# Enamel microwear texture properties of IGF 11778 (*Oreopithecus bambolii*) from the late Miocene of Baccinello, Italy

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**Summary** - Late Miocene Oreopithecus bambolii has been posited as a folivore from its pronounced molar shearing crests. However, scanning electron microscopy yields conflicting results with one study of Oreopithecus showing folivory and another indicating a coarser diet was consumed. To address this debate, the dietary proclivities of the well-known IGF 11778 Oreopithecus bambolii specimen are reconstructed by comparing the enamel texture properties of this specimen to extant Alouatta palliata (n = 11), Cebus apella (n = 13), Gorilla gorilla (n = 9), Lophocebus albigena (n = 15), Pan troglodytes (n = 17) and Trachypithecus cristatus (n = 12). Dental microwear is captured by scanning facet 9, a Phase II facet on the hypoconid surface, using white-light confocal microscopy at 100x. The scanning was followed by scale-sensitive fractal analysis, yielding four texture characteristics. These were ranked before ANOVA with post-hoc tests of significance and multivariate analyses were conducted. Oreopithecus specimen IGF 11778 does not match any of the extant taxa consistently but in some analyses is associated with Lophocebus, and secondarily with Pan, Gorilla and Cebus outliers suggesting mixed-fruit and hard-object feeding characterized at least a portion of its diet. The partially open habitat of late Miocene Baccinello may have had resources with mechanically resistant foods, or foods found near ground level were consumed. Hard, brittle foods, insects, and or extraneous grit may have contributed to the greater use-wear complexity of the enamel surface observed in IGF 11778 compared to extant folivores. IGF 11778 does not exhibit the degree of anisotropy characterizing Trachypithecus and Alouatta. The partial resemblance of IGF 11778 to some great ape specimens may indicate intermittent extractive and or terrestrial foraging.

Keywords - Lophocebus, Hard-object feeding, Leaf consumption, Hominoid, Miocene apes.

# Introduction

The "1958" or Florence skeleton, is a remarkably complete but severely crushed specimen found within the lignitic deposits of Baccinello, Tuscany. The fossil preserves the upper and lower limb skeleton, as well as jaws, teeth and cranial fragments providing insight into the relationship between the gnathic elements, cranial size and locomotion for a single individual. While more is known about IGF 11778 than any other Miocene hominoid individual (Begun, 2002), debate about its diet, taxonomy, anatomy and locomotion remain unresolved (Aiello, 1981; Delson, 1986; Drapeau & Ward, 2007; Harrison, 1986a,b; Jungers, 1987; Köhler & Moyà-Solà, 1997; Moyà-Solà *et al.*, 1999, 2005; Rook *et al.*, 1996, 1999, 2004; Sarmiento, 1987; Sarmiento & Marcus, 2000; Straus, 1962; Susman, 2004, 2005; Szalay & Delson, 1979; Szalay & Langdon, 1987; Wunderlich *et al.*, 1999).

Given its unusually primitive morphology (Begun, 2002), the phylogenetic placement of IGF 11778 and other fossils attributed to *Oreopithecus* has been equivocal (Delson, 1986; Rook *et al.*, 1996), echoing debates about the taxonomic attribution of the first *Oreopithecus* fossil discovered at Monte Bamboli in 1872 (Gentili *et al.*, 1998). A revitalization of interest in *Oreopithecus* occurred with the recovery of IGF 11778 (Hürzeler, 1958; Straus, 1958). Hürzeler (1958, 1960) suggested *Oreopithecus bambolii* belonged within the human lineage based on a morphological analysis of IGF 11778 and other specimens. Classified within the Cercopithecoidea from its cuspidate molars and other dental characteristics (Delson, 1986; Szalay & Delson, 1979), *Oreopithecus* was also referred to the Hominoidea on the basis of postcranial characteristics (Rook *et al.*, 1996; Straus, 1958), and to its own family, the Oreopithecidae (Carnieri & Mallegni, 2003; Harrison, 1986b; Hürzeler, 1958).

A reconstruction of the skull of IGF 11778 indicated a resemblance to the great apes (Clarke, 1997). The preservation of several long bones allowed for the relative lengths to be compared to other primates, and IGF 11778 is most similar to female Pongo (Jungers, 1987) suggesting slow quadramanous arboreal clambering. Body size for IGF 11778 from femoral head circumference was estimated to be 32 kg with 95% confidence limits providing a range of 30.2 - 33.9 kg (Jungers, 1987). This was surprisingly large because the teeth of Oreopithecus are proportionally small (Jungers, 1990; Rook et al., 2004). Oreopithecus bambolii can be characterized as microdont given the relatively small cheek teeth and canines with respect to reconstructed body mass (Alba et al., 2001). However, the use of tooth size as a proxy for body size is complicated by outliers, such as Australopithecus and Paranthropus (Jungers, 1987). Nevertheless, tooth size, shape and microwear provide unique insights into the dietary ecology of extinct forms.

# Paleoecology, chronology and paleogeography

*Oreopithecus* is considered highly autapomorphic in its craniodental and postcranial morphology, possibly stemming from its endemic isolation in the late Miocene Tuscan-Sardinia bioprovince (Begun, 2002; Gentili *et al.*, 1998). The unique fauna of Italy during the late Miocene suggests that *Oreopithecus* and early papionins such as

*Macaca* and colobines such as *Mesopithecus* entered Europe using different routes (Gentili *et al.*, 1998; Harrison, 1986a). *Oreopithecus* was probably the last surviving taxon of a broad radiation of western European Miocene hominoids. All of them except *Oreopithecus* appear to have become extinct by about 9.6 Ma during the "Vallesian Crisis" where deciduous species began to dominate the formerly tropical/subtropical landscapes, reflecting increased seasonality (Rook *et al.*, 2000).

