

Dental microwear texture analysis of late Pliocene *Procynocephalus subhimalayanus* (Primates: Cercopithecidae) of the Upper Siwaliks, India

Research Article

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Abstract: Late Pliocene *Procynocephalus subhimalayanus* from the Upper Siwaliks, India is known from only three specimens. The dietary proclivities of this taxon have implications for reconstructing the paleoecology of the Upper Siwaliks. The dental microwear texture properties of *Procynocephalus* are compared to those from extant tropical forest primates including *Alouatta palliata* (n = 11), *Cebus apella* (n = 13), *Gorilla gorilla* (n = 9), *Lophocebus albigena* (n = 15) and *Trachypithecus cristatus* (n = 12). Dental microwear textures are generated by scanning the surface enamel of Facet 9 using white-light confocal microscopy at 100x. Four variables were extracted from scale-sensitive fractal analysis, and the data were ranked before ANOVA with post-hoc tests of significance and multivariate analyses were performed. *Procynocephalus* clusters closest to *Lophocebus*, *Cebus* and some *Gorilla* specimens suggesting hard-object feeding characterized a portion of its diet. The dental microwear texture of *Procynocephalus* supports interpretations of widespread grasslands of the Late Pliocene Kansal Formation (Pinjor zone). The extreme enamel complexity characterizing *Procynocephalus* may derive from consumption of underground storage organs, or other foods with high grit loads. Foods consumed near ground level carry a heavy load of abrasive minerals possibly contributing to greater enamel surface complexity and textural fill volume.

Keywords: Pinjor • Kansal Formation • papionin • *Parapapio whitei* • *Paranthropus robustus*
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1. Introduction

Procynocephalus subhimalayanus [1, 2] was the first primate fossil to be formally described, and the first fossil recognized as a primate. Even 176 years later, little is known about the taxon which is represented by only three specimens, two of which were discovered in the 1830s and present difficulties in terms of provenance [3]. One spec-

imen was more recently discovered [4], and because its location was recorded at the time of discovery, has been ascribed a more definitive date of 2.5 to 1.7 Ma and probably close to 2 Ma based on paleomagnetic stratigraphy [3, 5]. This specimen was identified as *Procynocephalus pinjori* by Verma [4] and subsequent authors [5] although the remarkable similarity of this specimen to gnathic material attributed to *Procynocephalus subhimalayanus* discovered in the 1830s from the Kansal Formation gives the latter name priority [2]. *Procynocephalus subhimalayanus* is similar in its midfacial morphology and dentition to late Pliocene *Procynocephalus wimani* of Northern China

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[2, 4] which is associated with highly terrestrial postcranial adaptations such as slight dorsal rotation of the medial epicondyle of the humerus and an elongated olecranon process of the ulna [2].

The presence of *Procynocephalus* of the Kansal Formation (Pinjor zone) marks the entrance of cercopithecids into the foothills of the Himalaya, a rather isolated province with a high degree of endemic fauna [5]. *Procynocephalus* occurs after the appearance of *Equus* in the region at the Gauss-Matuyama boundary [5] (Figure 1). The appearance of *Procynocephalus* provides additional evidence for the turnover of fauna in the Upper Siwaliks after 2.5 Ma. Two other cercopithecoid monkeys from the Upper Siwaliks, *Theropithecus delsoni* and *Macaca paleoindica*, are roughly contemporaneous with *Procynocephalus*, and indicate several papionin taxa exploited the region [3].

There are no cercopithecoid taxa in the Upper Siwaliks before 6.3 million years ago suggesting the new arrivals came from elsewhere [3]. The first cercopithecoid monkey to inhabit the area is the colobine *Presbytis sivalensis*; however, no cercopithecine monkeys are noted in the Upper Siwaliks until the Pinjor stage [3]. Africa was probably the origin of cercopithecoid monkeys given the middle Miocene remains of *Victoriapithecus* (21–9 Ma) the earliest known Old World monkey [6–8]. After the Sahara desert initially formed 8–7 Ma [9], cercopithecoid taxa of western Eurasia and Africa became increasingly separated. By the late Miocene, *Macaca* is represented in Algeria and Libya [2]. *Macaca* is found by 5–4 Ma in France, and subsequently throughout Europe [10]. The relatively early dates for *Macaca* fossil taxa in Europe suggest a migration into the Upper Siwaliks from the West, represented by late Pliocene *Macaca paleoindica* [2, 3].

Alongside the migration eastward of *Macaca*, closely related macaque-like *Paradolichopithecus* and *Procynocephalus*—possibly representing the same genus—radiated broadly across Eurasia [2, 3, 11]. The shared maxillary sinus morphology of *Macaca* and *Paradolichopithecus sushkini* from Tajikistan indicates macaques radiated to the East through central rather than southern Asia [12]. Alternatively, *Paradolichopithecus sushkini* could have evolved its macaque-like maxillary morphology independently given its absence in early Pleistocene *Paradolichopithecus gansuensis* from China [13].

Although the relationship between *Macaca*, *Paradolichopithecus* and *Procynocephalus* is equivocal, the former has smaller teeth and jaws [2, 3]. Furthermore, *Macaca* exhibits the limbs of an arboreal animal while *Paradolichopithecus* and *Procynocephalus* can be characterized as baboon-like in their terrestrially adapted limb bone skeleton [2, 10, 11]. *Paradolichopithecus* has been posited as at

least partly terrestrial from postcranial adaptations convergent with A.L. 288-1, attributed to *Australopithecus afarensis*, an early hominin [14].

Procynocephalus subhimalayanus has been posited as possibly semi-terrestrial from its relatively large muzzle compared to most arboreal primates [2]. Additional support for semi-terrestriality in *Procynocephalus* is gleaned from paleoecological reconstructions which posit a further spreading of grasslands and the shrinking of forests in the Pliocene, a process initiated in the late Miocene in temperate Eurasia with the rise and subsequent spread of C₄ grasses [3, 15]. By 2.5 Ma, C₄ grasses dominated the ground cover of the region [15] coincident with the arrival of *Equus* [5]. *Procynocephalus* may have increased its adaptability to temperate Eurasia by including grassland products such as seeds, bark and possibly underground storage organs (USOs) of C₄ grasses in its dietary repertoire [16]. If the inferred grassland exploitation of early cercopithecoid monkeys in Eurasia, such as *Procynocephalus*, is correct, its dental microwear texture characteristics may not resemble those typical of arboreal forest primates.

