont teeth with slight traces of cingulum, strong internal column and the folded enamel on the outer surface. The enamel folding is more evident in the upper molars than the lower ones. The basal cingulum is absent and the median valley is deep excluding their attribution to C. sivalensis. The main difference between C. sivalensis and C. triplidens is that the basal cingulum is well developed in C. sivalensis. The deep median valley and the folded enamel on the outer surface differentiate the sample from Axis punjabiensis since these characters are absent in A. punjabiensis (Brown, 1926; Az zaroli, 1954; Arif et al., 1991b). The studied materials based on the above mentioned features are assigned to C. cf. triplidens.

Cervus cf. sivalensis Lydekker, 1880

(Figures 7-8)

Holotype: GSI B215, a right mandibular ramus with m2-3.

Occurrence: Upper Siwaliks, Maili, the Punjab province, India (Lydekker, 1880).

Diagnosis: A cervid with hypsodont molars and with relatively large body size. The skull and antlers resemble these portions in Rucervus duvaucelii, the skull by virtue of the frontal concavity at the orbits, and the forward swell at the pedicles. The lacrimal vacuity is smaller than in R. duvaucelii. The brow tine of the antler arises immediately above the burr and forms an obtuse angle with the beam (Colbert, 1935).

Referred Material: PUPC 84/119, a left mandibular fragment with m2-3 (Dhok Pathan). PUPC 87/279, a right mandibular fragment with m3 (Dhok Pathan).

Description: PUPC 84/119 is in the middle wear (Figure 7). The ectostylids are prominent, broad at base and narrow to the summit of the crown. The protoconid and the hypoconid are well preserved. The metaconid, the entoconid, the stylids, the median ribs and the talonid are washed away. In PUPC 87/279 median basal pillar, conids and stylids and median ribs are well preserved (Figure 8).

Discussion: PUPC 84/119 and PUPC 87/279 (Figures 7-8; Table 1) are referred to C. cf. sivalensis (Lydekker, 1880, 1884) because the teeth are hypsodont, the basal cingulum is well developed and the median valley is deep with strong ectostylid. These characteristics correspond to C. sivalensis from Siwaliks and the recovered remains can be assigned to C. cf. sivalensis.

Cervus cf. rewati Arif, Shah and Vos, 1991

(Figures 9-10)

Holotype: H – GSP J18388, a right mandible with p3-m3.

Occurrence: Rewat, Rawalpindi district, Upper Siwaliks, Potwar Plateau, the Punjab province, Pakistan (Arif et al., 1991a).

Diagnosis: The small size of the teeth, the presence of accessory columns and the pronounced anterior folds on the molars (Arif et al., 1991a).

Referred Material: PUPC 02/35, a right dentary fragment with m1-3 (Dhok Pathan) PUPC 05/12, a left dentary fragment with p2-m1 (Hasnot)

Description: PUPC 02/35 comprises three lower molars (Figure 9). The molars are in early wear. The ectostylid is strong in the m1 and weak in the m2-3. The principal conids are well preserved. The metastylid in the m1 is broken while it is weakly developed in the m2-3. The talonid in the m3 is also broken. PUPC 05/12 is a left dentary fragment with p2-m1 (Figure 10) and in early wear. The parastylid and the paraconid in the premolars are not fused and consequently form the anterior valley which is open lingually. It is wide in the p2 and the p3. The hypoconid is more prominent than the other
conids and inflated. The buccal furrow is deep in the p4. The posterior valley in the premolars is narrow and placed obliquely.

**Discussion:** PUPC 02/35 and PUPC 05/12 (Figures 9-10; Table 1) have small sized brachydont teeth. The basal cingulum is slightly developed distinguishing it from *C. sivalensis*. The presence of a strong ectostylid and the pronounced anterior folds differentiate this material from *A. punjabiensis*. The parastylid and the anterior folds are very pronounced in the studied samples. These characteristics are very close to *C. sivalensis* but the material size is small and corresponds to *C. rewati*. However, the studied samples are insufficient for the exact determination and assigned to *C. cf. rewati*.

**CONCLUSIONS**

The different species of the cervids (Figure 11) described here represent the stratigraphic range...
Figure 11. Bivariate scatter diagram showing dental proportions of the studied specimens (Referred data are taken from Colbert (1935), Arif et al. (1991a, 1991b) and Ghaffar (2005)).

from the Early Pliocene – Pleistocene times (5.3 – 1.6 Ma) contrary to the earlier workers whom stated that the cervids appeared in the Siwaliks in the late Pliocene times (3.5-1.6 Ma) (Matthew, 1929; Colbert, 1935; Barry et al., 2002). Barry and Flynn (1989) also mentioned the first appearance of family Cervidae from the Upper Siwaliks at 2.5 Ma. Perhaps one basic reason for this dispute was the stratigraphic confusions that have been resolved now as a result of refined magnetostratigraphy (Cheema et al., 1977; Johnson et al., 1982; Barry et al., 2002).

The primitive cervines were probably tropical in distribution, they certainly inhabited woodland or open country, not closed forest, and it probably lived in eastern Eurasia or probably India (not in western Eurasia or southern Asia) (Kahlke, 1976; Lister, 1984; 1986; Sommer et al., 2008). The open woodlands or grassy woodlands environments are also indicated by the carbon isotope record after 7.4 Ma (Barry et al., 2002). Analysis of hypsodonty and dietary structure of the mammalian plant–eater community in Europe shows that the Miocene–Pliocene boundary was marked by a strong decrease in mesodont species and mixed feeders, and an increase in brachydont species and omnivores (Fortelius et al., 2006).

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REFERENCES


Geist, V., 1971. The relation and the social evolution and dispersal in Ungulates during the Pleistocene, with emphasis on the Old World deer and the genus. Quaternary Researches, 1, 282-315.


Şen, S., Blieck, A., Bouvrain, G., Brunet, M., Gerards, D., Heintz, E., and Koufos, G.


