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2014 Dahlberg Award Winner: The effects of dietary toughness on occlusopalatal variation in savanna baboons

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ABSTRACT This study investigates the relationship between dietary toughness and craniofacial variation in two groups of savanna baboons. Standard craniofacial and malocclusion data were collected from a captive, soft-diet experiment group (n=24) and a sample of wild-captured baboons, raised on tougher, natural foods (n=19). We tested the hypothesis that in the absence of normal masticatory stress experienced during the consumption of wild foods, the captive baboons would exhibit higher levels of facial and dental structural irregularities. Principal component analysis indicates separation of the two samples. The soft-diet sample exhibits significantly shorter palates, greater variability in palate position, and higher frequencies of occlusal irregularities that correlate with the shorter palates. Results offer further support that long-term dietary chewing stresses have a measurable effect on adult craniofacial variation.

Malocclusions are the improper growth, positioning, and/or alignment of the teeth and jaws that lead to irregularities in occlusal surface contact and abnormalities of the surrounding bony structures. These deviations are due to multiple factors, but the reduced masticatory demands of modern diets have shown considerable influence (Corruccini, 1984; 1999; Corruccini et al., 1983; Corruccini and Lee, 1984; Varrela, 1990, 1992, 2006; Evensen and Øgaard, 2007). Notably, alterations in the proper growth trajectories of these areas due to decreased chewing forces are not unique to humans. By controlling for diet, laboratory animal studies have contributed to a broader understanding of occlusofacial variability (Beecher and Corruccini, 1981a, b; Corruccini and Beecher, 1982; Larsson et al., 2005; Grünheid et al., 2009; Jašarević et al., 2010; Ravosa et al., 2010; Dias et al., 2011; Makedonska et al., 2012).

This study expanded on the research of Corruccini and Beecher (1984), who found reduced facial growth, decreased structural correlations, narrower faces, and more occlusal irregularities in savanna baboons fed a soft diet. Using the same soft-diet sample as Corruccini and Beecher (1984), but a different research design and a wild comparative sample, the present study contrasted craniofacial and occlusal data between two groups of savanna baboons fed diets that differed in their mechanical properties. This study tested the hypothesis that in the absence of natural food consumption, the soft-diet baboon sample would exhibit higher levels of craniofacial variation due to their reduced chewing demands.

MATERIALS AND METHODS

The soft-diet experiment group consisted of 24 male *Papio cynocephalus* skulls housed at Southern Illinois University Carbondale. As part of a biomedical study in the 1970s, these individuals were fed "a very soft, atherogenic diet consisting of cholesterol, lard, butter, egg yolks, and powdered chow" for the last 27 months of their dental maturation (Corruccini and Beecher, 1984:136). Eighteen male *P. anubis* and one male *P. cynocephalus* individual housed at the Field Museum of Natural History were selected to be the wild-diet control sample because of their wild African origin. Although their exact diet was not known, their natural wild foods consist of grasses, roots, plants, leaves, bark, gums, seeds, fruit, berries, corn, small invertebrates, and even sheep and goats (Post, 1981; Barton, 1993; Wahungu, 1998; Akosim et al., 2010; Johnson et al., 2012). Visually, all individuals were dentally mature and had erupted third molars to suggest ages around 6-8 years (Phillips-Conroy and Jolly, 1988).

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Members of genus *Papio* are possibly populations of a single species and are sometimes referred to as *Papio hamadryas cynocephalus* and *P. hamadryas anubis* to reflect this subspecies distinction. *P. cynocephalus* and *P. anubis* have been known to interbreed (Samuels and Altmann, 1986; Alberts and Altmann, 2001; Charpentier et al., 2008; Tung et al., 2008) despite geographical distinctions in their genetic compositions (Williams-Blangero et al., 1990; Zinner et al., 2013). Further, Frost et al. (2003) noted cranial morphological clinal organization of genus *Papio* in Africa. Northern baboons (like *P. anubis*) exhibit broader, less flexed crania and rostra compared to the southern forms (such as *P. cynocephalus*) that display inferiorly flexed and narrower crania and rostra (Frost et al., 2003:1056, 1069). Because of their clinal organization and similar environments, general shape differences between these two groups observed by Frost et al. (2003) likely reflect genetic differences.