To test this hypothesis, the dietary proclivities of *Procynocephalus subhimalayanus* is compared to those from extant primate taxa with known diets (Figure 1) using white-light confocal microscopy followed by dental microwear texture analysis [17–24]. We anticipate that *Procynocephalus* will be more similar to larger-bodied taxa, such as grey-cheeked mangabey monkeys (*Lophocebus*) and perhaps *Gorilla*. Given the mineral accumulation on plants from grasslands and savannas [25], it may be the case that habitat heavily contributes to distinctions between primates living in tropical forests and those from temperate zones dominated by low lying shrubs, grasses and small trees. In this regard, *Procynocephalus* from the grasslands of the Upper Siwaliks may be distinct from extant forest primates from closed habitats, even those which are semi-terrestrial such as *Gorilla*.

2. Materials and Methods

2.1. Materials

Procynocephalus subhimalayanus originates from the late Pliocene deposits at Bunga, Haryana, Chandigarh, India [4], between Chandigarh and the town of Pinjor [5]. Its dentition has been described as indicating a generalized diet resembling that of extant baboons [2]. The maxilla is large compared to *Macaca*. The unverted mandibular corpus base and lack of gnathic fossae provides a super-

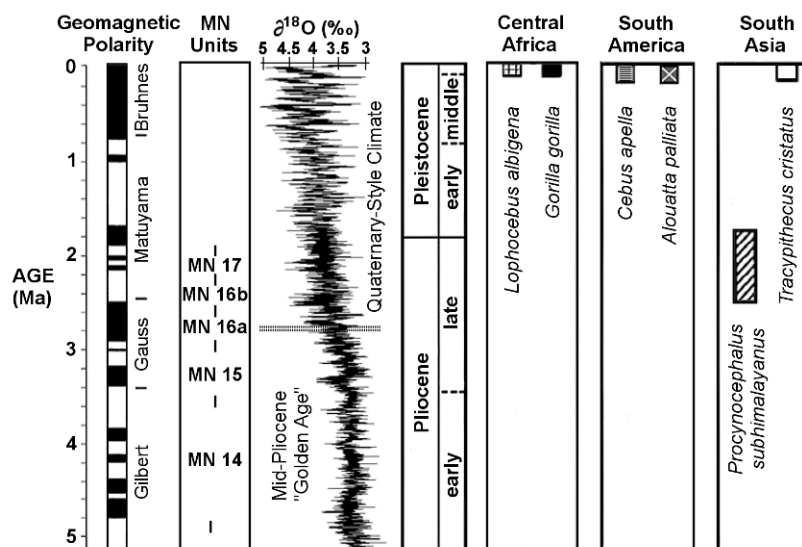


Figure 1. Geochronology of the Pliocene to the present provides a context for *Procynocephalus subhimalayanus* and the extant primates examined.

ficial resemblance to *Macaca*, *Parapapio* and other Plio-Pleistocene cercopithecoid monkeys [2, 11]. The specimen we examine (GSI 18453) is an adult female mandibular second molar from the Kansal Formation, or Pinjor zone, of the Upper Siwaliks [2, 3]. GSI 18453 is one of only three specimens attributed to *Procynocephalus subhimalayanus*, and the only specimen of this taxon with secure locality data [3].

Comparative observations from extant primate analogues are from Appendix 1 of [19], and include dedicated folivores which consume leaves, stems and some fruit such as in *Alouatta palliata* ($n = 11$) and leaves, stems and seeds such as in *Trachypithecus cristatus* ($n = 12$); a generalized folivore-frugivore which eats terrestrial herbaceous vegetation, ripe fruit, bark, pith and leaves such as *Gorilla gorilla gorilla* ($n = 9$), as well as mixed-fruit hard-object consumers and extractive foragers such as *Lophocebus albigena* ($n = 15$) and *Cebus apella* ($n = 13$). These primate taxa were chosen because of their reliability in other microwear studies in detecting fundamental distinctions in dietary profiles [18, 19, 23, 24]. Semi-terrestrial primates such as some species of *Macaca* and *Papio* were not considered because they have not yet been shown to yield distinct dental microwear texture characteristics. The opportunistic and idiosyncratic diets of *Macaca* and *Papio* may be extremely variable in dental microwear texture properties across individuals within and between species. *Procynocephalus* lacks the extreme dental specialization of tall columnar molars (hypsodonty) characterizing *Theropithecus gelada* which is terrestrial but was not included.

Microwear was observed on a high-quality epoxy resin dental cast, prepared from a mold, or impression, of the tooth using polyvinylsiloxine (Coltène-Whaledent). The original specimen was located at the American Museum of Natural History (New York) at the time the impression was created. The tooth was coated with shellac remover followed by isopropyl alcohol and molding material. The cast was prepared by pouring centrifuged epoxy resin and hardener (Buehler) directly onto the nested dental impression with the excess captured by putty walls, stabilized previously with hardener.

2.2. Data capture

The specimen was first examined under lower objectives to locate discernible evidence of microwear as many fossils lack any trace of dietary wear patterns [26] which further limits available fossil samples in studies of dental microwear [21]. The specimen GSI 18453 was examined under a white-light confocal microscope (Sensofar Plμ) at 100x equipped with an optical imaging system (Solarius Development Inc.). Microwear was scanned on the buccal surface of the hypoconid (facet 9) of the second mandibular molar corresponding to the surface of the cusp where foods are crushed (Phase II facet) rather than sliced. Four contiguous scans, shown for *Procynocephalus* in Figure 2, yielded a cloud of points with a viewing field of $138 \times 102 \mu\text{m}$ generated from a total area sample of $276 \times 204 \mu\text{m}$ [23]. A digital elevation map, derived from sampling the viewing field at $0.005 \mu\text{m}$ (y-axis) and $0.18 \mu\text{m}$ (x-axis),

was created to provide a visual assessment of surface complexity and distinctions in surface elevation such as those shown in Figure 3. The four scans were leveled using the software package SolarMap Universal.

