

## **Sumatran orangutan diets in the Late Pleistocene as inferred from dental microwear texture analysis**

### Author

Louys, J, Zaim, Y, Rizal, Y, Aswan, Puspaningrum, M, Trihascaryo, A, Price, GJ, Petherick, A, Scholtz, E, DeSantis, LRG

### Published

2020

### Journal Title

Quaternary International

### Version

Accepted Manuscript (AM)

### DOI

[10.1016/j.quaint.2020.08.040](https://doi.org/10.1016/j.quaint.2020.08.040)

### Rights statement

© 2020 Elsevier Ltd and the International Union for Quaternary Research (INQUA). Published by Elsevier Ltd. Licensed under the Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International Licence (<http://creativecommons.org/licenses/by-nc-nd/4.0/>) which permits unrestricted, non-commercial use, distribution and reproduction in any medium, providing that the work is properly cited.

### Downloaded from

<http://hdl.handle.net/10072/399186>

### Griffith Research Online

<https://research-repository.griffith.edu.au>

## Sumatran orangutan diets in the Late Pleistocene as inferred from dental microwear texture analysis

Julien Louys<sup>1\*</sup>, Yahdi Zaim<sup>2</sup>, Yan Rizal<sup>2</sup>, Aswan<sup>2</sup>, Mika Puspaningrum<sup>2</sup>, Agus Trihascaryo<sup>2</sup>, Gilbert J. Price<sup>3</sup>, Ansley Petherick<sup>4</sup>, Elinor Scholtz<sup>5</sup>, Larisa R.G. DeSantis<sup>4,5,\*</sup>

<sup>1</sup>Australian Research Centre for Human Evolution, Griffith University, Brisbane, Australia

<sup>2</sup>Paleontology and Quaternary Geology Research Group, Institut Teknologi Bandung, Indonesia

<sup>3</sup>School of Earth and Environmental Sciences, The University of Queensland, Brisbane, Queensland, Australia

<sup>4</sup>Department of Biological Sciences, Vanderbilt University, Nashville, TN, USA

<sup>5</sup>Department of Earth and Environmental Sciences, Vanderbilt University, Nashville, TN, USA

\*To whom correspondence should be addressed: [j.louys@griffith.edu.au](mailto:j.louys@griffith.edu.au),  
[larisa.desantis@vanderbilt.edu](mailto:larisa.desantis@vanderbilt.edu)

### Abstract

Orangutan (*Pongo* spp.) fossils have been found throughout much of Pleistocene Southeast Asia. Today, *Pongo* is restricted to three living species on the islands of Borneo and Sumatra. They are predominately frugivores, and during fruit masting events their diets can consist entirely of fruit. However, food procurement strategies between masting events differ between islands and thus species. Sumatran orangutans (*Pongo abelii*) are largely able to fall back on non-masting fruit species, such as figs, such that they can maintain higher quality diets compared to their Bornean counterparts (*Pongo pygmaeus*), who ingest more lower quality and tougher foods between mast events. However, diets of fossil orangutans remain largely unknown. We investigated the diets of Sumatran orangutans from the Pleistocene deposits of the Padang Highlands, western Sumatra, using dental microwear texture analysis. We tested whether the diets of the fossil species were similar to those of Bornean orangutans, all great apes generally, and macaques that occupy similar habitats to modern orangutans, in order to gain insights into palaeoenvironments present in western Sumatra. We found that fossil orangutans consumed foods less tough than modern Bornean *Pongo pygmaeus*, and thus presumably more fleshy fruits (absent of significant seed mastication). We found no differences in the amount of hard object feeding between modern and fossil orangutans. Taken together, we suggest that Pleistocene orangutans from western Sumatra had similar diets to *Pongo abelii*, indicating that masting events were not a significant contributing factor in their intake of fruit. Finally, we suggest anisotropy values in orangutan dental microwear may be an important marker for fruit masting events in the Pleistocene.

**Keywords:** Ngalau Gupin, Ngalau Sampit, Lida Ajer, Pandang Highlands, fruit masting, paleodiet

## 1. Introduction

Orangutans belong to a subfamily of Primates dating back to the Miocene, the pongines, that also includes *Sivapithecus*, *Gigantopithecus*, and potentially *Lufengpithecus* and *Ankarapithecus* (Finarelli and Clyde 2004; Welker et al. 2019). Pleistocene orangutans (*Pongo* spp.) were formally distributed across Southeast Asia, from southern China in the north through to Java in the south (Jablonski and Whitford 1999; Louys et al. 2007; Louys 2008; Spehar et al. 2018). Relict populations of the three modern species, *Pongo pygmaeus*, *P. abelii*, and *P. tapanuliensis*, are now found only on the islands of Borneo and Sumatra. Explanations on the loss of their geographic range as well as the potential extinction of fossil species have largely been related to sustained habitat loss brought about by southern shifts in the tropical and sub-tropical zones and increased seasonality during Pleistocene glacial conditions (Jablonski and Whitford 1999; Louys et al. 2007; Louys 2008; Spehar et al. 2018).