Linear measurements consisted of standard craniofacial measurements (Moore-Jansen et al., 1994) and posterior airway maximum lengths and breadths (Fig. 1, Table 1). These data were recorded using spreading and sliding Mitutoyo calipers calibrated to 0.01mm. Principal component analysis (PCA) was used to identify measurement loadings responsible for driving the observed variation. Pearson's product-moment correlation coefficient was used to analyze the strength of correlation between measures identified by the PCA.

Occlusal data (Table 2) consisted of molar class relationships (Angle, 1899), posterior crossbite, rotations, displacements, and incisor overbite and overjet following the summation in Harris and Corruccini (2008). For the purposes of our study, we reduced occlusal scores to a score of 0 for normal occlusion and 1 for any deviation from normal occlusion in each category. These values were summed to estimate the magnitude of occlusal irregularity for each individual, and significant differences between the samples were calculated using a Mann-Whitney U test.

Spearman's rank correlation coefficient tested for associations between relevant linear measures and occlusal scores. To attempt to account for potential variation in body size, shape ratios were calculated by dividing all linear measurements by foramen magnum breadth (simplified from area calculations found in Radinsky, 1967; Gould, 1975). The raw and scaled datasets produced highly similar results so that the data quality appears to be high, and only the scaled data are reported here. Statistical analysis was conducted by RMC using the R Project for Statistical Computing (R Core Team, 2013) and PAST: Paleontological Statistics software (Hammer, Harper, and Ryan, 2001).

RESULTS

The PCA results indicate that the combined first two principal components account for 81% of variation within the sample (Fig. 2). The first principal component (PC1) indicates a size increase, primarily in the measures with the highest loadings, along that axis (Fig. 3). There was clear separation between the wild-diet (maroon circles) and soft-diet (blue circles) samples primarily along the second principal component (PC 2). The loadings for PC 2 (Fig. 3) suggest that palate length (PAL) and incisivion (most distal point in the incisive foramen) to basion (IFB) distance contributed most to variation along this axis. Importantly, the single wild-diet *P. cynocephalus* (red circle) groups with the wild-diet *P. anubis* sample rather than the soft-diet *P. cynocephalus* sample, which suggests that the variation along

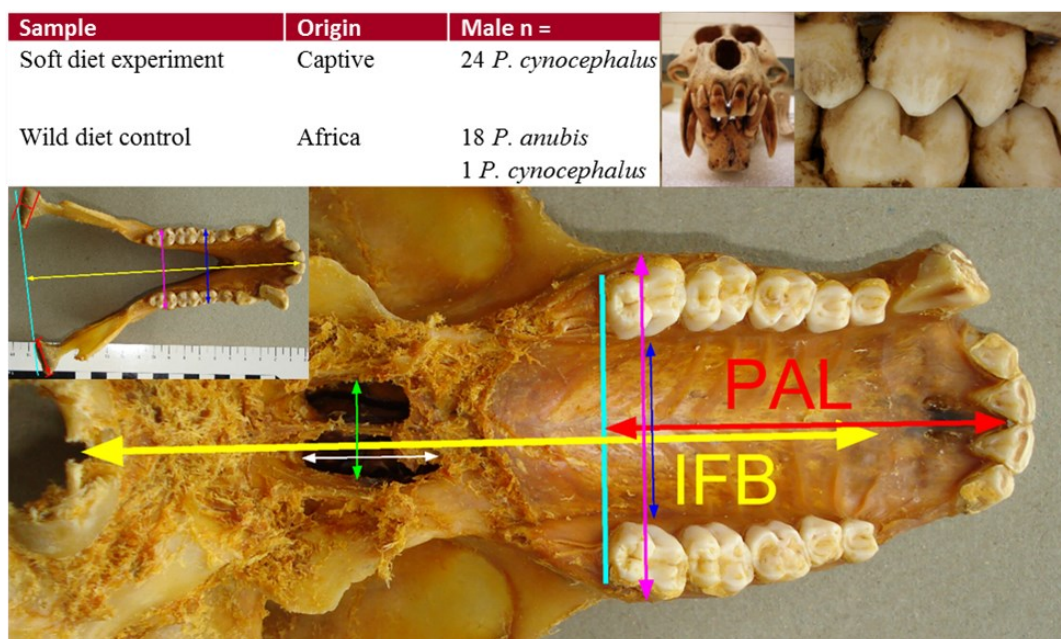| Sample	Origin	Male n =
Soft diet experiment	Captive	24 *P. cynocephalus*
Wild diet control	Africa	18 *P. anubis* 1 *P. cynocephalus*

Fig. 1. Illustration of relevant linear measures, palate length (PAL) and incisivion to basion (IFB).

