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Mesowear analysis and paleodiets of Middle Miocene artiodactyls from Chakwal, Punjab, Pakistan

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ABSTRACT: Mesowear analysis was performed to infer the paleodiet of the Middle Miocene artiodactyls by scoring the mesowear variables. In this analysis, the maxillary and mandibular cheek teeth (P4-M3 and p4-m3) of six bovid species (*Miotragocerus gluten*, *Tragoportax salmontanus*, *Helicoportax tragelaphoides*, *Elachistoceros khuristenensis*, *Eotragus* sp., and *Gazella* sp.), two giraffid species (*Giraffokeryx punjabiensis*, *Giraffa priscilla*), two tragulid species (*Dorcatherium majus*, *D. minus*) and two suid species (*Listriodon pentapotamiae*, *Conohyus sindiensis*) were included. The results show that the bovids were browse-dominated mixed feeders, the giraffids and the tragulids were preferably browsers, and most of the suids were browse-dominated mixed feeders with preferably grazers. These paleodietary analyses specify a browsing trend with a gradual shift towards mixed feeding during the Middle Miocene. These results also endorse the presence of mosaic habitats range from moist, humid forests more or less closed to grassland during the Middle Miocene of Punjab, Pakistan.

KEY WORDS: Bovidae, Tragulidae, Giraffidae, Paleoecology, Siwaliks.

INTRODUCTION

Mesowear is a dental wear technique that can be used to infer ancient herbivore's diets (herein referring to artiodactyls) by scoring of molar tooth cusps (Fortelius and Solounias, 2000; Ackermans, 2020). Mesowear provides the answers to the questions regarding paleoenvironments and has proven to be an appropriate method for paleodietary inference (Rivals and Semprebon, 2006; Semprebon and Rivals, 2007; Mihlbachler *et al.*, 2011; Fraser and Theodor, 2013; Ackermans, 2020). The cheek teeth experience two types of tooth wear during the buccolingual chewing stroke: attrition (tooth on tooth wear) and abrasion (food on tooth wear) (Fortelius and Solounias, 2000; Ackermans, 2020).

Attrition is the main cause of wear and occurs when opposing wear facets interact. The soft nature of a browse-based diet causes opposing teeth to wear themselves, as the diet itself does not provide resistance (Sanson, 2006). The teeth of browsing animals are, therefore, specialized for puncturing tough leaf tissue, which leads to the mutual sharpening of opposing wear facets (Fortelius and Solounias, 2000; Kaiser and Fortelius, 2003). On the other hand, abrasion occurs when the teeth interact with phytoliths (plant-borne abrasives) (Xia *et al.*, 2015; Merceron *et al.*, 2018) or exogenous grit (other ingested items) (Healy, 1967; Sanson *et al.*, 2007; Damuth and Janis, 2011; Lucas *et al.*, 2013). Grazing animals generally tend to feed close to the ground in open habitats, where plants become covered in external abrasives, for example dust and grit (Janis and Fortelius, 1988). Grazers ingest comparatively large amounts of exogenous grit that reduces the sharpness of wear facets (Fortelius and Solounias, 2000; Kaiser and Fortelius, 2003; Kaiser and Solounias, 2003; Damuth and Janis, 2011; Jardine *et al.*, 2012).

The degree of attrition and abrasion in the cheek teeth varies among species that feed on plant materials with different physical properties. Generally, the species feeding on leaves from trees and bushes (i.e. dicots or browse) experience the highest degrees of attrition while those feed on grasses (i.e. monocots or graze) experience the highest degrees of abrasion. An abrasion-attrition wear gradient is used to assign dietary categories to herbivores, with browsers generally showing a more attrition-based wear pattern, and grazers a more abrasion-dominated pattern (Fortelius and Solounias, 2000).

Fortelius and Solounias (2000) introduced the original mesowear technique (mesowear I) to reconstruct general paleodiets of fossil ungulates by observing the wear on their only upper second molars. Then this method has been extended to the mandibular and maxillary molars and fourth premolars of equids (Kaiser and Fortelius, 2003; Kaiser and Solounias, 2003). Franz-Odendaal and Kaiser (2003) applied this method to maxillary M3 and mandibular m2 in ruminants. In 2010, Fraser and Theoder adapted mesowear I for lagomorph's maxillary and mandibular P4-M2 while Purnell and Jones (2012) adapted it for P1 elements of Conodonta. Ulbrichtet *et al.*, (2015) adapted classical mesowear for