Oreopithecus survived the "Vallesian Crisis" in part because of its isolation, in part from its useful morphological adaptations but eventually became extinct around 7 Ma when the Tuscan-Sardinia paleobioprovince reconnected with peninsular Europe (Casanovas-Vilar et al., 2011). The occurrence of Oreopithecus was bracketed within a time interval between 9.5 and 6.0 Ma using biochronological controls from continental Europe (Rook et al., 2000). It was among the most abundant fossil taxa within the pre-Messinian mammal-bearing biostratigraphic units of southern Tuscany (Rook et al., 2011). Baccinello, from which IGF 11778 derives, was dated to the upper Miocene, corresponding to MN 12 and MN 13 (Begun, 2002; Gentili et al., 1998). A mean <sup>40</sup>Ar/<sup>39</sup>Ar date of 7.55 ± 0.03 Ma was obtained from an exposed tephra from the Passonaio section of the Baccinello-Cinigiano basin, corresponding to the middle of the Oreopithecus-bearing succession (Rook et al., 2000). More recently, paleomagnetostratigraphy has been applied to the Baccinello-Cinigiano basin and yielded dates over 8.1 Ma for the oldest deposits and between 7.1 and 6.7 Ma for the youngest (Rook et al., 2011).

Paleogeographic evidence suggested that the environment *Oreopithecus* inhabited was varied and likely included swampy, forested areas and drier uplands (Azzaroli *et al.*, 1986). *Oreopithecus* from Baccinello is part of the Baccinello-Cinigiano basin bordered by the Ombrone River valley and the Amiata Mountain in southern Tuscany (Benvenuti *et al.*, 2001; Rook *et al.*, 2000) and is distinct from other late Miocene bioprovinces in Italy (Rook *et al.*, 2006). The Baccinello deposits include four vertebrate-bearing levels. The V1, V2 and V3 layers were the first to be identified as distinct from the F1 and F2 layers bearing only molluscan faunas. An older vertebrate-bearing biostratigraphic unit was later identified as V0 (Benvenuti *et al.*, 2001; Rook *et al.*, 1996). Oreopithecus bambolii was found in the V0, V1 and V2 biostratigraphic units, but was replaced by Mesopithecus in V3 (Matson *et al.*, 2012). The endemic mammalian taxa of the Tuscan-Sardinian insular region from V0, V1 and V2 differed from continental European and African forms and have been identified as the Oreopithecus Zone Faunas (Bernor *et al.*, 2001; Chesi *et al.*, 2009; Delfino & Rook, 2008; Rook *et al.*, 2006), an ecological isolate for over 2 Ma.

The extinction of Oreopithecus may have possibly derived from increased variability in flooded zones and in fluvial discharge (Ligios et al., 2008). However, differences in pedogenic carbon from paleosols appeared to have been negligible suggesting that changes in flora may not have influenced the extinction of Oreopithecus, particularly at Baccinello (Matson et al., 2012). Instead, the insular Maremma fauna likely became extinct through competition with continental taxa when the Tuscan-Sardinian paleobioprovince connected with Europe during the Messinian or Tortonian-Messinian transition (Abbazzi et al., 2008; Chesi et al., 2009; Rook et al., 2000). This mammalian turnover apparently did not result in the extinction of fresh water turtle species preserved in the Messinian V3 deposits (Chesi et al., 2009). However, other reptiles, such as Crocodylus bambolii, appeared in V1 and V2, but not V3 assemblages (Delfino & Rook, 2008), suggesting the turnover of fauna associated with the extinction of Oreopithecus bambolii was pervasive in the peri-Tyrrhenian region.

## Reconstructing dietary proclivities in Oreopithecus bambolii

The paleoecology of the Baccinello-Cinigiano basin has dietary implications for such a large ape as *Oreopithecus*. The large body size estimated for IGF 11778 (Jungers, 1987) would suggest protein requirements derived from the consumption of large quantities of leaves or terrestrial herbaceous vegetation as in *Gorilla* (Head *et al.*, 2011), or leaves, large numbers of insects and other fauna as in *Pan* (McGrew, 1992). Considering the estimated body size of *Oreopithecus*, the relative brain size was small (Harrison, 1986b) perhaps the result of secondary de-encephalization related to a diet highly concentrated on folivorous resources (Begun, 2002). The high-cusped molars and small incisors of *Oreopithecus* are similar to those of extant colobines which show a number of adaptations to folivory (Szalay & Delson, 1979).

Researchers have also relied on dental microwear to reconstruct the dietary preferences of *Oreopithecus*. For example, Carnieri & Mallegni (2003) found a diet consistent with folivory. Ungar (1996) noted the dominant feature to be striations of various dimensions with only limited pitting. Galbany *et al.* (2005) observed a resemblance of *Oreopithecus* specimen Bac62 to *Papio* suggesting a coarser diet than predicted was consumed.

