

**DIETARY EVALUATIONS AND PALEOECOLOGY OF AN EXTINCT GIRAFFID
 (*GIRAFFOKERYX PUNJABIENSIS*) FROM SIWALIKS OF PAKISTAN**

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ABSTRACT

The dietary preferences and paleoecology of *Giraffokeryx punjabiensis* Pilgrim, 1910, an extinct giraffid species from Chinji Formation of Potwar Siwaliks of Pakistan, have been investigated by incorporating mesowear-I, mesowear-II and hypsodonty methods. The mesowear patterns of *Giraffokeryx punjabiensis* are very much consistent with the browsers as well as seasonal mixed feeders whereas hypsodonty index (1.31 ± 0.06) categorizes it within the browsers. Comparison of the results from these research tools suggest that the extinct giraffid reflects diverse dietary spectra ranging from browsers to seasonal mixed feeders and shows no affinities with grazers. The coexistence of *G. punjabiensis* with its mammalian paleocommunity reveals the persistence of mosaics of diverse habitats ranging from tropical evergreen forest to subtropical ones, closed seasonal woodlands to wooded savannas.

Key words: hypsodonty, Miocene, mesowear, ungulates, Sivatherines, biostratigraphy.

INTRODUCTION

The dietary preferences of large herbivorous mammals including giraffids can be evaluated on the basis of mesowear I, II and hypsodonty studies (Solounias and Semperebon, 2002; Damuth and Janis, 2011). The mesowear-I method is based on two major attributes named buccal cusp shape (either the paracone or metacone) and cusp relief, developed by attrition and abrasion, for estimating average life long diet of ungulates (Kaiser and Solounias, 2003; Franz-Odenaal and Solounias, 2004). Mesowear-II method combines the two variables such as cusp shape and occlusal relief (of mesowear-I) as a single variable and then mesowear scorings are scaled by relating them with a mesowear

“ruler” (Mihlbachler *et al.*, 2011). Hypsodonty is recognized as morphological proxy to interpret feeding adaptations and habitat inference in large herbivorous mammals (Fortelius *et al.*, 2003; Stromberg, 2006).

The diet of extinct Giraffidae was browse as in extant giraffes. The notion about the extinct giraffids as traditional browsers was changed when Solounias *et al.*, (1988) found that the *Samotherium boissieri* Major, 1888 (an extinct giraffid from the Miocene of Samos, Greece) was known to be mixed feeder to grazer. The premaxillary shape and dental microwear analyses showed that the diets of extinct Giraffidae were highly heterogeneous (e.g.) the *Bramatherium megacephalum* (Lydekker, 1878) and *Sivatherium giganteum* Falconer and Cautley, 1835 (Sivatheriinae) were grazers.



Fig.1. Map of Potwar Siwaliks displaying major biostratigraphic sections. (Behrensmeier and Barry, 2005 and the boundary dates were taken from Barry *et al.*, 2002; Dennell *et al.*, 2008 and Nanda, 2008). Rectangles mark the studied areas.

The Giraffinae and Palaeotraginae Pilgrim, 1911 also showed browsing, mixed feeding and grazing diet. Furthermore, *Okapia johnstoni* (Sclater, 1901) (the okapi), the second and very rare living species of Giraffidae, is a fruit-dominated browser instead of being regular browser whereas the *Giraffa camelopardalis* (Gmelin, 1788) is designated as a leaf-dominated browser (Solounias and Semperebon 2002). Studies on premaxillary shape and dental microwear also revealed that the Sivatheriinae, *Palaeotragus primaevus* Churcher, 1970 and *Helladotherium duvernoyi* Gaudry, 1860, were committed browsers whereas *Giraffokeryx punjabensis* Pilgrim, 1910, was a mixed feeder (Solounias and Moelleken, 1993; Solounias *et al.*, 2000). Other studies on dietary evaluations of herbivores including giraffids from Middle Miocene of Pakistani Siwaliks was based solely on general comparisons with their extant analogues (e.g., Barry *et al.*, 2002; Badgley *et al.*, 2008; Samiullah *et al.*, 2012). Considering this approach, Barry *et al.* (2002) and Badgley *et al.* (2008) assumed that the *Giraffokeryx punjabensis* was a browser similar to living giraffes whereas Samiullah *et al.* (2012) proposed its dietary spectrum ranging from a browser to a mixed feeder. During the last two decades, however, several approaches have been developed for dietary evaluations of fossil mammals. We have presently evaluated in detail the dietary adaptations of a Siwalik Sivathere; *Giraffokeryx punjabensis* based on mesowear-I, mesowear-II and hypsodonty index hoping to achieve better resolution than from mesowear-I and previous dietary inferences since it gives a very precise average life long diet of the species. Exploration of dietary adaptations in ungulate remains provide information concerning paleoecological conditions of individual species and ultimately of terrestrial paleocommunities of mammals (Kaiser *et al.*, 2000).