The leveled surface image was analyzed using scale-sensitive fractal analysis which allows for the identification of the scaled lengths, two and three-dimensional geometry and volumetric estimates of enamel surfaces. The programs Toothfrax and SFrax (Surfract.com) reduced the point cloud to raw data for subsequent analyses. Toothfrax estimated textural complexity (*Asfc*), scale of maximum complexity (*Smc*) and anisotropy (*epLsar*) while the program SFrax calculated textural fill volume (*Tfv*). Scale-sensitive fractal analysis incorporates principles from fractal geometry as idealized shapes deriving from Euclidean geometry are inadequate to describe the complex forms found in natural systems. Shapes in nature are often comprised of substructure units. These units can either be shaped similar to the whole (self-similarity) or be shaped differently to “fill” the larger unit completely. Detailed explanations of dental microwear texture analysis have been published elsewhere [17–24] but the variables we examine are relayed here in brief.

The complexity of a surface refers to its roughness which can differ with respect to the scale of observation (e.g., smooth at a lower resolution and rough at higher resolution). Complexity of surface enamel was estimated in two ways, *Asfc* and *Smc*. The *Asfc* variable is the change in surface roughness with the scale of observation and captures complexity at different scales (7200 μm^2 to 0.02 μm^2) identified as area-scale fractal complexity (*Asfc*), which derives from the steepest point of the slope for a plot of log-transformed relative length area against log-transformed scale of observation. Scale of maximum complexity (*Smc*) derives from the range of slope values from which *Asfc* is calculated [18, 21].

Anisotropy or *epLsar* (“exact proportion of Length-scale anisotropy of relief”) is a measure of the directionality, or orientation, of enamel surface relief. The relative lengths are calculated from different depth profiles and compared to straight line approximations across transects. These relative lengths were treated as vectors and sampled at 5° intervals for 36 units of observation to identify directionality. The vectors were normalized using the exact proportion method following Scott et al. [18]. The mean length of these vectors is a proxy for the degree to which microwear striations exhibit distinct patterning, or anisotropy, associated with folivory.

Textural fill volume (*Tfv*) was calculated using an algorithm which “fills” the surface of the scanned area with square cuboids. The resultant volume is then compared to

another volume fill calculated using cuboids with smaller facet lengths (10 μm versus 2 μm) to isolate the proportion of the fill which can be attributed to dental microwear [18].

The variable known as heterogeneity was not utilized in this study for a number of reasons. First, it is not available for the comparative sample from Ungar et al. [19]. Second, it is not utilized [23] or even mentioned [19, 20] in some studies of dental microwear texture analysis. In Scott et al. [22] it is a minor proxy for surface complexity (*Asfc*), although see Scott et al. [17, 18].

2.3. Analytical methods

Median values, rather than the means were calculated from the four scans to avoid a positive skewing of the central tendency [18] and descriptive statistics for each taxon are compared. Because scale-sensitive fractal analysis data are not normally distributed, they were rank-transformed [27] before group differences were identified using Analysis of Variance (ANOVA) with posthoc Tukey’s Honestly Significant Differences tests. *Procynocephalus* was excluded from this analysis because only a single individual is represented. However, the ANOVA serves to validate the existence of groups to which *Procynocephalus* is compared. Regression of each pair-wise comparison of microwear textural characteristics was conducted to identify significant covariation. Texture characteristics that are significantly associated are shown in bivariate plots with 95% confidence ellipses around group centroids for each taxon. Discriminant function analysis was included as a classification instrument. The first two canonical scores axes from a discriminant function analysis using all taxa were plotted with 95% confidence ellipses around group centroids.

3. Results

Descriptive statistics show important differences exist between groups (Table 1). For example, measures of central tendency for complexity (*Asfc*) cluster taxa into two groups. Extant folivores (*Alouatta* and *Trachypithecus*) are characterized by extremely low values while the other taxa exhibit much higher values. *Procynocephalus* with the greatest complexity is followed by *Cebus*. *Gorilla* and *Lophocebus* exhibit middle values. Scale of maximum complexity (*Smc*) separates the most folivorous of the extant primates and *Cebus* from *Lophocebus* and *Procynocephalus*. For anisotropy (*epLsar*) a number of distinctions are present. The highest value characterizes *Alouatta*, followed by *Gorilla*, *Trachypithecus* and *Lophocebus*. *Cebus*

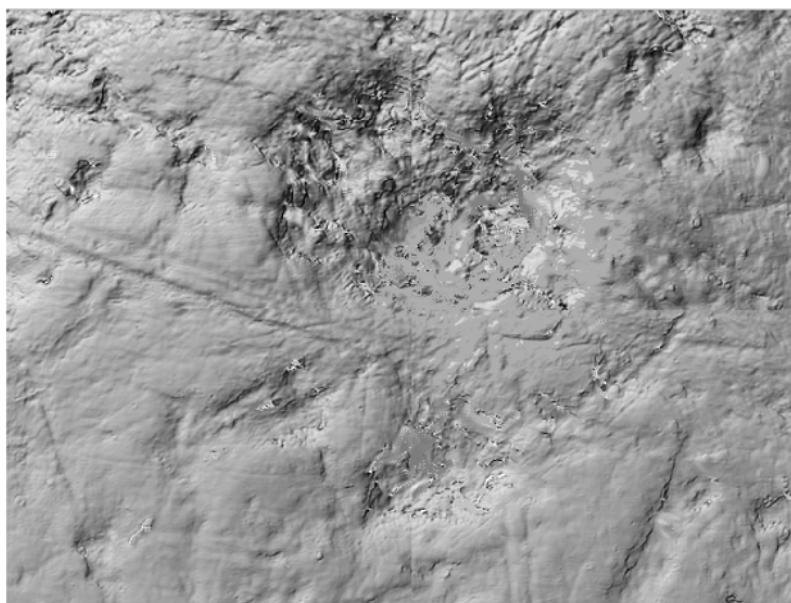


Figure 2. Reconstructed surface scans for *Procynocephalus subhimalayanus* GSI 18453.