To address this difference in observed versus expected dietary proclivities, the enamel surface of the Florence skeleton attributed to Oreopithecus bambolii was examined using whitelight confocal microscopy followed by scalesensitive fractal analysis (Merceron et al., 2009; Scott et al., 2005, 2006, 2009; Ungar et al., 2008, 2010). The dental microwear textures of several extant primates were included to infer the diet of the fossil specimen. It might be expected that IGF 11778 will be associated with Alouatta and Trachypithecus as its dental adaptations may be related to arboreal leaf consumption (Ungar, 1996). If the enamel complexity of IGF 11778 exceeds that of extant primate folivores, it may provide additional evidence to reconstruct the diet of this well preserved fossil and the paleoecology of late Miocene Baccinello, Italy.

# **Materials and Methods**

#### Materials

Oreopithecus bambolii specimen IGF 11778 is a fully articulated skeleton of a young adult male

catarrhine from the lignitic mines of Baccinello in the province Grossetto, southwestern Tuscany, Italy (Azzaroli *et al.*, 1986; Gentili *et al.*, 1998; Jungers, 1987). The original IGF11778 fossil is curated at the Museo di Storia Naturale, Sezione di Geologia e Paleontologia dell' Università di Firenze (originally the Istituto di Geologia di Firenze, or IGF). A cast of the left  $M_2$  of IGF 11778, on loan from the American Museum of Natural History, was examined (Fig. 1).

In order to provide an appropriate comparison to IGF 11778, two additional Oreopithecus bambolii specimens were investigated (IGF 10886 and IGF 4335, the originals also curated at the Museo di Storia Naturale, Sezione di Geologia e Paleontologia dell' Università di Firenze), but the preserved microwear was obscured by post-mortem taphonomy. Grine et al. (2012) posit that taphonomic damage often excludes a majority of fossil hominin teeth from providing an accurate portrayal of diet. However, King et al. (1999) investigated how taphonomic processes affect dental microwear using an experimental method in which both acidic and basic compounds and three size-based classes of sediment were included. They suggest that dental microwear is either completely destroyed by taphonomic processes or remains unchanged. The resulting destruction is easily discernible and is the principal factor involved in determining the appropriateness of a tooth for inclusion in a study of dental microwear (Williams & Patterson, 2010). The latter is true for IGF 11778 which does not exhibit postmortem taphonomic damage on facet 9 of M<sub>2</sub>.

The enamel texture characteristics of extant primates derive from Appendix 1 of Ungar *et al.* (2008). These include mantled howler monkeys, *Alouatta palliata* (n =11), which have a strong preference for young leaves, but eat substantial amounts of mature fruit, particularly from *Ficus* spp., along with flowers and leaf stems (Chamberlain *et al.*, 1993; Estrada, 1984; Rowe, 1996) as well as silvered langurs, *Trachypithecus cristatus* (n = 12), which primarily consume leaves (80%), some fruit (particularly figs) and at times, soil and sand (Brotoisworo & Dirgayusa, 1991;

Rowe, 1996). The comparative sample also includes western lowland gorillas, Gorilla gorilla gorilla (n = 9), which consume ripe fruit, leaves, herbs, seeds, bark, pith and insects (Doran-Sheehy et al., 2009) from 145 species (Head et al., 2011). Common chimpanzees, Pan troglo*dytes troglodytes* (n = 17), are classified as primary frugivores but also feed on social insects (Bogart & Pruetz, 2011), seeds, leaves, flowers, pith and vertebrate fauna from 116 species (Head et al., 2011). Also included are mixed-fruit hard-object consumers such as capuchin monkeys, Cebus apella (n = 13), and grey-cheeked mangabeys, Lophocebus albigena (n = 15). Cebus consumes insects, bromeliads, seeds, vertebrate prey and extracts "fight-back foods" with physical defenses against predation (Jack, 2011). To resist fracture from hard and brittle food items, Cebus has the thickest enamel per body size among primates (Kay, 1981). Lophocebus also has exceptionally thick enamel and eats ripe and unripe fruit as well as rotten fruit and insects (Lambert et al., 2004). These anthropoids have been featured in other studies because they represent folivores (Alouatta and Trachypithecus), frugivore-folivores (Gorilla), frugivores (Pan) and mixed-fruit hardobject consumers such as Cebus and Lophocebus (Merceron et al., 2009; Scott et al., 2006; Ungar et al., 2008). The anthropoids in this study all consume various amounts of leaves, fruit and insects such that a broad overlap in dental microwear texture properties is expected. Differences may be present when particular food items are consumed such as palm nuts in Cebus.

#### Data capture

Oreopithecus specimen IGF 11778 was examined at 100x under a white-light Sensofar Plµ confocal microscope with an optical imaging system designed by Solarius Development Inc. Microwear was observed on facet 9, a Phase II facet on the hypoconid, a buccal-distal cusp on the second mandibular molar which corresponds to a grinding rather than a shearing surface (Fig. 1) (Gordon, 1982; Kay & Hiiemae, 1977; Krueger *et al.*, 2008). Lower objectives were utilized to detect microwear devoid of taphonomic



Fig. 1 - The reconstructed enamel surface scans for Oreopithecus bambolii IGF 11778 showing individual scans A, B, C and D were obtained from adjoining views on the distolingual surface of the hypoconid corresponding to facet 9, a "Phase II" facet. The scanned area is marked by a black square on the enlarged second mandibular molar on this 1984 mandibular reconstruction of IGF 11778 (courtesy of and copyright Eric Delson). The white arrow shows from where the enlarged second mandibular molar of this figure is available at the JASs website.