Abbreviations GCUPC= Govt. College University Lahore Paleontological Collection, ca= Circa, H= crown height, W= crown width, l= left, r= right, M= upper molar, m= lower molar, Ma= mega annum, MN= Mein

Zones, HI= Hypsodonty Index, MS= mesowear scale, N= number of samples.

MATERIALS AND METHODS

Specimens (molar teeth) of *Giraffokeryx punjabensis* unearthed from the Chinji Type locality and Bin Mir Khatoon (Chinji Formation) of Pakistan were examined. The HI was calculated based on the metrics of completely unworn seven m3s following Janis (1988). Seventeen M2s were selected for mesowear analysis following Fortelius and Solounias (2000) and Muhlbachler *et al.* (2011). The mesowear method is based on two variables namely cusp shape and occlusal relief and were determined by direct observation and the percentage of teeth with high/low cusps and sharp/round/blunt cusps was calculated for the species. The variables were then plotted against HI, as recommended by Fortelius and Solounias (2000). The cusp sharpness and degree of relief are dependent variables. Higher occlusal relief tends to be sharper as compared to low relief cusps and cusps with zero relief are obviously blunt. Hence, old mesowear (Mesowear Type I) were treated as a single variable (Mesowear Type II) during which cusp apices are continuously assigned to stages ranging from the sharpest cusps displaying highest relief to the bluntest cusps showing lowest relief. Mesowear scorings were digitized by relating them with a mesowear “ruler” designed by Muhlbachler *et al.* (2011). Having recorded the mesowear scorings, the percentages for each variable were calculated which in turn were examined by hierarchical cluster analyses using PAST version 14 software to evaluate the dietary and habitat interpretations of the studied taxon.

RESULTS

Mesowear analysis: The mesowear signatures of *Giraffokeryx punjabensis* reflect affinities with extant browsers and mixed feeders.

Table.1. Absolute and relative mesowear scorings of upper M2s of *Giraffokeryx punjabensis* Pilgrim, 1910.

N	Mesowear Counts					Percentages				
	Cusp relief			Cusp shape		Cusp relief		Cusp shape		
	High	Low	Sharp	Round	Blunt	%High	%Low	%Sharp	%Round	%Blunt
17	17	0	11	6	0	100	0	64.70	35.29	0

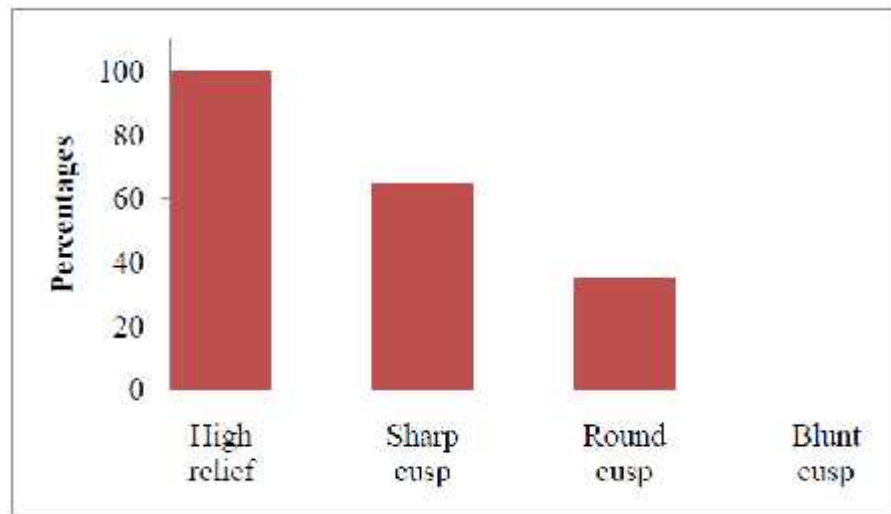


Fig. 2. Mesowear scorings displaying cusp relief (100% high) and cusp shape (64.70% sharp and 35.29% round) of M2 of *Giraffokeryx punjabiensis* Pilgrim, 1910. No specimens with low cusp relief and blunt cusp shape were observed.