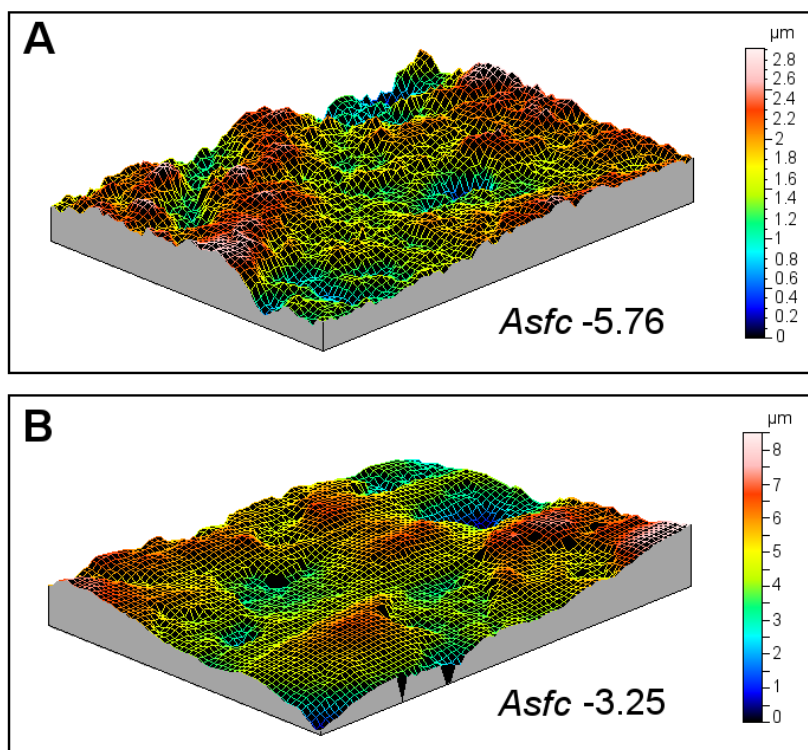


Figure 3. Digital elevation maps show surface complexity distinctions in (a) *Parapapio whitei* MP 62 and (b) *Paranthropus robustus* SK 47. Complexity in *Procynocephalus subhimalayanus* is more similar to *P. robustus* SK 47 than to *Pp. whitei* MP 62.

Table 1. Descriptive statistics for complexity (*Asfc*), scale of maximum complexity (*Smc*), anisotropy (*epLsar*) and textural fill volume (*Tfv*)

<i>Genus</i>	<i>N</i>		<i>Asfc</i>	<i>Smc</i>	<i>epLsar</i>	<i>Tfv</i>
<i>Alouatta</i>	11	Median	0.315	-0.574	5.7×10^{-3}	1351
		s.d.	0.183	1.050	2.142×10^{-3}	3225.70
<i>Cebus</i>	13	Median	2.882	-0.574	2.9×10^{-3}	9707.0
		s.d.	6.304	1.101	1.859×10^{-3}	4931.705
<i>Gorilla</i>	9	Median	1.247	-0.626	4.25×10^{-3}	6784
		s.d.	1.012	0.567	1.784×10^{-3}	5702.802
<i>Lophocebus</i>	15	Median	1.018	0.886	3.5×10^{-3}	11324
		s.d.	1.740	1.064	1.962×10^{-3}	3389.76
<i>Procynocephalus</i>	1	Median	3.260	47.580	1.200×10^{-3}	34064.52
		s.d.	—	—	—	—
<i>Trachypithecus</i>	12	Median	0.514	-0.626	3.65×10^{-3}	10126.5
		s.d.	0.660	0.547	2.601×10^{-3}	5687.205

Table 2. Analysis of Variance results

Dental microwear textures	F value	p value
Complexity (<i>Asfc</i>)	13.933	0.000
Scale of maximum complexity (<i>Smc</i>)	2.003	0.106
Anisotropy (<i>epLsar</i>)	2.046	0.099
Textural fill volume (<i>Tfv</i>)	6.778	0.000

displays middle values, while *Procynocephalus* exhibits the lowest value. A number of groupings also characterize textural fill volume (*Tfv*). *Alouatta* exhibits low values while *Procynocephalus* shows an elevated value. The extant primates (except *Alouatta*) show largely middle range values for textural fill volume (*Tfv*) with the highest value belonging to *Lophocebus*.

variable for this surface texture and do not significantly differ from each other. Significant differences are not evident in scale of maximum complexity (*Smc*) and anisotropy (*epLsar*) (Tables 3 and 4). For textural fill volume (*Tfv*), *Alouatta* is distinct from *Cebus*, *Lophocebus*, and *Trachypithecus* and is nearly distinct from *Gorilla* ($p = 0.56$) (Table 4).

3.1. ANOVA results with post-hoc tests of significance

Two of the four ANOVA comparisons yield significant differences among the taxa ($p \leq 0.001$). These are complexity (*Asfc*) and textural fill volume (*Tfv*). For both anisotropy (*epLsar*) and scale of maximum complexity (*Smc*), the F values intimated substantial between-group variation exists albeit insignificant (Table 2). The F values for textural fill volume (*Tfv*) and complexity (*Asfc*) ranged from 6.778 to 13.933 respectively further supporting the observation that the dental microwear texture properties of the taxa are distinct (Table 2).

The results of Tukey's posthoc significance tests suggest that important distinctions exist among some of the pair-wise comparisons of taxa. For complexity (*Asfc*), *Alouatta* and *Trachypithecus* are distinct from all taxa except each other (Table 3). *Cebus*, *Gorilla* and *Lophocebus* are quite