artifacts before the specimen was scanned. Many fossils lack any trace of use-wear scars while others exhibit confounding taphonomic and casting damage (Galbany et al., 2005; Teaford, 2007; Williams & Holmes, 2011). Four contiguous scans for IGF 11778 (Fig. 1) were obtained from a viewing field of 138 x 102 µm from a total area sample of 276 x 204 µm (Merceron et al., 2009). Before scanning, the degree of tilt at 100x was reduced using the fine elevation control for the z axis. Prior to data extraction, the scans were leveled using the program SolarMap Universal. Scale-sensitive fractal analysis was employed to analyze the cloud of points from the scans to identify scaled lengths, two and threedimensional geometry and estimates of texture fill volume. One program, Toothfrax, calculated complexity (Asfc), scale of maximum complexity (Smc) and anisotropy (epLsar). Textural fill volume (Tfv) was estimated by the program SFrax developed by Surfract.com. The resulting data derive from algorithms embedded within these programs thus eliminating interobserver error (Scott et al., 2006).

#### Enamel texture properties

Surface complexity changes with respect to the scale of observation such that rough surfaces at a high resolution may appear smooth at a lower resolution. Area-scale fractal complexity (Asfc) is the difference in surface roughness with the scale of observation (7200  $\mu$ m<sup>2</sup> to 0.02  $\mu$ m<sup>2</sup>). Complexity (Asfc) is calculated as the steepest point slope from a log-log comparison of relative length area compared to scale of observation. The range of slope values from which the textural characteristic Asfc was calculated offers another measure of enamel complexity identified as scale of maximum complexity (Smc) (Scott et al., 2006, 2012; Ungar et al., 2010). Scale of maximum complexity (Smc) measures different aspects of hard-object consumption than captured by complexity (Asfc) revealing extremes, such as Lophocebus, compared to other tropical forest primates (Scott et al., 2006, 2012).

The orientation of enamel surface relief, or *epLsar* ("exact proportion of Length-scale anisotropy of relief") is associated with folivory (Scott *et al.*, 2006, 2009). Relative lengths of features are estimated from different depth profiles. The depth profiles are then compared to their straight line approximations across transects. These relative lengths, or vectors, were sampled at 5° intervals for 36 units of observation to estimate anisotropy, or patterning of surface relief. To normalize the vectors, the exact proportion method

was employed (Scott *et al.*, 2006). The mean length of the vectors approximates the extent to which micro-striations show a distinct orientation, or anisotropy.

Textural fill volume (*Tfv*) was obtained from an equation which calculates the surface fill of the scanned area, first with square cuboids with facet lengths of 10  $\mu$ m followed by cuboids with facet lengths of 2  $\mu$ m. These two volumes are compared to approximate the amount of surface damage derived from dental microwear (Scott *et al.*, 2006).

#### Analytical methods

Median values were obtained for the four textural properties to remove a positive skew of the central tendency (Scott *et al.*, 2006). Scalesensitive fractal analysis of the point cloud exhibits a nonparametric distribution so the data were rank-transformed (Conover & Inman, 1981). This obviated the need for normality tests and subsequent use of nonparametric statistics.

To identify whether the taxonomic (and dietary) groups were distinct, an Analysis of Variance (ANOVA) with Tukey's Honestly Significant Differences and Bonferroni adjustments was conducted; however since the two post-hoc tests for pairwise comparisons revealed the same pattern of significance, only the former was included. To account for IGF 11778 in statistical tests, the four scans were treated as individuals. Each pair-wise comparison of microwear textural characteristics was regressed to locate significant covariation. Texture properties that were significantly related were plotted together with 95% confidence ellipses around the centroids for each taxon. These confidence ellipses are centered on the means of the x and y variables and the standard deviations of x and y determine the axis values while the correlation coefficient between x and y specify its Discriminant Function Analysis orientation. was employed to locate classification rates and plots of the first two canonical scores axes were included to identify which texture characteristics best accounted for the distribution of individuals across the axes. Using the 95% confidence ellipses around group centroids the canonical scores axes show the polarization of taxa using multiple variables. Mahalanobis distances  $(D^2)$  of all four *Oreopithecus* scans to the group centroids are provided along with post-hoc probabilities of group membership to identify similarities between *Oreopithecus* and the compared samples. Finally, a cluster analysis, using a single linkage of squared Euclidean distances was conducted using the means of the dental microwear textures for each extant taxon and the four scans for IGF 11778. The cluster analysis provided a multivariate approximation of dietary preferences in extant primates and IGF 11778.

# Results

Fundamental group differences characterize the sample (Tab. 1). Alouatta and Trachypithecus exhibit low values for complexity (Asfc) while the other taxa show elevated values with a range of variation. Cebus with the greatest degree of complexity is followed by Pan and two of the four IGF 11778 scans. Scale of maximum complexity (Smc) separates Alouatta, Cebus, Gorilla and Pan with negative values from Lophocebus and IGF 11778 with positive ones. Pan shows the highest negative, Oreopithecus IGF 11778 a moderately high, and Lopohocebus the highest positive mean value for scale of maximum complexity (Smc). Alouatta exhibits the highest mean value for anisotropy (epLsar), followed by Trachypithecus and Gorilla, while Oreopithecus (IGF 11778) has the lowest value. For textural fill volume (Tfv) IGF 11778 followed by Alouatta exhibit the lowest values while Lophocebus shows the highest value.