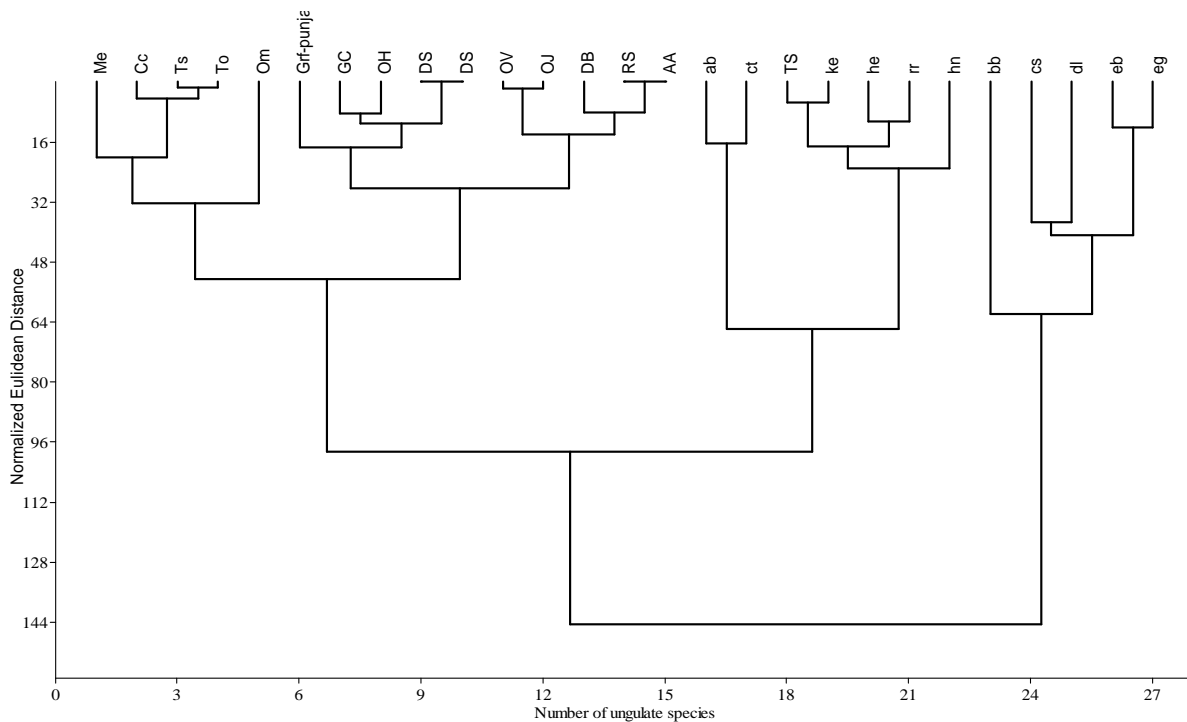


Fig.3. Dendrogram showing the hierarchical cluster analyses of *Giraffokeryx punjabiensis* Pilgrim, 1910, amongst dataset of 27 extant species of ungulates comprising of browsers, mixed feeders and grazers from Fortelius and Solounias (2000). Abbreviation for the fossil species: Grf, punj= *Giraffokeryx punjabiensis*. Abbreviations for the extant species-Browsers: OH= *Odocoileus hemionus*, OV= *Odocoileus virginianus*, OJ= *Okapia johnstoni*, RS= *Rhinoceros sondaicus*, DS= *Dicerorhinus sumatrensis*, DB= *Diceros bicornis*, AA= *Alces alces*, GC= *Giraffa camelopardalis*. Grazers: ab= *Alcelaphus buselaphus*, bb= *Bison bison*, cs= *Ceratotherium simum*, ct= *Connochaetes taurinus*, dl= *Damaliscus lunatus*, eb= *Equus burchelli*, eg= *Equus grevyi*, he= *Hippotragus equines*, hn= *Hippotragus niger*; ke= *Kobus ellipsiprymnus*, rr= *Redunca redunca*. Mixed feeders: Me= *Aapyceros melampus*, Cc= *Cervus Canadensis*, Gg= *Gazella granti*, Gt= *Gazelle thomsoni*, Om= *Ovibos moschatus*, To= *Taurotragus oryx*, Ts= *Tragelaphus scriptus*, Ts= *Tragelaphus strepsiceros*.

The living analogues for browsers are a giraffid; *Giraffa camelopardalis* Linnaeus (1758), and a cervid; *Capreolus capreolus* Linnaeus (1758). The extant analogues for mixed feeders are *Tragelaphus imberbis* (Blyth, 1869) and *Procavia capensis* Pallas (1766) (Table 1, Appendix 2).

The graphical representation indicates that the *Giraffokeryx punjabiensis* may be placed within the dietary spectrum of browsers and seasonal mixed feeders. As regards cusp shape, the specimens have 36.84% round cusps, 63.15% sharp and 0% blunt cusps (Table 1, Fig.2). Bivariate plots of Mesowear results for *Giraffokeryx punjabiensis* versus mesowear variable outlined by Fortelius and Solounias (2000) for extant species of ungulates were prepared.

Hypsodonty Index: Hypsodonty index shows that *Giraffokeryx punjabiensis* is a brachydont browser. Nevertheless, it is somewhat more hypsodont than the living brachydont giraffe *Giraffa camelopardalis* (HI= 1.2) (Janis, 1988). The Hypsodonty Index (HI) for *Giraffokeryx punjabiensis* calculated here is 1.31 ± 0.06 (n=6) (Appendix 1). The purpose of incorporation of hypsodonty index (HI) is primarily to evaluate the mesowear results and to compare with its extant analogues i.e. *Giraffa camelopardalis*, *Okapia johnstoni* for drawing ecomorphic inferences. The HI of 1.31 ± 0.06 is utilized for *Giraffokeryx punjabiensis* in all bivariate representations (Appendix 1). The graphical representation indicates that the *Giraffokeryx punjabiensis* is placed within the dietary spectrum of browsers (Figs. 4-7 A, B, C).