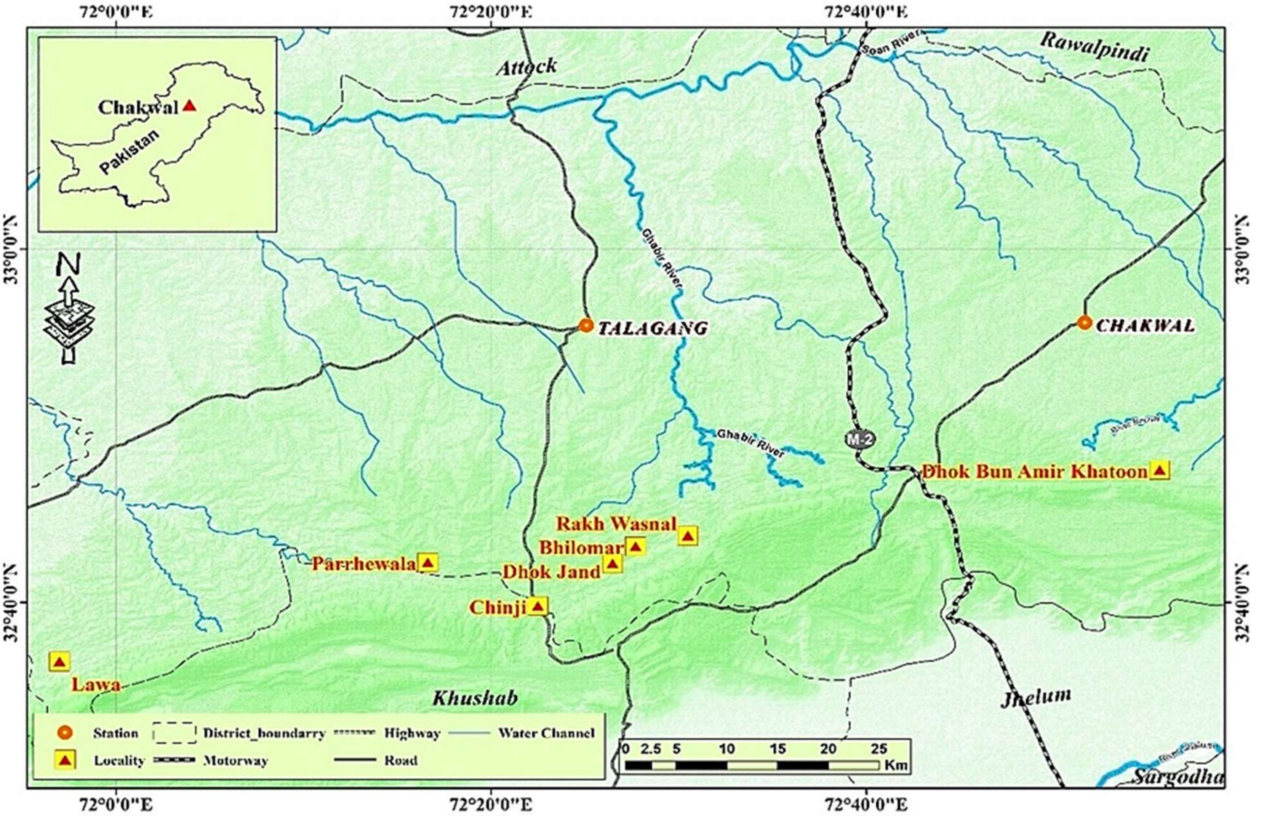

Fig. 1. Map showing the studied sites of district Chakwal, Pakistan.

the maxillary M1–M2, and mandibular p3 in Leporinae and distal side of the maxillary M1 and mandibular m1 in Murinae. Kropacheva *et al*. (2017) applied this method for maxillary M1–M2 and mandibular m1 of voles.

Belmaker *et al*. (2007) studied *Selenoportax,* Hipparionini and *Tragoceridus* sp. from the Siwalik of Pakistan but Tariq (2010) provided his valuable addition in the analysis of paleodiet of extant and extinct ungulates by using microwear and mesowear technique. Tariq and Jahan (2014) investigated the paleodiet and paleoecology of *Giraffokeryx punjabiensis* with the help of mesowear-I, mesowear-II and hypsodonty methods. Nawaz *et al*. (2022) and Ghaus *et al*. (2024) analyzed the paleodiets of Middle Miocene mammalian species from Lower Siwaliks of Pakistan using dental Mesowear I and the principal author was the part of these works. No other significant work has been done up to now for the interpretations of paleodiets from the Siwaliks of Pakistan.