TABLE 1. Metric variables

Measure	Description
MWCond	Mediolateral width of the mandibular condyle taken at the longest ML axis
MLCond	Maximum AP length of the mandibular condyle, perpendicular to MWCond
MDC	Maximum depth of the mandibular corpus from the superior edge of the alveolar
MWCorp	Maximum width of the mandibular corpus from the labial to lingual side of the mandibular corpus at the midpoint of M1
MMdW	Maximum mandibular arch width at M1 taken on alveolar bone with calipers at the midpoint of LM1 and RM1
NMdW	Minimum mandibular arch width at M3 taken on the alveolar bone with calipers at the midpoint of LM3 and RM3
MandL	Mandibular length from the anterior point of projection on the alveolar bone of the mandible to the most posterior projection of the mandibular condyles (infradentale to condylion)
MMW	Maximum maxillary arch width taken at the widest point of the alveolar bone on the maxilla regardless of field or adjacent tooth
NMW	Minimum maxillary arch width at M3 taken on the alveolar bone (lingual surface) at the midpoints of LM3 & RM3
NSB	Minimum snout breadth between L & R maxilla, with calipers in the fossae
PAL	The length of the palate measured from prosthion to the plane of the posterior projection of the maxilla (using a rubber band to delineate the posterior border)
IFB	From the most posterior point on the incisive foramen to basion (incisivion was estimated in poorly mascerated soft-diet individuals)
PAB	The greatest medio-lateral breadth of the posterior airway, taken with the calipers held just posterior to the palate
PAH	The anterio-posterior length of the internal nares, from the posterior margin of the palate to the anterior margin of the opening
BZB	The widest breadth across L & R zygomatic arches (zygion to zygion)
FB	The breadth of the frontal bone across brows
FMW	The medio-lateral breadth of the foramen magnum, measured from within the margins of the occipital with the "inside" arms of the caliper

PC 2 is not the result of genetic differences.

A two-sample t-test demonstrates that mean differences in PAL were significantly smaller (P<0.000), and an F statistic indicates that IFB was significantly more variable (p<0.010) in the soft-diet sample (Fig. 4, Table 3). Again, the bivariate plot of PAL and IFB (Fig. 5) implies that the wild-diet *P. cynocephalus* individual groups with the wild-diet *P. anubis* group, as a this is a reflection of the PCA measures responsible for driving the observed variation. Although a Pearson's correlation coefficient for the soft-diet group (r=0.752) was only slightly lower than the wild-diet sample (r=0.780), results suggest that the soft-diet sample displays significantly shorter palate lengths relative to IFB distances. A Mann-Whitney U test (Table 4) indicates that the soft-diet sample exhibits significantly greater overall occlusal scores than the wild-diet group. Spearman's correlation coefficient (Table 5) demonstrates a relatively weak yet significant (p<0.050) negative correlation between PAL and occlusal scores and suggests that occlusal patterns become more variable as palate length reduces.

DISCUSSION

The hypothesis that the soft-diet baboon sample would exhibit higher levels of craniofacial variation due to decreased masticatory loading during ontogeny is supported. Specifically, the soft-diet group exhibits greater occlusopalatal variation. The single wild-diet *P. cynocephalus* offers support that our results are not the mere reproduction of clinal shape differences of genus *Papio* as noted by Frost et al. (2003). Although genetics undoubtedly play a considerable role (Carlson, 2005; Harris, 2008; Koussoulakou et al., 2009), our study supports the potential for environmental factors to alter developmental trajectories.