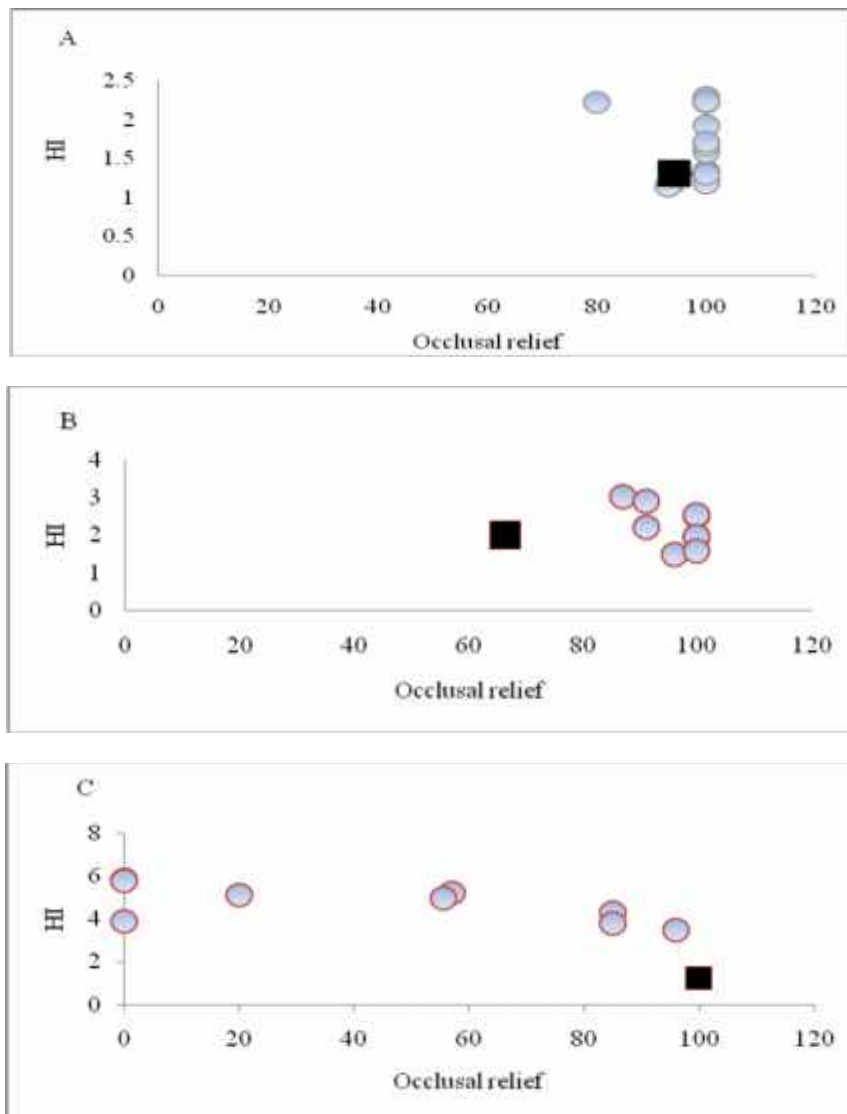


Fig. 4 A, B, C. Bivariate plots of hypsodonty index (HI) versus percentage of high occlusal relief. A= browsers, B= mixed feeders, C= grazers. Hypsodonty data from Janis (1988), mesowear data from Fortelius and Solounias (2000) (■), *Giraffokeryx punjabiensis* (●) Pilgrim, 1910.