The current work adds new information in the field of paleoecology and help to infer the paleodiet and paleoenvironment of the Middle Miocene artiodactyls from the Lower Siwalik Subgroup. This study also extends the mesowear I method to the maxillary and mandibular cheek teeth of artiodactyls.

MATERIALS AND METHODS

The studied material was collected from the seven Middle Miocene sites of district Chakwal, Pakistan: Dhok Bun Amir Khatoon (Lat. 32°47′ N; Long. 72°55′E), Chinji Rest House (Late. 32°40′N; Long. 72°22′E), Parrewala (Late. 32°70′N; Long. 72°27′E), Lawa (Lat. 32°36′N, Long. 71°56′E), Bhilomar (Lat. 32°71′N: Long. 72°46′E), Rakh Wasnal (Late. 32°72′N: Long. 72°50′E) and Jand (Late. 32°70′N: Long. 72°44′E; Fig. 1). Total 111 samples were selected for mesowear, and this collection is placed at Dr. Abu Bakr Fossil Display & Research Center, Institute of Zoology, University of the Punjab, Lahore, Pakistan.

Mesowear I technique was employed as it is a straightforward, relying on cusp height and sharpness and easily categorize the diets without any training or using complex equipment (Ackermans, 2020; Mihlbachler *et al*., 2023). This proxy is applied on maxillary and mandibular cheek teeth (P4-M3 and p4-m3) of six bovid species (*Miotragocerus gluten*, *Tragoportax salmontanus*, *Helicoportax tragelaphoides*, *Elachistoceros khuristenensis*, *Eotragus* sp. and *Gazella* sp.), two giraffid species (*Giraffokeryx punjabiensis* and *Giraffa priscilla*), two tragulid species (*Dorcatherium majus* and

Table 1. Mesowear frequency of twelve Middle Miocene species of district Chakwal with percentage of OR (High and Low) and CS (Sharp, Round and Blunt).

Taxon	N	Occlusal relief (OR)				Cusp shape (CS)					
		high	%High	low	%Low	Sharp	%Sharp	Round	%Round	Blunt	%Blunt
Miotragocerus gluten	19	5	26.32	14	73.68	5	26.32	13	68.42	1	5.26
Tragoportax salmontanus	8	7	87.5	1	12.5	4	50	4	50	0	0
H. tragelaphoides	4	1	25	3	75	1	25	3	75	0	0
E. khauristenensis	2	1	50	1	50	1	50	1	50	0	0
Eotragus sp.	9	4	44.44	5	55.56	2	22.23	5	55.56	2	22.23
Gazella sp.	28	19	67.86	9	32.14	14	50	14	50	0	0
G. punjabiensis	29	23	79.31	6	20.69	16	55.17	13	44.83	0	0
G. priscilla	15	12	80	3	20	12	80	2	13.33	1	6.67
D. majus	6	5	83.33	1	16.67	4	66.67	2	33.34	0	0
D. minus	7	6	85.71	1	14.29	6	85.71	1	14.29	0	0
L. pentapotamiae	37	22	59.46	15	40.54	13	35.14	23	62.16	1	2.7
C. sindiensis	11	0	0	11	100	0	0	11	100	0	0

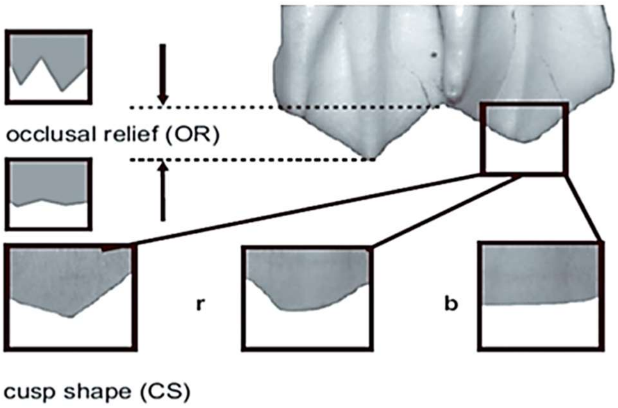

Fig. 2. The mesowear scoring convention for cheek teeth as defined by Fortelius and Solounias (2000) for upper second molars. The convention is extended to other tooth positions (P4-M3, p4-m3).

D. minus) and two suid species (*Listriodon pentapotamiae* and *Conohyus sindiensis*), collected from the Middle Miocene Siwalik Group. The buccal cusps of the maxillary cheek teeth and the lingual cusps of the mandibular cheek teeth were scored because they are analogous. Only those specimens included in the study that have intact maxillary and mandibular cheek teeth at an intermediate stage of the wear. Individuals with highly worn (old) or unworn (young) cheek teeth were excluded from the analysis, following Fortelius and Solounias (2000). The teeth were examined (from buccal surfaces) at close range using a hand lens.