3.2. Bivariate and multivariate analyses

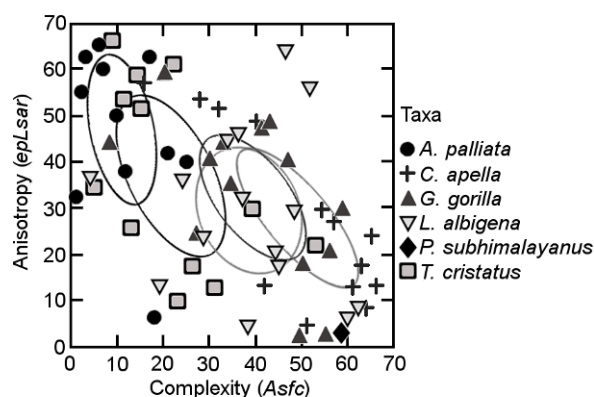
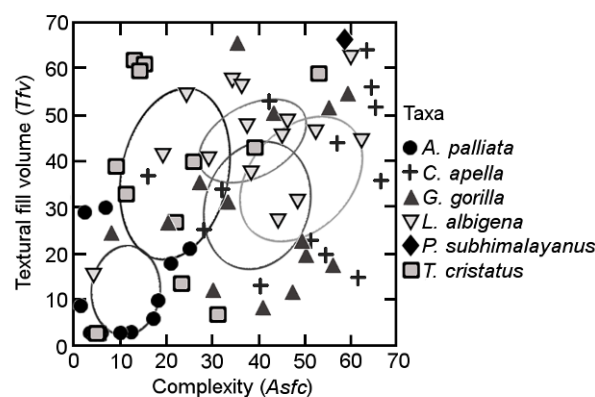
Linear regression of each pair-wise comparison of dental microwear texture properties shows whether significant associations are present (Table 5). Complexity (*Asfc*) and anisotropy (*epLsar*), shown in Figure 4, are associated with a relatively large r value (Table 5) and a highly significant p value ($p < 0.001$). Similarly, textural fill volume (*Tfv*) and complexity (*Asfc*), shown in Figure 5 are highly significantly related ($p < 0.001$) as are scale of maximum complexity (*Smc*) and complexity (*Asfc*) shown in Figure 6. Scale of maximum complexity (*Smc*) and anisotropy (*epLsar*) (not shown) are also significantly associated. In Figures 4 the fossil is distinct from *Alouatta* in showing higher complexity and lower anisotropy values. Figure 5 also shows distinctions exist between *Procynocephalus* and the extant taxa. However, *Lophocebus* most closely approximates *Procynocephalus* in scale of maximum com-

Table 3. Tukey HSD multiple comparisons for complexity, *Asfc* (below) and scale maximum complexity, *Smc* (above)

	<i>Alouatta</i>	<i>Cebus</i>	<i>Gorilla</i>	<i>Lophocebus</i>	<i>Trachypithecus</i>
<i>Alouatta</i>		0.998	0.946	0.472	0.997
<i>Cebus</i>	0.000		0.990	0.257	1.000
<i>Gorilla</i>	0.000	0.403		0.090	0.994
<i>Lophocebus</i>	0.000	0.291	1.000		0.254
<i>Trachypithecus</i>	0.384	0.000	0.019	0.027	

Table 4. Tukey HSD multiple comparisons for anisotropy, *epLsar* (below) and textural fill volume, *Tfv* (above)

	<i>Alouatta</i>	<i>Cebus</i>	<i>Gorilla</i>	<i>Lophocebus</i>	<i>Trachypithecus</i>
<i>Alouatta</i>		0.005	0.056	0.000	0.004
<i>Cebus</i>	0.100		0.875	0.688	1.000
<i>Gorilla</i>	0.287	0.973		0.152	0.809
<i>Lophocebus</i>	0.136	0.999	0.995		0.798
<i>Trachypithecus</i>	0.704	0.725	0.962	0.827	

**Figure 4.** Bivariate comparison between anisotropy (*epLsar*) and complexity (*Asfc*) is shown with 95% confidence ellipses around group centroids.**Figure 5.** Bivariate comparison between textural fill volume (*Tfv*) and complexity (*Asfc*) is shown with 95% confidence ellipses around group centroids.

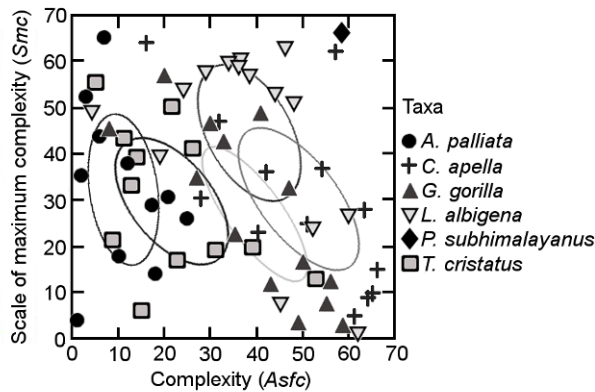
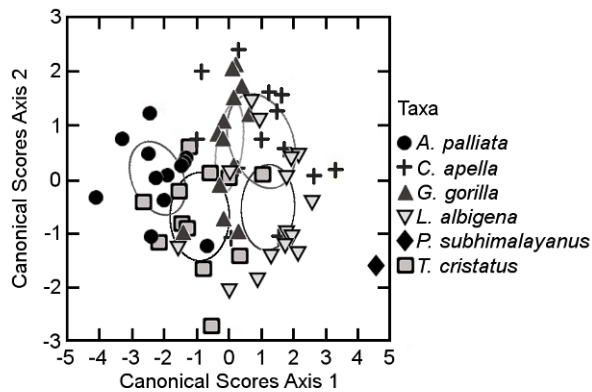
plexity (Figure 6).

Discriminant function analysis shows one *Cebus* is misclassified as *Procynocephalus*. Canonical Scores axes show *Procynocephalus* does not fall within the 95% confidence ellipses for any extant taxon (Figure 7). Canonical Scores Axis 1 separates *Alouatta*, and to a lesser degree, *Trachypithecus*, with lower anisotropy (*epLsar*) values from *Procynocephalus* followed by two *Gorilla* specimens and several *Lophocebus* individuals (Figure 7). This distinction between extant folivores specializing in tough foods versus *Procynocephalus* and some extreme hard-object consumers from equatorial forests, such as some *Gorilla* and most *Lophocebus* derives from the greater complexity (*Asfc*) and scale of maximum complexity (*Smc*)

values in the latter group (Table 6). Canonical Scores Axis 2 separates *Procynocephalus*, and several *Lophocebus* and *Trachypithecus* specimens from *Gorilla*, *Cebus* and *Alouatta* (Figure 7). This vector contrasts those individuals with high values for textural fill volume (*Tfv*) such as *Procynocephalus* from specimens with high values for anisotropy (*epLsar*) and complexity (*Asfc*) such as *Gorilla* (Table 6). Taxa with elevated values for either anisotropy (*epLsar*) such as *Alouatta* or complexity (*Asfc*) such as *Cebus* were also projected positively on Canonical Scores Axis 2. However, *Alouatta* and *Cebus* exhibit at least a middle value for anisotropy (*epLsar*) and complexity (*Asfc*)—a criterion which excluded *Procynocephalus* from a positive projection on Canonical Scores Axis 2 given its pronounced complexity (*Asfc*) but low anisotropy (*epLsar*)