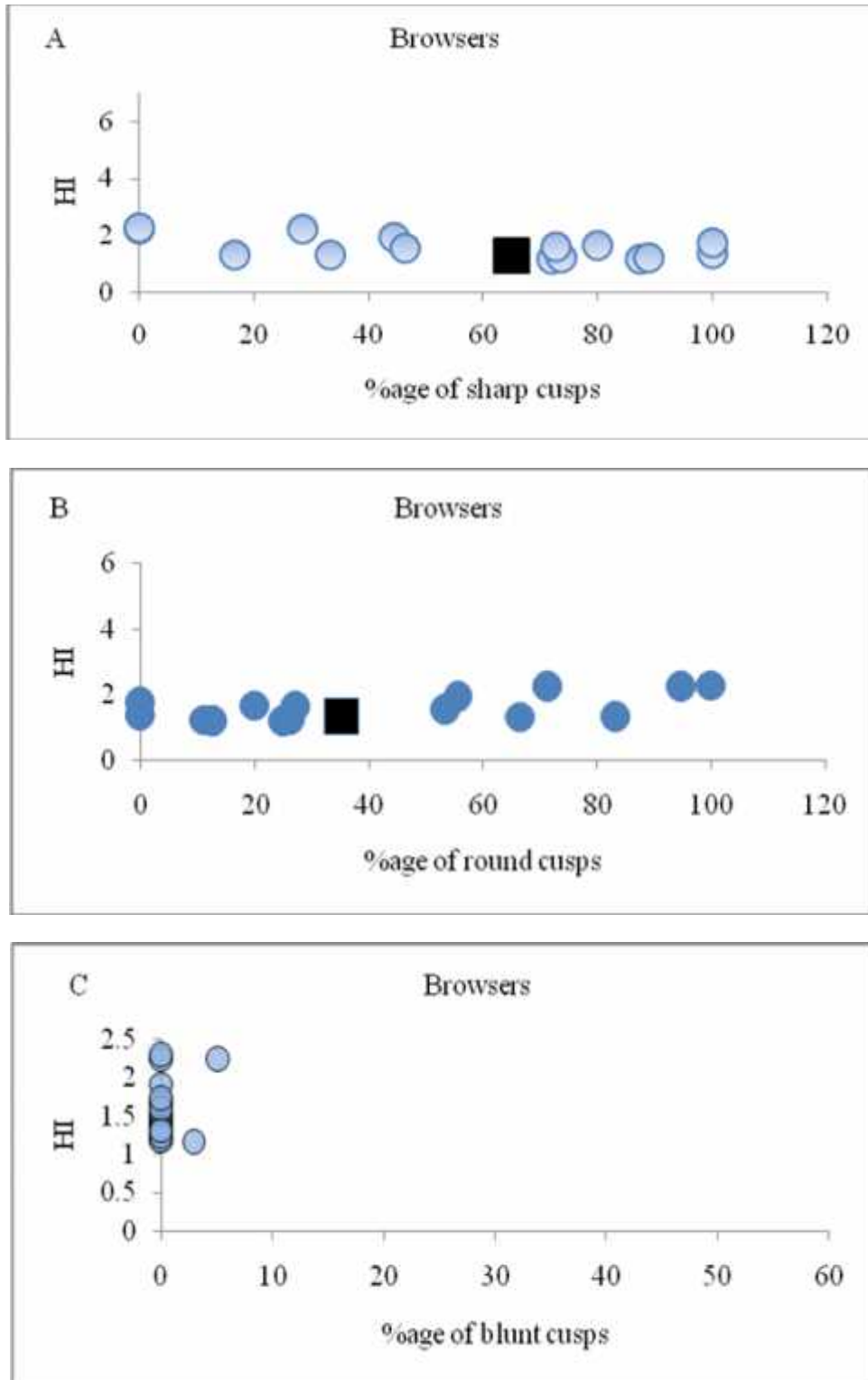


Fig. 5A, B, C. Mesowear analyses of cusp shape in *G. punjabiensis* Pilgrim, 1910. *G. punjabiensis*(○) data for upper teeth are plotted against extant species of ungulates (●) from Fortelius and Solounias (2000). In all bivariate plots, hypsodonty index is taken on y-axis and x-axis is represented by one of the three (% age of cusp shape) mesowear variables.