The two variables of mesowear i.e. the occlusal relief (OR) and cusp shape (CS) were scored according to the method proposed by Fortelius and Solounias (2000; Fig. 2). The teeth were scored only for unbroken cusps and selected the sharpest cusp as per Fortelius and Solounias (2000). The occlusal relief categories were high (h) and low (l) depending on how high the cusps rise above the valley between them (Fortelius and Solounias, 2000). The cusp shape categories were sharp (s), rounded (r) and blunt (b) according to the degree of facet development. The degrees of relief and cusp sharpness are dependent

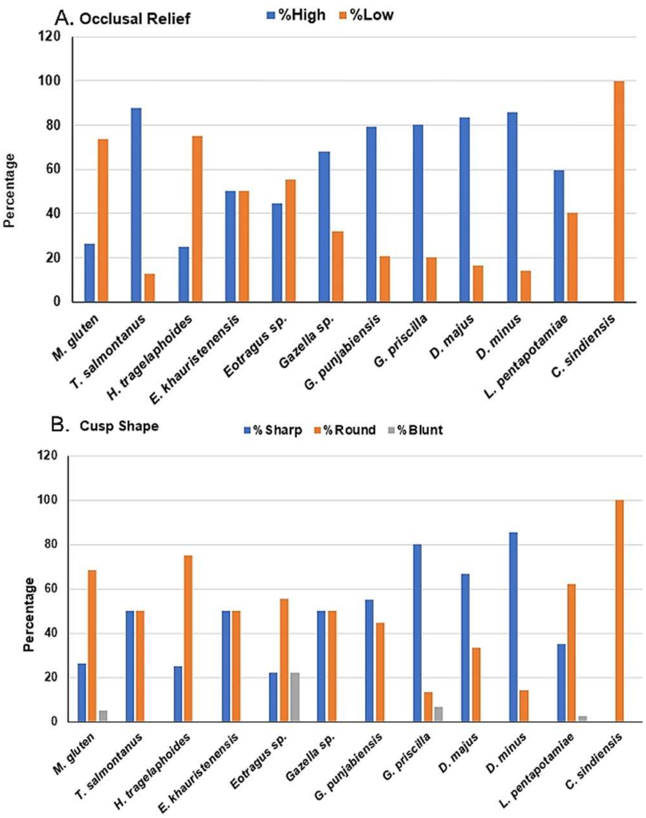

Fig. 3. Histogram of mesowear variable of the Middle Miocene artiodactyls of district Chakwal, Pakistan. **A.** Occlusal Relief (OR). **B.** Cusp Shape (CS)

variables. Higher occlusal relief tends to be sharper compared to low relief cusps and cusps with zero relief are obviously blunt. After each specimen had been recorded for cusp shape and occlusal relief in tabulated form, the percentages of individuals of each species exhibiting sharp, blunt, and high cusps were calculated. The mean mesowear variables were calculated for the dietary construction of histograms based on the percentage of sharp, round, or blunt cusps; along with the percentage of high or low relief.

RESULTS

The classical mesowear I method was tested by comparing the individual scored frequencies for the mesowear variables i.e. OR (perhigh, perlow) and CS (persharp, perround and perblunt). The mesowear scored specimens belonging to four families of Artiodactyla: Bovidae, Giraffidae, Tragulidae and Suidae. The occlusal relief and cusp shape data of the studied families is given in Table 1. The occlusal relief in Bovidae (Table 1; Fig. 3A) ranged between 87.5% (*Tragoportax salmontanus*) to 25% (*Helicoportax tragelaphoides*) high and 73.68% (*Miotragocerus gluten*) to 12.5% (*T. salmontanus*) low. The cusp shape (Table 1; Fig. 3B) ranged between 50% (*T. salmontanus, Elachistoceros khuristenensis* and *Gazella* sp.) to 22.23% (*Eotragus* sp.) sharp, 75% (*H. tragelaphoides*) to 50% (*T. salmontanus, E. khuristenensis* and *Gazella* sp.) round and 22.23% (*Eotragus* sp.) to 0% (*T. salmontanus, H. tragelaphoides*, *E. khuristenensis* and *Gazella*) blunt. Comparing the histograms, we find similarity in the occlusal relief data (perhigh, perlow); three bovid species among six *M. gluten, H. tragelaphoides* and *Eotragus* sp. show high relief with round cusp shape while rest three *T. salmontanus, E. khuristenensis and Gazella* sp. demonstrate low relief with sharp and round cusp shapes in equal proportion. However, it is notable that the histogram of *T. salmontanus, H. tragelaphoides*, *E. khuristenensis* and *Gazella* sp. is more similar while having no blunt cusp scores (Fig. 3B).