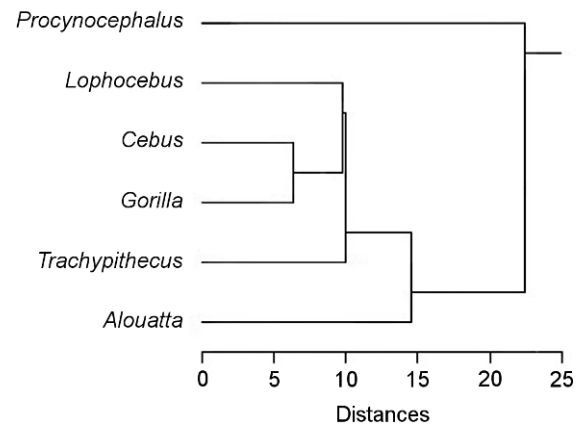
Table 5. Regression results for all pair-wise comparisons of dental microwear textures.

Pair-wise comparisons	R	p value
Complexity-scale of maximum complexity (<i>Asfc-Smc</i>)	0.318	0.009
Complexity-anisotropy (<i>Asfc-epLsar</i>)	0.319	<0.001
Complexity-textural fill volume (<i>Asfc-Tfv</i>)	0.153	0.001
Scale of maximum complexity-anisotropy (<i>Smc-epLsar</i>)	0.370	0.002
Scale of maximum complexity-textural fill volume (<i>Smc-Tfv</i>)	0.010	0.938
Anisotropy-textural fill volume (<i>epLsar-Tfv</i>)	0.195	0.116

**Figure 6.** Bivariate comparison between scale of maximum complexity (*Smc*) and complexity (*Asfc*) is shown with 95% confidence ellipses around group centroids.**Figure 7.** Canonical Scores Axes 1 and 2 are shown with 95% confidence ellipses around group centroids.

values (Figure 7; Table 6).

A cluster analysis of the means for all four dental microwear texture characteristics provides an overall picture of the dietary signatures for extinct and extant taxa (Figure 8). On a first approximation, *Procynocephalus* is distinct from the extant taxa. In the cluster containing all

**Figure 8.** A cluster analysis shows the longest branch lengths exists between *Procynocephalus* and the extant taxa, all of which (except *Alouatta*) are tightly clustered.

extant taxa, there is little difference among extant folivore-seed predators (*Trachypithecus*), folivore-frugivores (*Gorilla g. gorilla*), frugivore-extractive foragers (*Cebus*) as well as mixed-fruit hard-object consumers such as *Lophocebus*, although folivorous *Alouatta* differs from all of these. The close clustering of most extant tropical forest taxa suggests that the differences among them are difficult to parcel out when they are compared to *Procynocephalus*.

4. Discussion

Procynocephalus exhibits relatively complex enamel surface textures and is characterized by high values for scale of maximum complexity and textural fill volume (*Tfv*). The tropical forest primates have lower values for these textural characteristics.

High values for complexity (*Asfc*) are found in several extant primates that regularly consume hard and brittle foods, particularly *Cebus* while low values typify dedi-

Table 6. Canonical discriminant functions standardized by within variances

Dental microwear textures	Canonical Scores Axis 1	Canonical Scores Axis 2
Complexity (<i>Asfc</i>)	0.906	0.860
Scale of maximum complexity (<i>Smc</i>)	0.906	-0.375
Anisotropy (<i>epLsar</i>)	-0.324	0.593
Textural fill volume (<i>Tfv</i>)	0.384	-0.705

cated folivores that consume tough foods, such as *Trachypithecus* and *Alouatta* [19, 23]. *Procynocephalus* exhibits relatively complex surfaces compared to *Trachypithecus* and *Alouatta*. In fact, *Procynocephalus* exceeds the mean value for complexity (*Asfc*) found in *Cebus*.

For scale of maximum complexity (*Smc*), *Procynocephalus* also exhibits extreme values. *Lophocebus* exhibits relatively high values for *Smc* indicating hard and brittle resources may have been included in the diet of *Procynocephalus*. *Lophocebus* exhibits among the thickest enamel of any extant primate, and consumes more fruit (35.5%), fewer insects (36.4%) and leaves (9%), but more bark (8.9%) and seeds (8.6%) compared to *Cercopithecus ascanius* (redtail guenons) [28]. Some of the seeds include those with stony layers, such as *Diospyros abyssinica*, the distinctive crunching of which can be heard from several meters away. Bark, while surprisingly nutritious, is a very hard fallback food for *Lophocebus* as well as *Gorilla*. The hardness of bark and seeds with stony layers may mimic the resistant fracture properties, and possibly the resulting deformation of the enamel surface texture, of grit found on foods located close to the ground (or underground). *Gorilla* exhibits high values for complexity (*Asfc*) which explains the similarity of at least two *Gorilla* specimens to *Procynocephalus* along Canonical Scores Axis 1 (Figure 7). Similarities in dental microwear between *Gorilla gorilla* and *Procynocephalus subhimalayanus* have been noted elsewhere [16].

Two extant primates commonly described as folivores, *Alouatta* and *Trachypithecus*, while variable, exhibit some of the highest values for anisotropy (*epLsar*) [18]. *Procynocephalus* exhibits relatively low values for anisotropy (*epLsar*) indicating that food items, such as leaves, were not dragged along the molars. The high values for anisotropy (*epLsar*) for the two arboreal folivores may derive from local dietary ecology or forest canopy level [29].