#### ANOVA results with post-hoc tests of significance

All of the ANOVA comparisons yield significant differences among the taxa for each of the dental microwear textures with the *P* values ranging from *P* < 0.001 for complexity (*Asfc*) and textural fill volume (*Tfv*) to *P* = 0.009 for scale of maximum complexity (*Smc*). The F values ranged from 3.079 for scale of maximum complexity (*Smc*) to 10.071 for complexity (*Asfc*) demonstrating strong between-group differences exist.

Genus	N		Asfc	Smc	epLsar	Tfv
Alouatta	11	Mean	0.360	-0.188	6.0 x 10 <sup>-3</sup>	2610.909
		s.d.	0.183	1.050	2.1 x 10 <sup>-3</sup>	3225.700
Cebus	13	Mean	5.466	-0.178	4.0 x 10 <sup>-3</sup>	9674.846
		s.d.	6.304	1.101	1.9 x 10 <sup>-3</sup>	4931.705
Gorilla	9	Mean	1.597	-0.384	4.0 x 10 <sup>-3</sup>	8099.714
		s.d.	1.012	0.567	1.8 x 10 <sup>-3</sup>	5702.802
Lophocebus	15	Mean	1.769	0.623	4.0 x 10 <sup>-3</sup>	11388.333
		s.d.	1.740	1.064	2.0 x 10 <sup>-3</sup>	3389.758
Pan	17	Mean	2.246	-0.497	3.0 x 10 <sup>-3</sup>	9344.529
		s.d.	1.523	0.520	1.0 x 10 <sup>-3</sup>	5476.855
Trachypithecus	12	Mean	0.734	-0.365	5.0 x 10 <sup>-3</sup>	9532.250
		s.d.	0.660	0.547	2.6 x 10 <sup>-3</sup>	5687.205
IGF 11778		Mean	1.80	0.150	1.6 x 10 <sup>-3</sup>	<0.001
IGF 11778a			2.633	0.150	1.7 x 10 <sup>-3</sup>	264.116
IGF 11778b			0.965	0.150	1.4 x 10 <sup>-3</sup>	<0.001
IGF 11778c			3.041	0.150	1.6 x 10 <sup>-3</sup>	<0.001
IGF 11778d			0.907	0.150	3.4 x 10 <sup>-3</sup>	<0.001

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

Tukey's posthoc Honestly Significant Differences tests show significant distinctions are found between some taxa. For enamel surface complexity (Asfc), Alouatta is distinct from all taxa except *Trachypithecus* (Tab. 2a). The variation in this enamel surface texture property among the other taxa precludes many significant differences although Cebus and Pan are distinct, and Gorilla is nearly so (P = 0.053), from Trachypithecus (Tab. 2a). The only significant difference apparent for scale of maximum complexity (*Smc*) is between *Lophocebus* and *Pan* (Tab. 2a). For anisotropy (*epLsar*), both IGF 11778 and Pan are distinct from Alouatta. For textural fill volume (Tfv), Alouatta is distinct

from all extant taxa except *Gorilla*, while IGF 11778 is significantly different from all taxa except *Gorilla* and *Alouatta* (Tab. 2b).

#### Bivariate analyses

Several pair-wise comparisons of dental microwear textural characteristics are significant. The relationship between scale of maximum complexity (*Smc*) and complexity (*Asfc*) shown in Figure 2a is significantly associated (P = 0.001). Similarly, a linear regression of anisotropy (*epLsar*) and complexity (*Asfc*), shown in Figure 2b, is associated with a relatively large r value (r = 0.570) and a highly significant P value (P < 0.001), as is textural fill volume (*Tfv*) and complexity (*Asfc*) (P = 0.002)

	ALOUATTA	CEBUS	GORILLA	IGF 11778	LOPHOCEBUS	PAN	TRACHYPITHECUS
Alouatta		1.000	0.990	0.808	0.573	0.635	1.000
Cebus	0.000		0.999	0.682	0.344	0.762	1.000
Gorilla	0.000	0.479		0.456	0.116	0.958	0.999
IGF 11778	0.008	0.984	0.999		1.000	0.133	0.679
Lophocebus	0.000	0.372	1.000	0.997		0.005	0.353
Pan	0.000	0.958	0.942	1.000	0.812		0.798
Trachypithecus	0.681	0.000	0.053	0.165	0.066	0.002	

Tab. 2a - Tukey's HSD multiple comparisons for complexity, Asfc (below) and scale of maximum complexity, Smc (above).

Tab. 2b - Tukey's HSD multiple comparisons for anisotropy, epLsar (below) and textural fill volume, Tfv (above).

	ALOUATTA	CEBUS	GORILLA	IGF 11778	LOPHOCEBUS	PAN	TRACHYPITHECUS
Alouatta		0.008	0.090	0.962	0.000	0.005	0.007
Cebus	0.162		0.960	0.010	0.857	1.000	1.000
Gorilla	0.443	0.995		0.059	0.254	0.931	0.930
IGF 11778	0.008	0.475	0.227		0.000	0.008	0.008
Lophocebus	0.210	1.000	0.999	0.365		0.782	0.924
Pan	0.005	0.896	0.491	0.898	0.760		1.000
Trachypithecus	0.858	0.869	0.995	0.095	0.884	0.174	

shown in Figure 2c. Scale of maximum complexity (*Smc*) and anisotropy (*epLsar*) are significantly related (P < 0.001), but not shown.