Histogram of *M. gluten* reveals that high occlusal relief was scored as 26.32% and low as 73.68% (Fig. 3A). The cusp shape was scored 26.32% as sharp, 68.42% as round and 5.26% as blunt (Fig. 3B). The occlusal relief of *T. salmontanus* was recorded high as 85.5% and low as 12.5% (Fig. 3A). The cusp shape was recorded sharp and round as 50% and no specimen was scored as blunt (Fig. 3B). The high occlusal relief and sharp cusp shape of *H. tragelaphoides* were scored as 25% while low relief and round was recorded as 75%. No specimen scored as blunt (Fig. 3B). No specimen of *E. khuristenensis* was blunt and 50% specimens were recorded as high and sharp compared with low and round (Fig. 3B). The occlusal relief 44.44% specimens of *Eotragus* sp. were recorded as high and 55.56% as low (Fig. 3A). The cusp shape of 22.23% specimens were scored as sharp and blunt while 55.56% as round (Fig. 3B). Histogram of *Gazella* sp. shows that the occlusal relief 67.86% specimens were recorded as high and 32.14% as low (Fig. 3A). No specimen was scored as blunt while 50% specimens were observed as sharp relief with round cusp shape (Fig. 3B).

The occlusal relief data of Giraffidae (Table 1; Fig. 3A) ranged between 80% (*Giraffa priscilla*) to 79.31% (*Giraffokeryx punjabiensis*) high and 20.69% (*G. punjabiensis*) to 20% (*Giraffa priscilla*) low. The cusp shape (Table 1; Fig. 3B) ranged between 80% (*Giraffa priscilla*) to 55.17% (*G. punjabiensis*) sharp, 44.83% (*G. punjabiensis*) to 13.33% (*Giraffa priscilla*) round and 6.67% (*Giraffa priscilla*) to 0% (*G. punjabiensis*) blunt. Histogram of both giraffid species show resemblance in occlusal relief and cusp shape while having high and sharp cusps for maximum specimens as compared with low and round cusps. Some specimens of *Giraffa priscilla* were recorded as blunt (Fig. 3B). Histogram of *G. punjabiensis* indicates that no specimen (0%) was scored as blunt, 79.31% were high, 20.69% were low, 55.17% sharp and 44.83% round (Fig. 3A, B). Histogram of *Giraffa priscilla* specifies that high and sharp were 80%, low 20%, round 13.33% and blunt were 6.67% (Fig. 3A, B).

The occlusal relief of Tragulidae (Table 1; Fig. 3A) extended between 85.7% (*Dorcatherium minus*) to 83.33% (*Dorcatherium majus*) high and 16.67% (*D. majus*) to 14.29% (*D. minus*) low. The cusp shape (Table 1; Fig. 3B) ranged between 85.71% (*D. minus*) to 66.67% (*D. majus*) sharp, 33.34% (*D. majus*) to 14.29% round (*D.* minus) and no specimen (0%) was found blunt (Fig. 3B). By comparing the histogram, high degree of similarity can be seen in occlusal relief and cusp shape while having maximum specimens with high and sharp cusps compared with low and round and lacking blunt specimen in both *Dorcatherium* species. Histogram of *D. majus* designates that no specimen (0%) was recorded as blunt, 83.33% high, 16.67% sharp and 33.34% round. Like *D. majus* none of the specimen of *D. minus* was scored as blunt, high and sharp were 85.71% and low and round were 14.29% (Fig. 3A, B).

The occlusal relief data of Suidae (Table 1; Fig. 3A) ranged between 59.46% (*Listriodon pentapotamiae*) to 0% (*Conohyus sindiensis*) high and 100% (*C. sindiensis*) to 40.54% (*L. pentapotamiae*) low. The cusp shape data (Table 1; Fig. 3B) ranged between 35.14% (*L. pentapotamiae*) to 0% (*C. sindiensis*) sharp, 100% (*C. sindiensis*) to 62.16% (*L. pentapotamiae*) round and 2.7% (*L. pentapotamiae*) to 0% (*C. sindiensis*) blunt. The histogram shows that low and round were maximum as compared to high and sharp, respectively, and minimum specimens were scored as blunt. The specimens of *L. pentapotamiae* indicate that 59.46% was high, 40.56% was low and 35.14% sharp, 62.16% round and 2.7% was blunt (Fig. 3A, B). The specimen of *C. sindiensis* designates that no specimen was high, sharp, and blunt while 50% specimens were low and 50% were round (Fig. 3A, B).