Procynocephalus exhibits higher textural fill volumes (*Tfv*) than those characterizing extant analogues. High values for textural fill volume (*Tfv*) have been interpreted as evidence of hard and brittle food consumption [21] as *Cebus* and *Lophocebus* are characterized by higher values while *Alouatta* exhibits a low *Tfv*. Although *Alouatta* and *Trachypithecus* both consume considerable quantities of

folivorous resources, *Trachypithecus* does not exhibit low *Tfv* values, perhaps because it consumes large quantities of seeds. Merceron et al. [23] suggest that, like *Trachypithecus*, *Mesopithecus* exhibits a high textural fill volume (*Tfv*) from seed-predation. The low textural fill volumes (*Tfv*) of several *Alouatta* and one *Trachypithecus* specimen suggest a lack of seed predation in these individuals. The exceptionally pronounced textural fill volume (*Tfv*) in *Procynocephalus* may indicate items with even higher fracture resistant properties were consumed compared to the foods found in tropical forests. Scott et al. [24] suggest that higher values for textural fill volume (*Tfv*) correspond to large, deeply incised symmetrical pitting on the enamel surface characteristic of hard-object consumption.

Although only one individual of *Procynocephalus subhimalayanus* with known provenance, GSI 18453, could be included in this study, so little is known about this taxon [2, 3], that any information gleaned from the fossil can inform reconstructions of the Upper Siwaliks subsequent to a fauna turnover event [3]. This specimen is associated with paleomagnetic dates [5] providing a diachronic context for the dietary signal.

4.1. Faunal reconstruction in the Upper Siwaliks

Ecological changes occurred in the Upper Siwaliks after 7 Ma, probably from the evolution of the monsoonal system [15]. Prior to the late Miocene, more forested areas existed as indicated by the presence of the somewhat orangutan-like *Sivapithecus* [2]. Colobines were present at the end of the Miocene, such as *Presbytis sivalensis* dated to 6.3 Ma [3]. Extant *Presbytis* taxa of the Colobinae are known for their leaf-based diets. *Presbytis sivalensis* shows some similarities to *Mesopithecus*, a late Miocene colobine from Europe [30] both of which disappear from the Eurasian fossil record by the end of the Miocene [3, 31]. Cercopithecoid monkeys recolonized western Eurasia by 5–4 Ma [10], reaching the Upper Siwaliks after 2.5 Ma [3, 5].

These changes in fauna indicate substantial ecological perturbations occurred, coinciding with the spread of grasslands and the reduction of forests in temperate Euro-

sia beginning in the late Miocene and intensifying in the Plio-Pleistocene. Increasingly hot, wet summers interspersed with cool, dry winters furthered the spread of C₄ grasslands in Northern India and nearby Northern Pakistan [15]. By the early Pliocene, C₄ grasslands covered up to 90% of the region [15]. A faunal transition at 2.5 Ma separates the Tatrot and Pinjor stages [3]. Comparisons of the abundance of fossil taxa in the Pinjor zone indicate that the most common derive from proboscideans, bovids and *Equus*, suggesting a grassland habitat [15].

First appearance dates for *Procynocephalus* correspond to various taxa attributed to *Elephas*, *Equus*, *Rhinoceros*, *Punjabitherium*, *Sivatherium*, *Bubalus*, *Crocota*, *Hystrix* and *Sus* [5]. Some early Indian Villafranchian fauna survived the Gauss-Matuyama turnover, while others migrated to the Upper Siwaliks thereafter. The Pinjor stage also includes middle and late Villafranchian assemblages [5]. These faunal communities differ substantially from their tropical forest counterparts, and suggest grasslands increasingly governed the ground cover corresponding to the dispersal of *Equus* in the region.

4.2. Southern Africa as a parallel example

Temperate southern Africa during the Plio-Pleistocene also experienced an intensification of grassland expansion resulting from global (Intensification of Northern Hemispheric Glaciation), and later, regional (Walker Circulation) climate changes [32]. Faunal turnover in the region has been explored using dental microwear texture analysis. For example, Scott et al. [17] suggest that *Australopithecus africanus* and *Paranthropus robustus* from Plio-Pleistocene southern Africa exhibit distinct diet signals, although both exhibit a complex enamel surface texture. *Paranthropus robustus* in particular has been described as exhibiting substantial complexity of enamel surface texture and low anisotropy [21], more similar to *Cebus* and *Lophocebus* than to *Alouatta* [24]. This suggests hard-object feeding and extractive foraging, characterized at least a portion of the diet of *Paranthropus robustus* and to a lesser extent, *Australopithecus africanus*. A strong C₄ signal is also exhibited by *Paranthropus* and *Australopithecus* [33], possibly from corm and bulb consumption [34]. Differences in surface texture complexity may correspond to changes in habitat from a more closed environment of late Pliocene *Australopithecus africanus* compared to the relatively open savannas and grasslands associated with early Pleistocene *Paranthropus robustus*.

Underground storage organs contain particles with relatively resistant fracture properties [34]; grit adhering to USOs would cause additional microwear [35, 36]. The

enamel textural complexity of *Procynocephalus* may stem from the consumption of USOs, hard-object feeding, or both, given its enamel texture complexity exceeds that characterizing *Lophocebus* and *Cebus*.

Williams [37] suggests the dental microwear texture properties of *Procynocephalus* resemble those of *Parapapio whitei*, a middle Pliocene (2.9 Ma) papionin monkey from Makapansgat, South Africa; the two taxa were similarly projected in multivariate analyses, and *Procynocephalus* fell within the 95% confidence ellipse for *Parapapio whitei* on axes derived from a principal components analysis. Although the stable carbon isotopes of *Procynocephalus* are not available, those for *Parapapio whitei* from Makapansgat are, and show a mixed C₃/C₄ signal. Trace element analysis suggests the consumption USOs from both C₃ and C₄ plants [38]. Meanwhile, forest animals from closed canopies routinely exhibit a C₃ signal [39]. Plio-Pleistocene southern Africa and northern India probably exhibited more open habitats than the tropical forests of the extant primates in the comparative sample. The consumption of C₄ grassland resources has been identified in a variety of Plio-Pleistocene fossil papionins of southern Africa [40] and may stem from the consumption of USOs [16].