Figure 2a shows fundamental distinctions exist between *Alouatta* and to a lesser extent *Trachypithecus* with relatively low values contrasting with those of *Cebus* and *Pan* with relatively high values for complexity (*Asfc*). *Lophocebus*, *Gorilla* and two IGF 11778 scans exhibit moderately elevated values for complexity (*Asfc*), while two IGF 11778 scans exhibit much greater values and fall within the 95% confidence ellipse for *Lophocebus*. For scale of maximum complexity (*Smc*), *Lophocebus* and IGF 11778 show high values which contrasts with *Pan* which exhibits lower values (Fig. 2a). In Figure 2b, only one of the IGF 11778 scans falls within the confidence ellipse for *Lophocebus* while the other three are highly distinct from *Alouatta* in showing greater complexity and lower anisotropy values. A few *Pan, Gorilla, Cebus* and *Lophocebus* outliers also show relatively high complexity and lower anisotropy values, resembling the textural properties characterizing IGF 11778.

Figure 2c shows differences exist between *Lopohocebus* with high values, and *Alouatta* and



Fig. 2 - Bivariate comparison between (A) scale of maximum complexity (Smc) and complexity (Asfc); (B) anisotropy (epLsar) and complexity (Asfc); and (C) textural fill volume (Tfv) and complexity (Asfc) with 95% confidence ellipses around group centroids (centered on the means of the x and y variables)—group centroids are outlined in black for each taxon. The colour version of this figure is available at the JASs website.

IGF 11778 with lower values for textural fill volume (Tfv). However, IGF 11778 differs from *Alouatta* in showing the combination of high values for complexity (*Asfc*) and low values for textural fill volume (Tfv). *Oreopithecus* specimen IGF 11778 is distinct from the majority of extant primates in this comparison. However, one *Pan*, one *Trachypithecus* and two *Gorilla* outliers approximate the combination of dental microwear textural properties exhibited by the four IGF 11778 scans (Fig. 2c).

#### Multivariate analyses

Classification rates from a discriminant function analysis show that all of the four scans for IGF 11778 are classified correctly as *Oreopithecus*. The extant taxa exhibit classification rates as high as 82% for *Alouatta* and 60% for *Lophocebus*, and as low as 29% for *Pan* and 42% for *Gorilla*. A jackknifed classification matrix yields lower classification rates for the extant taxa.

On Canonical Scores Axis 1, the 95% confidence ellipse for the four IGF 11778 scans cannot be excluded from any of the tropical forest taxa except Alouatta. The four IGF 11778 scans cluster together on the positive projection of the first canonical scores axis, and are closely approximated by Pan and Gorilla outliers but distinct from folivores, particularly Alouatta (Fig. 3). For extant taxa, Canonical Scores Axis 1 is a contrast vector separating individuals with high values for anisotropy (epLsar) such as Alouatta, and to a lesser degree, Trachypithecus, from hard-object consumers such as Pan, Gorilla, Lophocebus and Cebus based on the greater complexity (Asfc), and scale of maximum complexity (Smc) in the latter as shown by canonical discriminant functions-standardized by within-group variance. Canonical Scores Axis 2 separates IGF 11778 from all extant taxa with the exception of a few Pan, Gorilla and Trachypithecus outliers (Fig. 3). On Canonical Scores Axis 2, individuals with low textural fill volumes (Tfv), such as IGF 11778, and to a lesser extent, Alouatta, are polarized from individuals with elevated textural fill volumes (Tfv) as shown by canonical discriminant functions-standardized by within-group variance.

Mahalanobis distances  $(D^2)$  of group centroids from each of the Oreopithecus IGF 11778 scans to the comparative taxa show distinctions exist between the fossil and the extant species (Tab. 4). The  $D^2$  distances between IGF 11778 scans are among the smallest in the comparison, with the exception of "scan d" which shows a smaller posterior probability of group membership than do the other scans. However, even "scan d" is characterized by a much smaller distance to the Oreopithecus group centroid than any of the Oreopithecus samples are to the group centroids for the comparative taxa. The extant species are uniformly distinct from Oreopithecus. Cebus, Pan and Gorilla show smaller  $D^2$  distances to the group centroid for IGF 11778 than do Alouatta and Trachypithecus.

A cluster analysis divides the specimens into two groups. One of these comprises all of the IGF 11778 scans and the other includes all of the extant taxa (Fig. 4). Two of the scans for IGF 11778 (a and c) cluster with the shortest distance in the cluster tree while the other two scans are grouped with the *Oreopithecus* cluster albeit with rather long branch lengths. The cluster containing extant taxa divides *Alouatta* from all others. *Pan, Cebus* and *Gorilla* are closely clustered, and secondarily join *Trachypithecus* and *Lophocebus*.

#### Discussion

The dietary proclivities of Oreopithecus bambolii, and specifically of IGF 11778, have been explored by several researchers (Carnieri & Mallegni, 2003; Galbany et al., 2005; Szalay & Delson, 1979; Ungar, 1996; Ungar & Kay, 1995). In this study, Oreopithecus bambolii specimen IGF 11778 exhibits a relatively complex enamel surface texture (Tab. 1). The ectocranial superstructures exhibited by Oreopithecus indicate heavy chewing (Begun, 2002) consistent with relatively elevated values for enamel textural complexity (Asfc) and scale of maximum complexity (Smc). Furthermore, the forward projection of the zygomatic arch and the presence of a sagittal crest suggest masticatory functional affinities with Australopithecus perhaps indicative of a rather coarse fiber-rich diet (Harrison, 1986b).