Statistical analyses were performed by using independent t-test and one-way ANOVA to test the significant differences in mesowear variables (occlusal relief and cusp shape) with significance set at $p<0.05$. Independent samples t-test revealed no significant differences between the high and low relief mesowear variables (Fig. 4A; Table 2). This indicates that the difference in means between the high and low relief groups was not large enough to be considered statistically significant.

Table 2. Difference between means of Occlusal Relief (OR) and Cusp Shape (CS) analyzed by independent t-Test.

Sr No.	OR	Mean ± SE	F value	P value	DF
1	High	8.75 ± 2.39	1.07	0.3123	1
2	Low	5.83 ± 1.50			
Sr No.	**CS**	**Mean ± SE**	**F value**	**P value**	**DF**
1	Sharp	6.50 ± 1.64	6.66	0.0037	2
2	Round	7.67 ± 2.02			
3	Blunt	0.42 ± 0.19			

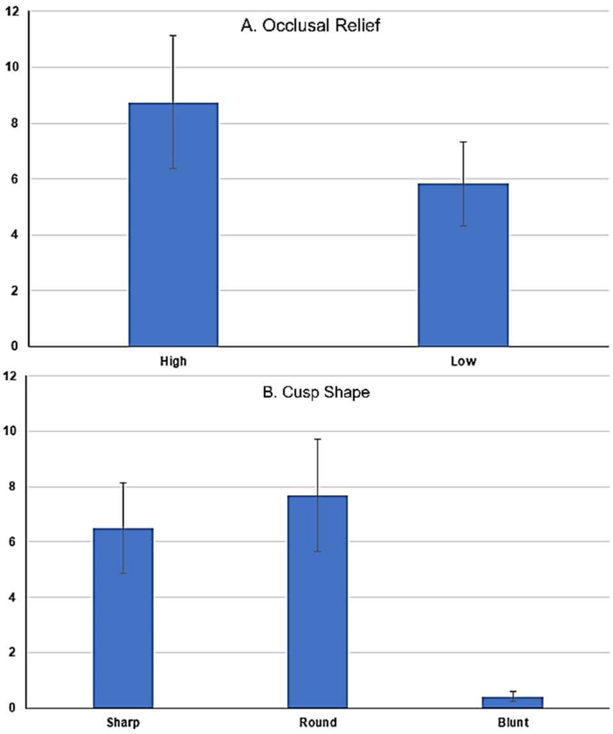

Fig. 4. Difference between means of **A.** Occlusal Relief analyzed by independent t-test. **B.** Cusp Shap analyzed by one-way ANOVA.

One-way Anova test was applied on the cusp shape and found that, means of CS differ significantly at P = 0.002 ≤ 0.05 (Fig. 4B; Table 2). This indicates there is a significant difference in mean cusp shape between at least two of the groups being compared. Overall, these findings highlight the importance of cusp shape as a marker for dietary habits or environmental factors among artiodactyls whereas occlusal relief may not be as indicative in the current results. However, it is important to mention that mesowear analysis is a subjective technique, and the categorization of occlusal wear can vary between observers. Previous studies have shown that interobserver error does not significantly affect the results, but it is still a potential source of variability.

DISCUSSION

Dental mesowear has been a valuable technique in evaluating the paleodiets of various herbivorous groups (Fortelius and Solounias, 2000; Solounias *et al*., 2010, 2013; Mihlbachler *et al*., 2011; Nawaz *et al*., 2022; Ghaus *et al*., 2024; Table 3). The newly recovered specimens from seven Middle Miocene sites of district Chakwal were tested for the interpretation of palaeodiets of four herbivorous families of Artiodactyla by roughly measuring the relative amounts of attrition and abrasion experienced by the maxillary and mandibular cheek teeth using mesowear I, a classical method designed by Fortelius and Solounias (2000). This method categorized the cheek teeth on the basis of two variables: cusp relief (high, low) and cusp shape (sharp, round, blunt) (Fortelius and Solounias, 2000). Individuals who experience high attrition (browsers) tend to have high relief and sharp cusps, while individuals who experience high abrasion (grazers) have low relief and blunt cusps. Intermediate or mixed feeders (10–90% grass consumption) tend to have low or high relief cusps with rounded tips, depending on whether their diet is dominated by grasses or browse diet (Fortelius and Solounias, 2000).