4.3. Abrasive grit

There is some experimental evidence suggesting extraneous mineral particles adhering to foods rather than plant phytoliths, may be the primary cause of dental microwear [41], and resources consumed in the upper forest canopy may exhibit less abrasive mineral particles than dietary resources found in lower levels [29]. Whether grit is associated with a particular type of diet—such as the consumption of USOs—is possible, but the presence of a heavy grit signal is equally likely to be a reflection of habitat as it is of diet [25]. In xeric habitats, leaves, fruit and herbs can be covered by a thin layer of grit, particularly those proximate to ground level [42]. Underground storage organs may be consumed without leaving a large degree of enamel texture complexity as some bulbs and corms have outer tunics that are easy to skin or hand-wash [34]. In addition, semi-terrestriality does not always indicate a reliance on USOs. African apes such as gorillas and chimpanzees are partially terrestrial but actively search for fruit [43, 44]. However, the marked similarity in enamel surface texture properties between *Procynocephalus* and *Parapapio*, and the inferred USO consumption in *Parapapio* [38], suggests that *Procynocephalus* is likely to have also consumed the underground parts of plants in the C₄ grasslands of late Pliocene northern India. *Procynocephalus* may have also consumed pith

and/or bark, similar to extant *Gorilla gorilla* [16].

Both male and female *Gorilla gorilla* actively search for ripe fruit and two rare herbs even when fruit is abundant [43]. When fruit is scarce, fallback foods are consumed, including leaves and second choice fruits and herbs, bark, pith and insects (particularly among females). Herbs are close to ground level and may be covered with fracture resistant particles more often than arboreal leaves and fruits [25]. The two *Gorilla* that approximate *Procynocephalus* on the first canonical scores axis (Figure 7) may exhibit extremes in textural complexity values ($Asfc$) from the consumption of abrasive grit on preferred herbs such as the shoots of *Haumania danckelmaniana* and the swamp herb *Hydrocharis chavalieri* both of which are eaten year round [43].

Although similarities between *Procynocephalus* and *Gorilla* are apparent in some analyses, the relationship between *Procynocephalus* and *Lophochebus* is more consistent. This is to be expected from similarities in body size and phylogeny. Papionins are opportunistic feeders, and less discriminating about fruit preferences compared to *Gorilla* (excepting *G. beringei*), *Pongo* and *Pan*, all of which favor ripe fruit low in chemical defenses and high in sugar. In contrast, *Lophochebus* eats ripe and unripe fruit as well as fruit rotting on the ground, and includes seeds, legumes and fruit equipped with a range of defensive toxins. Old World monkeys differ from the great apes in having less differentiated diets, often including lower quality leaves than can be consumed by hominoids [43]. Like its tropical forest relative *Lophochebus*, *Procynocephalus* probably also exhibited a less differentiated diet than characterized by the great apes, and may have included durophagy (hard-object feeding) as a fallback strategy in the grasslands of the Upper Siwaliks of the late Pliocene.

4.4. Durophagy

Hard-object feeding requires a suite of anatomical features including thick dental enamel and enlarged craniofacial superstructures to process mechanically resistance food items. Objects in nature present differences in fracture properties. Fracture in this context can be defined as a perforation in plant tissues as a function of the force applied [34]. The degree to which tissues respond to displacement from the teeth reflect the mechanical properties of the fibers. There is a range of toughness and stiffness among foods. For example, leaves of C_4 grasses are much more fracture resistant than USOs which are geophytic plant parts and include corms, bulbs, rhizomes and tubers [45]. Underground storage organs are com-

mon in arid habitats given their capacity to store water, starches and nutrients [38]. Fracture resistance is variable among USOs with some (rhizomes and tubers) exhibiting extremes in mechanical properties when compared to other organic substances. Rhizomes, or root stalks, present much more resistance to fracturing than do tubers, followed by bulbs. Corms, vertically implanted thickened stems, are the least fracture resistant [34]. However, corms are stiffer than bulbs as shown by a higher Young's modulus value [34]. Both corms and bulbs are good candidate foods to accounted for the strong C_4 signature noted for *Australopithecus* and *Paranthropus* [45] and are consistent with the dental microwear signal which suggests hard and brittle foods were consumed [34]. Corms and bulbs of C_4 plants could have also played a role in the diet of *Procynocephalus*, particularly as fallback foods. The abrasive grit clinging to the outer tunics of USOs could be responsible for the extreme complexity ($Asfc$) and textural fill volume (Tfv) noted in GSI 18453 (as well as in *Parapapio whitei* from Makapansgat [37], and *Paranthropus robustus* from Swartkrans [17], unpublished data). Fallback foods were probably an important resource in the increasingly xeric habitat recorded in the Kansal Formation of the Upper Siwaliks.

5. Conclusions

Most primate taxa are found in tropical forests, but during the Pliocene, large-bodied cercopithecoid monkeys ventured into seasonal and more open terrain. Evidence of these new habitats should be preserved in the enamel surface texture. For example, given the grit adhering to plant parts underneath or close to the ground, consumption of these foods should result in greater complexity of the enamel surface, greater fill volume due to dental microwear, and limited patterning of textural relief typical of folivores.

Procynocephalus subhimalayanus from the Upper Siwaliks (Pinjor zone) can be characterized in this manner. *Procynocephalus*—and *Parapapio* from Makapansgat—are distinct from extant forest primates [37]. The closest approximation to *Procynocephalus* among the extant taxa is *Lophochebus*, a large-bodied monkey observed to engage in hard-object feeding (e.g., seeds with stony layers and bark) and to a lesser extent, *Gorilla* and *Cebus*, both of which consume variable amounts of fracture resistant foods. *Procynocephalus* may have consumed foods with even harder properties than the brittle ectoderm of forest nuts and seeds, and concentrated at least some of its foraging efforts on foods close to, or underneath ground level, at least on a seasonal basis [46]. The relationship between

semi-terrestriality and consumption of foods with a high Young's modulus values is in part borne out by these analyses. The grit adhering to foods may be a fundamental source of dental microwear, both in the canopy [29] and with respect to habitat [25].

Procynocephalus is distinct from most of the extant comparative taxa suggesting it was not a folivore with some seed consumption such as *Trachypithecus*, or folivorous with some fruit consumption as is the case for *Alouatta*. These inferred dietary proclivities corroborate habitat reconstructions of the Kansal Formation of the Upper Siwaliks which postulate an expansion of grasslands in the region corresponding with the arrival of *Equus*.

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