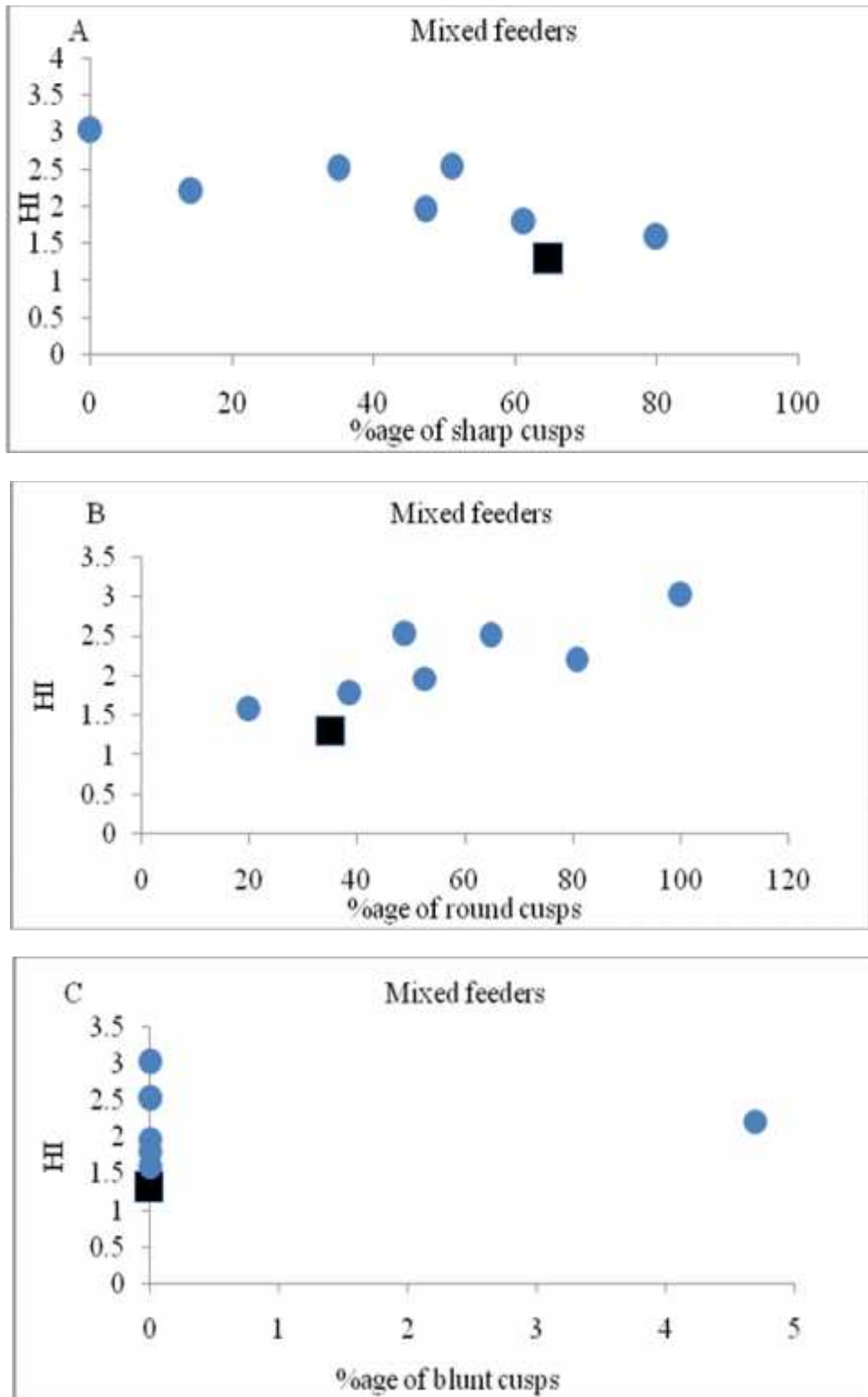


Fig. 6 A, B, C. Mesowear analyses of cusp shape in *G. punjabiensis* Pilgrim, 1910. *G. punjabiensis*() data for upper teeth are plotted against the extant species of ungulates () from Fortelius and Solounias (2000). In all bivariate plots, hypsodonty index is taken on y-axis and x-axis is represented by one of the three (% age of cusp shape) mesowear variables.