The graphical representation of *Miotragocerus gluten* (Fig. 3A, B) shows that they are browse-dominated mixed feeder. Tariq (2010) inferred *M. gluten* as a browser/mixed feeder in closed/semi-closed habitat, leaf and herb-eater in shrubland-light woodland habitats (Gentry and Kaiser, 2009). Nawaz *et al*. (2022) placed *Miotragocerus gluten* as an open habitat browser and closed habitat mixed feeder in dietary spectra (Merceron *et al*., 2007, 2010).

The mesowear pattern of *Tragoportax salmontanus* (Fig. 3A, B) places it within the dietary spectrum of the browse-dominated mixed feeder as the cusp shape of the specimens are sharp and round in equal proportions. But high occlusal relief shows its diet may be preferably browsing. Mesowear scorings of *Tragoportax* sp. specifies that it may be placed within browsing category and shows affinity with browsing living analogues (two cervids; *Odocoileus hemionus* and *Capreolus capreolus*) (Tariq, 2010). *Tragoportax* sp. has been a browser before 8 Ma and after that, became a mixed feeder by incorporating fruit and grass in their diet (Belmaker *et al*., 2007; DeMiguel *et al*., 2019).

The graphical representation of *Elachistoceros khauristanensis* and *Helicoportax tragelaphoides* (Fig. 3A, B) places them within the dietary spectrum of the browse-dominated mixed feeding. These inferences are in line with that of Tariq (2010) as he placed these small sized boselaphines in the category of selective browsers/fruigivores. The Mesowear analysis of *Eotragus* sp. shows (Fig. 3A, B) that they are mixed feeders that spending equal time in browsing and grazing. All the dental material on which Mesowear I is applied belong to mandibular dentition. This taxon was placed as mixed feeders or browse dominantly mixed feeders (Ghaus *et al*., 2024)

Dental Microwear analysis confirms that *Gazella* species were generally mixed feeders and browsers (Merceron *et al*., 2006). In current study, the *Gazella* sp.

Table 3. Dietary comparison of Middle Miocene artiodactyls species with previous studies.

No.	Species	Dietary category in previous studies	Dietary category in present Study
Family Bovidae			
1.	*M. gluten*	Browser or mixed feeder in closed habitats (Tariq, 2010; Gentry and Kaiser, 2009), Browser (Merceron *et al*., 2007, 2010; Nawaz *et al*., 2022)	Browse-dominated Mixed
2.	*T. salmontanus*	Browser before 8 Ma (belmaker *et al*. 2007; Tariq, 2010), Mixed (DeMiguel *et al*., 2019)	Browse-dominated Mixed
3.	*E. khauristanensis*	selective browsers/fruigivores (Tariq, 2010)	Browse-dominated Mixed
4.	*H. tragelaphoides*	selective browsers/fruigivores (Tariq, 2010)	Browse-dominated Mixed
5.	*Eotragus* sp.	Mixed feeders or browse dominantly mixed feeders (Ghaus *et al*., 2024)	Mixed feeder with spending equal time in browsing and grazing
6.	*Gazella* sp.	Mixed feeder in closed habitats (Badgley *et al*., 2008; Tariq, 2010), Mixed feeder or browse dominated mixed feeder (Nawaz *et al*., 2022; Ghaus *et al*., 2024)	Browse-dominated Mixed
Family Giraffidae			
7.	*G. punjabiensis*	Regular, selective, high-level browser (Janis,1988; Badgley *et al*., 2008; Damuth and Janis, 2011; Patnaik *et al*., 2019), Browser or mixed feeder in closed habitats (Tariq, 2010; Tariq and Jahan, 2014), Browser (Nawaz *et al*., 2022)	Preferably browser
8.	*G. priscilla*	Browser (Janis,1988; Badgley *et al*., 2008; Damuth and Janis 2011; Patnaik *et al*., 2019), High-level browser (Tariq, 2010; Tariq and Jahan, 2014), Browser (Nawaz *et al*., 2022)	Preferably browser
Family Tragulidae			
9.	*D. majus*	Browser (Thomas, 1977, 1984; Solounias *et al*., 1995; Barry *et al*., 2005; Bibi, 2007; Khan *et al*., 2010, 2012; Khan and Akhtar, 2013; Patnaik *et al*., 2019)	Preferably browser
10.	*D. minus*	Frugivore/browser (Badgley *et al*., 2008), Selective browser (Tariq, 2010) Browser (*Dorcatherium* sp.) (Patnaik *et al*., 2019), Browser (Nawaz *et al*., 2022; Ghaus *et al*., 2024)	Preferably browser
Family Suidae			
11.	*L. pentapotamiae*	Browser (Leinders, 1976; Made, 1996; Agusti *et al*., 1999; Pickford and Morales, 2003; Badgley *et al*., 2008; Ghaus *et al*., 2024), Regular browser (Tariq, 2010), Mixed feeder or browse dominated mixed feeder (Nawaz *et al*., 2022)	Browse-dominated Mixed
12.	*C. sindiensis*	Browser (Tariq, 2010; Ghaus *et al*., 2024)	Mixed feeder