In a study of molar buccal microwear using scanning electron microscopy (SEM), Oreopithecus bambolii specimen Bac62 is distinct from Gorilla gorilla, Pan troglodytes, Pongo pygmaeus, Cercopithecus mitis, Cercopithecus neglectus, Papio anubis and Dryopithecus laietanus in exhibiting a much smaller total density of scratches (although Colobus spp. exhibited the smallest total number of scratches) (Galbany et al., 2005). This is in contrast to the predominance of scratches observed on the Phase II molar facets in an Oreopithecus bambolii sample from Baccinello, Monte Bamboli and Ribolla (Ungar, 1996). Oreopithecus bambolii specimen Bac62 is classified as Papio anubis in a discriminant function analysis, and the two are more closely grouped in a cluster analysis than are the other taxa with the exception of Pan and Gorilla (Galbany et al., 2005). Similarly, Smith & Williams (2010) suggest that Oreopithecus bambolii was more similar in dental microwear to



Fig. 3 - Canonical Scores Axes 1 (57%) and Axis 2 (24.2%) with 95% confidence ellipses around group centroids (centered on the means of the x and y variables) -group centroids are outlined in black for each taxon. The colour version of this figure is available at the JASs website.

Papio ursinus than to the great apes. The feeding behavior of Papio includes fruits, leaves, flowers, herbs and the underground parts of plants (Rowe, 1996). These dietary proclivities differ from that reconstructed for Oreopithecus bambolii (IGF 11778 and IGF 4335) by Ungar & Kay (1995) who suggest a diet consistent with folivory from observed versus expected shearing-crest lengths. Ungar (1996) observed fewer pits on the M2 Phase II facets in Oreopithecus bambolii compared to Dryopithecus spp. and Ouranopithecus macedoniensis using SEM. However, for feature density, Oreopithecus bambolii is not distinct from Dryopithecus laietanus and Dryopithecus Feature density is much higher in brancoi. Ouranopithecus macedoniensis which probably consumed hard foods (Ungar, 1996) given its thick enamel (de Bonis & Koufos, 1994). The molar Phase II facets of Oreopithecus bambolii show a proliferation of long and narrow striations in contrast to Ouranopithecus macedoniensis in which pits are the dominant feature (Ungar, 1996). Ungar (1996) considers Oreopithecus to be distinct from the other Miocene catarrhines

he examined. According to Ungar (1996), both *Ouranopithecus*, a hard-object consumer, and *Oreopithecus*, a presumed folivore, present unique feeding adaptations, indicating the range of diets among Miocene hominoids was much broader than observed in extant apes.

The results presented here agree in part with Galbany et al. (2005) who suggest that Oreopithecus bambolii specimen Bac62 is distinct from Colobus spp. and likely consumed some coarse food items rather than having an exclusive leaf-based diet. Similarly IGF 11778 is not aligned with Trachypithecus and Alouatta in anisotropy (Fig. 2b). Although a direct comparison of texture characteristics and SEM of buccal microwear has not been performed, Gorilla gorilla and Pan troglodytes are included here and in Galbany et al. (2005). In terms of total number of scratches, the two African apes are similar to one another and exhibit overlapping ranges (Galbany et al., 2005). They are distinct from Cercopithecus spp. and are most similar to Papio anubis and Oreopithecus specimen Bac62. Furthermore, Gorilla and Pan are among the

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Fig. 4 - Cluster analysis of the four scans for IGF 11778 with the comparative taxa shows the fossil samples are distinct from extant species. The colour version of this figure is available at the JASs website.

most similar to *Oreopithecus* specimen Bac62 in scratch length (Galbany *et al.*, 2005) although for other buccal microwear traits, Bac62 differs from the African apes. The mean value for complexity (*Asfc*) in *Oreopithecus* specimen IGF 11778 falls between those for *Gorilla* and *Pan* (Tab. 1). For the other texture characteristics, IGF 11778 differs from the African apes, although IGF 11778 is similar to *Pan* and *Gorilla* outliers in bivariate and multivariate comparisons (Figs. 2 and 3).

Oreopithecus specimen IGF 11778 exhibits a relatively complex enamel textural surface (Asfc and Smc) and has lower anisotropy values than Trachypithecus and Alouatta, indicating the fossil exhibited a brittle and less leafy diet than extant folivores. Pronounced enamel complexity (Asfc) is noted in a number of extant primate taxa, particularly those which consume hard and brittle food items, such as Cebus. Lophocebus and secondarily IGF 11778 exhibit relatively high values for scale of maximum complexity (Smc) indicating some hard and brittle resources may have been included in the diet of this Oreopithecus individual. However, IGF 11778 is distinct in textural fill volume (Tfv) by exhibiting lower values than most extant individuals characterized as hard-object feeders, and is not significantly different from *Gorilla* and *Alouatta* in this textural characteristic (Tab. 2).

Elevated textural fill volume (Tfv) is associated with the consumption of hard and brittle foods. For example, Cebus and Lophocebus both exhibit high values for textural fill volume (Tfv)while *Alouatta* exhibits a low Tfv as its diet comprises a substantial quantity of young and mature leaves, but Trachypithecus exhibits relatively elevated Tfv values. Soil and sand consumption (Brotoisworo & Dirgayusa, 1991) or perhaps seed predation may be at least partially responsible for the higher textural fill volume (Tfv) characterizing Trachypithecus (Merceron et al., 2009) compared to Alouatta. The low textural fill volume (Tfv) of Oreopithecus specimen IGF 11778 approximates the values of several Alouatta and one Trachypithecus individual within the sample (Ungar et al., 2008, Appendix 1) suggesting the fossil does not exemplify pronounced hard-object consumption.