Incisivion (Mew, 1974; Frost et al., 2003) should be utilized when investigating basicranial flexion. By using incisivion to construct multivariate ratios, it may be possible to test for the functional and taxonomic significance of the palate's effect on basicranial flexion (Corruccini, 1978; Oxnard, 1983). Through dietary manipulation of living animals, radiographs could be used to investigate the relationships between ontogenetic shape changes, adult cranial form, allometric scaling, heterochrony, and differential

TABLE 2. Occlusal variables

Measure	Description
Anterior Overjet	The maximum distance between the most inferior point on the upper central incisors, and the most superior point on the lower central incisors
Anterior Overbite	The maximum distance between the labial surface of the lower central incisors and the labial surface of the upper central incisors
Posterior Crossbite	The buccolingual interrelationship between upper and lower first molar antagonists
Normal occlusion	The buccal cusp of the upper molars overhang the lower buccal cusps, with the lowers reaching proper centric occlusion
Buccal crossbite	The upper molars are atypically buccally located, such that the lowers do not reach proper centric occlusion
Lingual crossbite	The upper molars are atypically lingual, such that the buccal cusps of the uppers do not overhang the lowers
Buccal Segment Relationship	The interrelationships between the upper and lower first molars in the parasagittal plane
Class 1	The mesiobuccal cusp of the M1 is parasagittal to the buccal groove of M1
Class 2	The mesiobuccal cusp of M1 is mesial to the buccal groove of M1
Class 3	The mesiobuccal cusp of M1 is distal to the buccal groove of M1
Rotation	Refers to a tooth in its normal position in the dental arcade but rotated about its long axis. The sum of rotated teeth are recorded for each side. Recorded for both maxilla and mandible
0	Unrotated
1	Rotated < 45°
2	Rotated > 45°
Displacement	Refers to a tooth that is out of ideal alignment. The summed value is recorded. Recorded for both maxilla and mandible
0	Not displaced
1	Displaced < 2mm
2	Displaced > 2mm

growth (Frost et al., 2003; Leigh, 2006; Trenouth and Joshi, 2006). This could broaden allometric understanding, as Gilbert (2011) reminds us that a large percentage of shape information is lost during allometric correction, and our results suggest that masticatory behavior also confounds shape analyses.

These implications are also important for humans. Many authors have used the hunter-gatherer/agricultural transition to illustrate how changes in dietary selective pressures produced skull morphologies able to cope with new masticatory functional demands (Carlson, 1976a, b; Carlson and Van Gerven, 1977; Hinton and Carlson, 1979; Paschetta et al., 2010). Clinically, Haskell et al. (2009) noted correlations between snoring, sleep apnea, and the structures of the face and mouth. However, this study cannot

conclude about the taxonomic significance of airway dimensions in the two samples specifically, nor the relationships between dental variation and airway dimensions in general. There could be multiple reasons why smaller airway dimensions were not found in the soft-diet group. Although the tight confines of the airway's location could have prevented the caliper arms from accurately touching the landmarks, there also exists the possibility that there does not exist significant morphological differences in this area.