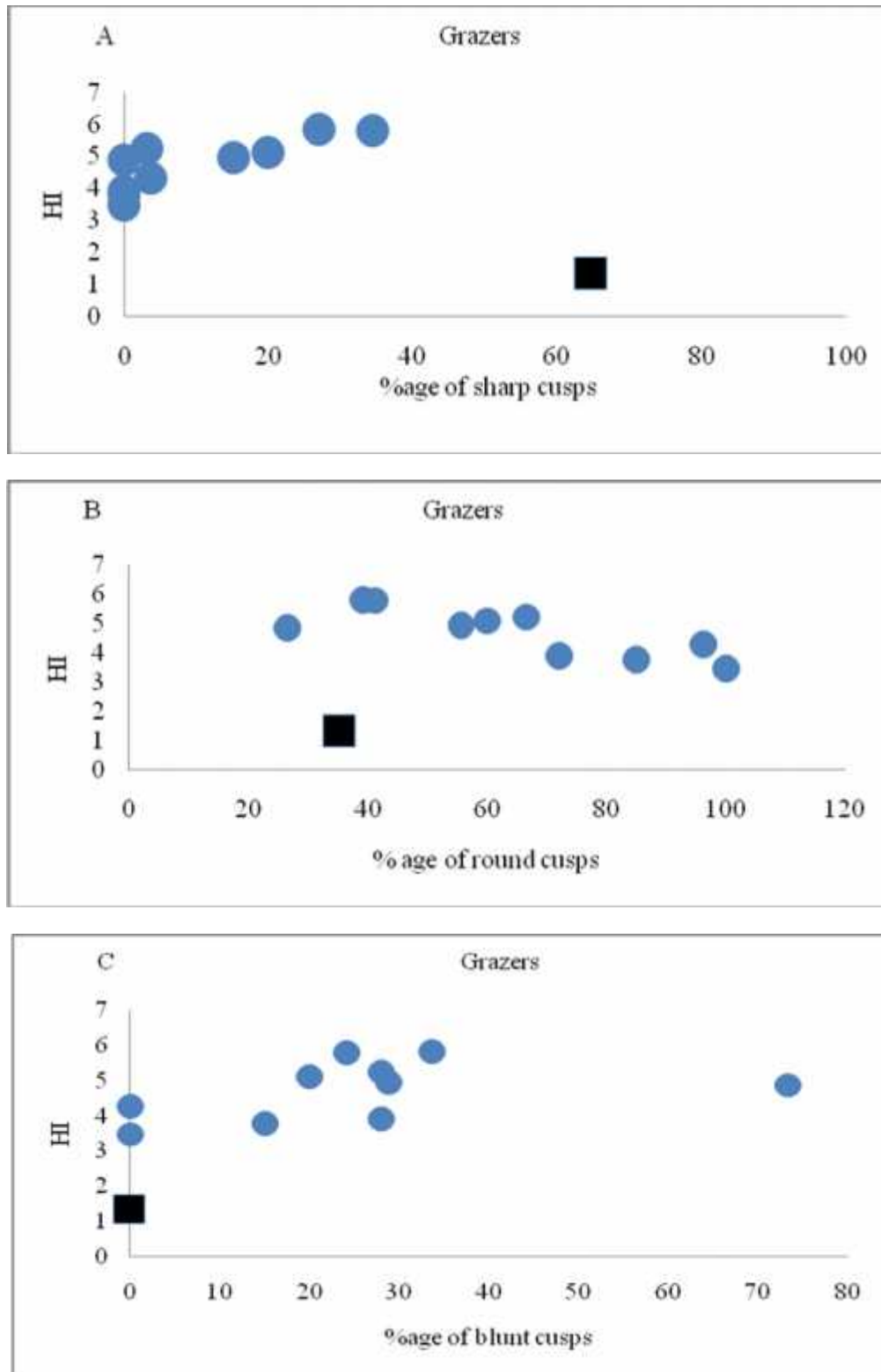


Fig.7 A, B, C. Mesowear analyses of cusp shape in *G. punjabiensis* Pilgrim, 1910. *G. punjabiensis*() data for upper teeth are plotted against the extant species of ungulates () from Fortelius and Solounias (2000). In all bivariate plots, hypsodonty index is taken on y-axis and x-axis is represented by one of the three (% age of cusp shape) mesowear variables.

DISCUSSION

Mesowear: Although cusp relief in the extant giraffe, *G. camelopardalis*, and *Giraffokeryx punjabiensis* are similar, yet the cusp shape markedly differs. As regards numbers, *Giraffa camelopardalis* shows 74% sharp and 26% round shaped cusps (Fortelius and Solounias, 2000) as compared to the less marked pattern in *Giraffokeryx punjabiensis* (63.15% sharp, 36.84% round) (Table 1, Fig.2). Bivariate representations of mesowear variables show that diet of *G. punjabiensis* was different from that of the living giraffes. The species under study is analogous to *Tragelaphus imberbis* (Blyth, 1869) and *Procapra capensis* Pallas (1766). Consequently, the diet of *G. punjabiensis* seems to be most consistent with browsers and seasonal mixed feeders. It indicates no evidence for a pure grazer (Table 1, Fig. 2).

Hypsodonty study: The HI (1.31 ± 0.06) for *Giraffokeryx punjabiensis* suggests its placement within the brachydont browsers. Considering Janis (1988), Damuth and Janis (2011) hypsodonty interpretations, *Giraffokeryx punjabiensis* may be categorized within the dietary spectrum of two sub-types of brachydont browsers such as regular browsers (BB) and high level browsers (HB). Furthermore, the HI of *Giraffokeryx punjabiensis* is similar to the average for four regular browsers (BB); *Odocoileus virginianus*, *Hylochoerus minertzheni*, *Mazama mazama americana*, *Choeropsis liberiensis*, and three high-level browsers (HB); *Alces alces* (Erxleben, 1777), *Litocranius walleri* and *Okapia johnstoni*. Having compared the HI and body size/mass of *Giraffokeryx punjabiensis* to the previously published HI and body size of 127 species of extant ungulates (Janis, 1988), *G. punjabiensis* HI seems most similar to that of its multiple extant analogues i.e. one cervid; *Alces alces* (Linnaeus, 1758) (moose), a giraffid; *Okapia johnstoni* (Sclater 1901) (okapi), a Hippopotamid; *Choeropsis liberiensis* (Morton, 1849) (pygmy hippos), a suid; *Hylochoerus minertzheni* (Thomas, 1904) (giant forest hog) (Janis 1988). The *Alces alces* and *Okapia johnstoni* have been classified by Janis (1988) as high-level browsers (HB), while *Choeropsis liberiensis* and *Hylochoerus minertzheni* as regular browsers (BB) and *Muntiacus reevesi* as mixed feeders in closed habitats (MFC). Both of the regular and high level browsers have body weights nearly equivalent to the estimated body weight for *G. punjabiensis* (233 kg) by Barry *et al.* (2002). Comparison of the results from these research techniques reveals that the *G. punjabiensis* is categorized within the dietary spectra of browsers as well as seasonal mixed feeders and shows no affinities with grazers (Table 1, Fig. 2, Appendix 2).