Given the swampy habitat reconstructed for late Miocene Baccinello (Azzaroli *et al.*, 1986), the elevated complexity (*Asfc*) and scale of maximum complexity (*Smc*) values observed for IGF 11778 could have resulted from the consumption of edible aquatic rhizomes, particularly those similar to

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cans of IGF 11778 to the group centroids of the com- oup membership).
PECIMEN IGF 11778

OREOPITHECUS BAMBOLII SPECIMEN IGF 11778								
TAXON	SCAN A	SCAN B	SCAN C	SCAN D	AVERAGE D <sup>2</sup>			
LOPHOCEBUS	10.0 (0.01)	10.4 (0.01)	13.3 (0.00)	6.8 (0.05)	10.125			
CEBUS	8.3 (0.2)	11.2 (0.01)	10.7 (0.01)	5.9 (0.08)	9.025			
OREOPITHECUS	0.6 (0.96)	1.6 (0.95)	1.6 (0.98)	2.0 (0.56)	1.45			
TRACHYPITHECUS	18.5 (0.00)	13.6 (0.00)	23.4 (0.00)	8.4 (0.02)	15.975			
GORILLA	10.6 (0.01)	10.6 (0.01)	13.7 (0.00)	4.7 (0.15)	9.9			
ALOUATTA	19.1 (0.00)	13.0 (0.00)	23.4 (0.00)	6.0 (0.07)	15.375			
PAN	10.1 (0.01)	9.9 (0.02)	13.4 (0.00)	6.2 (0.07)	9.875			

Tab. 3- Mahalanobis distances (D<sup>2</sup>) of all four s parative taxa (with post-hoc probabilities of g

Nymphea lotus and Phragmites australis, which lack the fracture resistant properties associated with most terrestrial rhizomes, or the enamel complexity could have derived from extraneous grit (Dominy et al., 2008). Herbs close to ground level may be covered with fracture resistant particles more often than arboreal leaves and fruits. The close proximity of two Gorilla individuals to IGF 11778 (Fig. 3) may have resulted from the consumption of abrasive grit clinging to herbs which are consumed by gorillas even during months when ripe fruit is plentiful. These include the shoots of Haumania danckelmaniana and the swamp herb Hydrocharis chavalieri (Doran-Sheehy et al., 2009).

Another possibility is that the consumption of insect exoskeletons may be related to elevated complexity (Asfc). Insectivory and specifically termitivory, constitutes up to 60% of the diet of Pan troglodytes verus at Fongoli, Senegal, arguably a unusual chimpanzee habitat (Bogart & Pruetz, 2011). Although direct observations of insectivory at central African sites have been lacking, insect remains, particularly those of weaver ants, are frequently found in fecal material. The highest values for complexity (Asfc) in the extant sample occur in Cebus and Pan, both of which consume large quantities of insects compared to the other taxa. Insect exoskeletons are among the stiffest non-mineral reinforced biological materials known (Dirks & Taylor, 2012; Vincent &

Wegst, 2004). While a dental microwear texture analysis of insectivory has not been conducted, SEM results suggest the consumption of insect exoskeletons results in the formation of large pits on the enamel surface of Muridae species (Rodrigues et al., 2009) as well as among small primates and microchiropterans (Strait, 1993). The somewhat elevated textural complexity (Asfc) exhibited by Oreopithecus specimen IGF 11778 could have resulted from a heavy exploitation of social insects; its large body size and small, but high-cusped molars are not incompatible with feeding on insects, although abrasive grit or food items with resistant mechanical properties could also be responsible for the elevated complexity (Asfc) observed. Rodrigues et al. (2009) caution against attributing a strong relationship between grit load and dental microwear given the equivocal results obtained from micromammals with known habitats and dietary proclivities.

It was expected that IGF 11778 would align with extant folivores in textural characteristics given the high crests of its molars and its small brain to body size estimates. However, the fossil does not group with Alouatta or Trachypithecus in any consistent fashion. While this observation does not exclude the possibility of leaves from the diet of Oreopithecus, it does indicate that some coarse food items atypical of extant folivores were also consumed, at least by IGF 11778.

#### Conclusions

Oreopithecus specimen IGF 11778 does not align with extant folivores suggesting its diet may have included some hard, brittle items, such as extraneous grit, insects or foods with physical defenses. The fossil is similar to Lophocebus and some Pan, Gorilla and Cebus outliers, although none of the extant individuals exhibit the same combination of textural properties as IGF 11778. This Oreopithecus specimen is distinct from the comparative taxa suggesting it was not a strict folivore with some fruit, soil and sand consumption such as in Trachypithecus, or folivorous with considerable fruit consumption as in Alouatta. Parallel results were obtained by Galbany et al. (2005) who found Oreopithecus bambolii specimen Bac62 to be classified as Papio anubis rather than extant folivores (Colobus spp.). Oreopithecus may have exhibited an eclectic diet, concentrating its feeding strategy on a wide range of foods like Pan and Gorilla. Given the complexity of its enamel surface texture, and the relative lack of anisotropy, Oreopithecus specimen IGF 11778 was possibly only partly committed to a folivorous diet, and may have consumed some "fight-back" foods, insects, or may have periodically traveled to the ground to obtain foods with higher grit loads than are found in the forest canopy.

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