Anthropologically, it should be remembered that diet influences our reconstructions of biodistance, phylogeny, and taxonomy whether we account for it or not. Eshed et al. (2006) and Halcrow et al. (2013) rightfully remind us that simple linear relationships between diet and the denti-
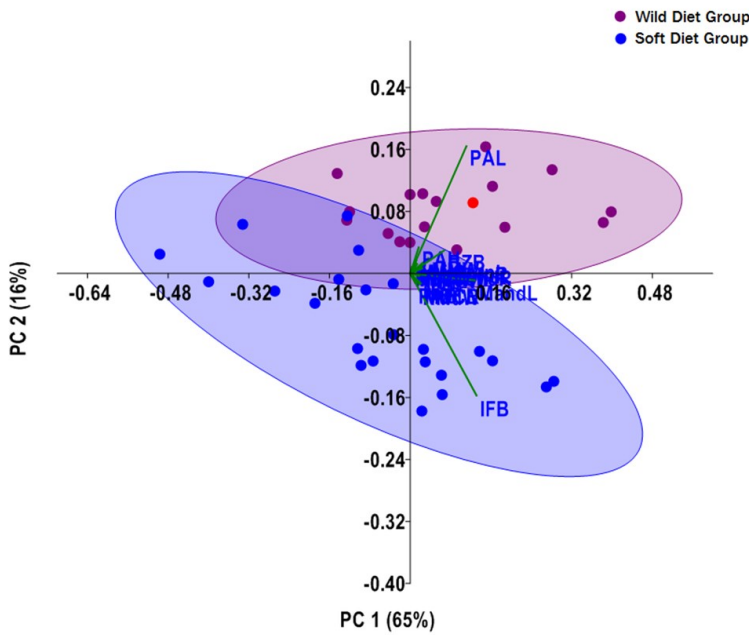
Fig. 2. PCA on scaled data. Maroon circles = wild diet sample; blue circles = soft diet sample; red circle = the single wild-diet *P. cynocephalus.*
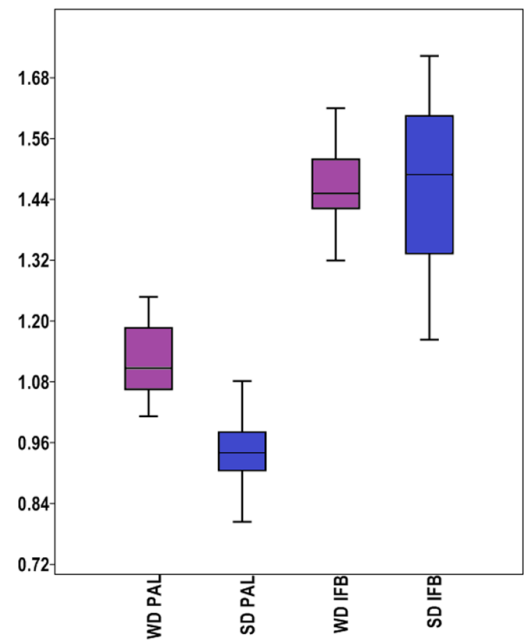
Fig. 4. Boxplot for scaled data. WD = wild-diet sample; SD = soft-diet sample. PAL = palate length; IFB = incisivion to basion.
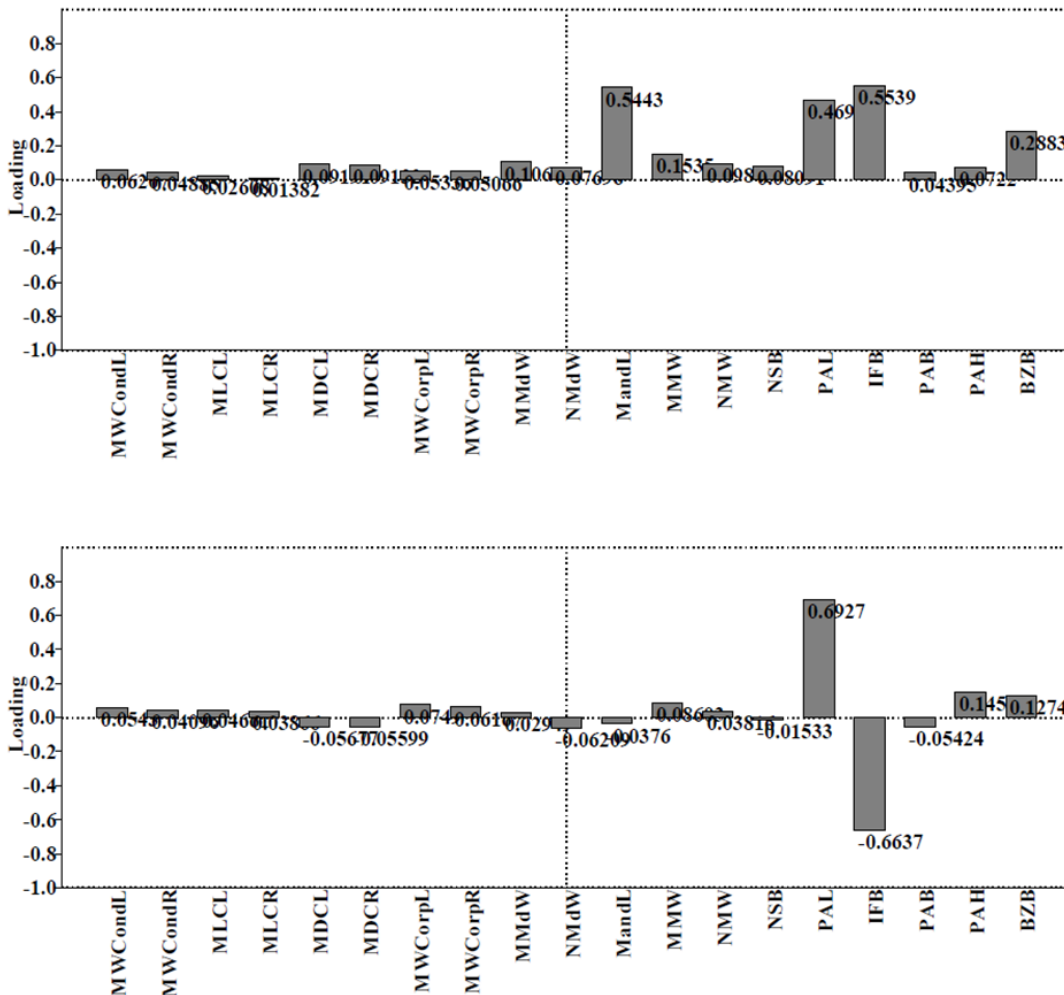