is placed in the browse-dominated mixed dietary category (Fig. 3A, B). Nawaz *et al*. (2022) and Ghaus *et al*. (2024) also positioned *Gazella* sp. as a mixed feeder or browse dominated mixed feeder in dietary spectra. Tariq (2010) placed *Gazella* in the mixed feeding group. The mixed feeding lifestyle endorses the occurrence of plentiful herbaceous vegetation in the Middle Miocene of the Siwaliks.

The present mesowear findings for *Giraffokeryx punjabiensis* and *Giraffa priscilla* (Fig. 3A, B) indicate that they are preferably browsers but later shows little interest in grazing. The results are in line with Tariq (2010) who found both lineages as high-level browsers. Based on hypsodonty interpretations by Janis (1988), and Damuth and Janis (2011), *G. punjabiensis* may be classified as regular, selective, and high-level browsers. Nawaz *et al*. (2022) results of *G. punjabiensis* and *Giraffa priscilla* dietary categories are in line with the current study.

Dorcatherium majus and *D. minus* (Fig. 3A, B) make their position in the browsing group based on current analysis. The browsing habit of *Dorcatherium* also suggested by Thomas (1977, 1984), Solounias *et al*. (1995), Barry *et al*. (2005), Bibi (2007), Khan *et al*. (2010, 2012) and Khan and Akhtar (2013). Nawaz *et al*. (2022) and Ghaus *et al*., 2024 placed *D. minus* as browser in dietary spectra in recent studies. These species fed on a broad array of buds, leaves and shoots with high protein content, as well as on limited amounts of vegetation with abrasive particles (Bouvrain, 1994; Khan *et al*., 2009, 2010, 2012). Their dry-land dietary habits include fruits and leaves (Dubost, 1978).

In case of Suidae family, *Listriodon pentapotamie* fall in the category of the browse-dominated mixed feeder. The high occlusal relief shows its diet was preferably browsing and the round cusp shape pointing toward mixed feeding category. The *Conohyus sindiensis* is regarded as mixed feeders as all the specimens show low occlusal relief with round cusp (Fig. 3A, B). Tariq (2010) placed the medium sized suids, *L. pentapotamie* and *C. sindiensis* as a regular browser. Wooded or forested environment may point towards the browsing nature of the listriodonts (Agusti *et al*., 1999). *Listriodon* were lophodont, herbivores and browse on vegetation (Leinders, 1976; Made, 1996; Pickford and Morales, 2003; Ghaus *et al*., 2024). Nawaz *et al*. (2022) characterized *L. pentapotamie* as a mixed feeder on the basis of dental mesowear analysis.

The deviation in current findings of above-mentioned dietary category of different taxa may be due to the incorporation of mandibular teeth and forth premolar in mesowear analysis. It seems that the mesowear score of mandibular cheek teeth is responsible for the variations as the lower cheek teeth lose their sharpness because of the effects of unloaded food (gravity), relaxation of maxillary tooth over the mandibular tooth cusp and experience greater wear because of prolonged contact with the food (Fraser *et al*., 2014).

CONCLUSIONS

Mesowear analysis was conducted to assess the dietary categories of the Middle Miocene artiodactyls from district Chakwal, Punjab, Pakistan, based on two variables. Based on the current mesowear dietary analysis, it is concluded that mostly the bovids are browse-dominated mixed feeders, giraffids and tragulids are preferably browsers, and suids are browse-dominated mixed feeder. These paleodietary analysis specify that, there was a browsing trend with a gradual shift towards mixed feeding during the Middle Miocene. This analysis reflects that browsers were more dominant than grazers during the Middle Miocene. These results also endorse presence of mixture of habitats, ranging from moist, humid forests more or less closed to grassland during the Middle Miocene of district Chakwal, Punjab, Pakistan.

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