Biostratigraphy and Paleoecology: The Giraffokerycinae appeared sporadically in the Chinji beds of the Siwaliks (Bhatti *et al.*, 2007). *Giraffokeryx punjabiensis* has been

documented from several localities of Siwalik late Middle Miocene (Bhatti, 2005), occupying a long geochronologic ranges from Western Europe to Indian subcontinent (Bohlin, 1926; Bosscha-Erdbrink, 1977; Gentry *et al.*, 1999). *G. punjabiensis* in association with *Listriodon pentapotamiae*, *Conohyus sindiensis*, *Gaiotherium browni*, *Brachypotherium fatehjangense*, *Sivapithecus* sp. and *Deinotherium pentapotamie* are considered to be zonal marker elements of Chinji Formation (Sarwar, 1977; Barry *et al.*, 2002). The Chinji fauna is in favor of Middle Miocene age because the comparison of the material with several representatives of the fauna indicates a Middle Miocene age (Pilgrim, 1937, 1939; Heissig, 1972). The faunal assemblage contains elements significant enough to be compared with Astaracian of Europe and Greco-Iranian Province spanning from middle Miocene to earliest Late Miocene (Khan *et al.*, 2011). It shows overlapping of temporal ranges with that of the Chinji stratotype which correspond to the MN6 as well as MN7/8 (Heissig, 1972; Colbert, 1935; Pickford and Morales, 2003).

The dietary preferences of giraffes provide a baseline for interpretation of their ecology. The reconstruction of palaeoecology of ungulate remains is largely dependent on their palaeodietary inferences (Bibi and Gulec, 2008). The great diversity of the ungulate paleocommunity reveals the predominance of forest frugivores/selective browsers, browsers and browsing mixed feeders during Middle Miocene to earliest Late Miocene of Siwaliks in Pakistan (Badgley *et al.*, 2005, 2008). Frugivores/selective browsers, and browsers are indicators of tropical evergreen forest to subtropical one whereas browsing mixed feeders are markers of woodlands and wooded savannas (Janis, 1988; Damuth and Janis, 2011). The coexistence of *G. punjabiensis* with mammalian paleocommunity suggests the persistence of mosaics of diverse habitats ranging from tropical evergreen forests to subtropical ones, closed and seasonal woodlands to woodedsavannas.

Conclusions: Mesowear signatures, in association with HI, indicated that the diet of *G. punjabiensis* was most consistent with browsers as well as seasonal mixed feeders. *G. punjabiensis* was not an exclusively browser or grazer. Rational for the abrasion-attrition gradients within the mixed feeding adaptation is that the Middle Miocene mammalian assemblage is represented by a diverse populations or cohorts of organisms that accumulated over 3.9 Ma (ca.14.2-10.3 Ma) and it is most likely that animals died at different intervals of the year and therefore had paleodiets which varied seasonally. The paleoecology of studied taxon reveals the persistence of mosaics of diverse habitats ranging from tropical evergreen forests to subtropical ones, closed and seasonal woodlands to wooded savannas. This study contributes to the understanding of evolution of dietary

preferences and paleoecology among Siwalik Sivatherines.

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APPENDIX 1: Specimens used to determine the hypsodonty index for *Giraffokeryx punjabiensis* Pilgrim, 1910.

Catalogue No.	Tooth Position	H	W	HI
GCUPC 1286/10	lm3	21.16	17.45	1.21
GCUPC 1308/11	rm3	18.00	15	1.20
GCUPC 1242/10	lm3	27.00	22.75	1.67
GCUPC 1243/10	lm3	21.00	17.00	1.23
GCUPC 1240/10	rm3	25.16	18.00	1.38
GCUPC 1249/10	lm3	22.12	17.50	1.25

Mean HI= 1.31±0.06

APPENDIX 2: Raw mesowear-I and II data of *Giraffokeryx punjabiensis*, Cusp relief is categorized as high (H) or low (L) based on how high the projection of cusps above the inter-cusp valley. The mesowear “ruler” is utilized by matching the dental cusp apex of fossil species with one of the seven (0-6) reference cusps to assign the score and standardize the data.

Catalogue No.	Tooth Position	Mesowear-I		Mesowear-II
		Cusp relief	Cusp shape	MS
GCUPC 1329/11	M2	H	S	0-1
GCUPC 1335/11	M2	H	S	0-1
GCUPC 1305/11	M2	H	S	0-1
GCUPC 1276/10	M2	H	S	0-1
GCUPC 1272/10	M2	H	S	0-1
GCUPC 491/02	M2	H	R	2-3
GCUPC 1336/11	M2	H	R	2-3
GCUPC 1142/09	M2	H	R	2-3
GCUPC 1166/09	M2	H	R	2-3
GCUPC 490/02	M2	H	R	2-3
GCUPC 1320/11	M2	H	S	0-1
GCUPC 1138/09	M2	H	R	2-3
GCUPC 1325/11	M2	H	S	0-1
GCUPC 1174/09	M2	H	S	0-1
GCUPC 1172/09	M2	H	S	0-1
GCUPC 1135/09	M2	H	S	0-1
GCUPC 1275/10	M2	H	S	0-1