Fig. 3. Loadings for PC1 (top) and PC2 (bottom). Note the inverse relationship between PAL and IFB for PC2.

tion should not be assumed as the ambiguity of genetic, environmental, and cultural influences have the potential to produce a multitude of skeletal adaptations and alterations. By expanding on the research of Corruccini and Beecher (1984), we were able to demonstrate that a variety of research designs can strengthen discussions about the gene-environment interaction and other complex anthropological topics. Luckily, a stronger understanding of genetic influences will better contextualize environmental factors of phenotypic variation. Kuang et al. (2013) have documented the involvement of regulatory genes in mice with long-term, laboratory induced malocclusions. New discoveries such as this continue to enable anthropology to pioneer explanations of observed skeletal variation.

ACKNOWLEDGEMENTS
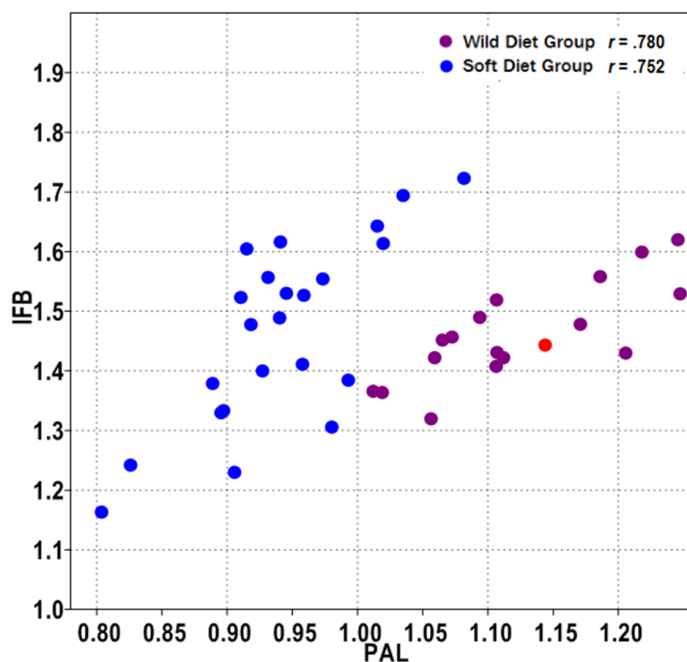
Fig. 5. Biplot showing the relationship between PAL and IFB. Maroon circles = wild-diet sample; blue circles = soft-diet sample; red circle = the single wild-diet *P. cynocephalus.*

TABLE 3. Summary statistics for relevant linear measurements scaled for body size

	n	$\bar{x}$	SD	F	*p*	t	*p*
PAL WD	18	1.12	0.07	1.35	0.500	8.49	2.16E-10**
PAL SD	23	0.94	0.06				
IFB WD	18	1.46	0.08	3.668	0.008*	-0.13	0.90
IFB SD	23	1.47	0.15				

*significant at P<0.010, **significant at p<0.000; WD = wild-diet sample, SD = soft-diet sample; PAL = palate length, IFB = incisive foramen to basion

TABLE 4. Mann-Whitney U Test for wild-diet and soft-diet occlusal scores

	n	Median	U	*p*
Occlusal WD	19	0	122	0.035*
Occlusal SD	20	1		

*significant at p<0.050

TABLE 5. Spearman correlation for relevant linear measures and occlusal scores

	r's	*p*
PAL + Occlusal	-0.3782	0.017*
IFB + Occlusal	-0.2260	0.172

*significant at p<0.050

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