Human interactions with orangutans are known from at least c. 50 ka, with evidence of orangutans and other primate hunting discernible from the archaeological deposits of Niah Cave, Borneo (Piper and Rabbett 2009). Earlier interactions are inferred based on the common presence of humans and orangutans in the Lida Ajer fossil deposits in Sumatra, dated to 62-72 ka (Westaway et al. 2017). However, a synthesis of palaeontological, archaeological, and palaeoecological data pertaining to orangutan and human interactions suggest that significant human influence on the distribution and extirpation of these apes became prevalent only in the last 10,000 years or so (Spehar et al. 2018).

In Sumatra, orangutans are found predominately north of Lake Toba and represented by *P. abelii*; the only substantiated exception is the second Sumatran species *P. tapanuliensis*, found in a 1000 km<sup>2</sup> area of Batang Toru, South Tapanuli (Nater et al. 2017). Meanwhile, fossil orangutans

on the island are only known from the Padang Highlands in west Sumatra. The largest collection of these are from the ‘Dubois Caves’, fossil deposits excavated by M. Eugene Dubois in the late 19<sup>th</sup> Century (Dubois 1891). Orangutan fossils from the sites of Lida Ajer, Sibrambang, Djamboe, and several unnamed caves were described in detail by Hooijer (1948) and Drawhorn (1994). Additional orangutan fossils were subsequently reported from two nearby caves by Louys et al. (2017), Ngalau Gupin and Ngalau Sampit.

The evolutionary and biogeographical relationship between fossil and modern Sumatran orangutans has not been adequately addressed. It seems likely that the absence of fossil orangutans in the north of the island are a function of the lack of suitable fossil sites recorded in this region coupled with limited exploration. However, it is interesting that Binjai Tamieng, one of the only Quaternary sites known north of Lake Toba, records no fossil orangutans despite modern orangutans found nearby (Gruwier 2017). Presumably, orangutans were once found throughout the island and their current geographic range is a product of the extinction of the Padang Highland populations/species. Critical disparities in ecological or environmental tolerances between modern and fossil orangutans may have played a role in the latter’s extinction. Notable differences between fossil specimens and modern species include generally larger tooth sizes and higher average enamel thickness in Pleistocene individuals (Hooijer 1948; Drawhorn 1994; Smith et al. 2011). These differences may be associated with processing harder, more brittle, or more abrasive foods in fossil orangutans (Smith et al. 2011).

Modern orangutans have the broadest range of plant species included in their diet of all the great apes (Russon et al. 2009). Nevertheless, they are predominately frugivores who prefer large quantities of fruit that are high in calories, soft in pulp, and occur in large crops (MacKinnon 1974; Galdikas 1988; Knott 1998; Djojosedharmo and van Schaik 1992; Leighton 1993). When fruit is

unavailable, orangutans eat a variety of other food types including flowers, shoots and leaves, vines, pith, bark, insects, and occasionally smaller mammals (Hardus et al. 2012; Russon et al. 2009; Delgado and van Schaik 2000).

Dramatic fluctuations in fruit availability are common in Southeast Asia due to masting – a phenomenon produced largely by dipterocarp and other canopy trees species that fruit in synchrony every 2-10 years (Ashton et al. 1988). Masting events are thought to be initiated by drier conditions and sharp drops in night-time temperatures associated with the El Niño Southern Oscillation (Ashton et al. 1988; Newbery et al. 1998; Wycherley 1973; Wich and van Schaik 2000). During masting events, orangutan diets may consist of 100% fruit (Knott 1998; Kanamori et al. 2010). Between masting events, orangutans adopt one of two strategies related to the availability of fruit. In habitats dominated by dipterocarps, where fruiting is strongly controlled by masting events, orangutans adopt a sit and wait strategy in order to limit energy expenditure. In habitats where fruit is available more reliably, such as forests which have a high density of strangling figs, orangutans are constantly moving and feeding (Morrogh-Bernard et al. 2009).

Sumatra and Borneo differ significantly in terms of habitat productivity and climate, which have large impacts on the dietary ecology of orangutans living on these islands. Sumatran forests yield larger numbers of orangutan-preferred foods (Russon et al. 2009; Wich et al. 2006) and produce less severe masting effects on diet (Knott 1998; Delgado and van Schaik 2000; Wich et al. 2006). The net effect of these differences produces higher densities of Sumatran orangutans compared to Bornean, with Sumatran orangutans eating more high-quality foods (fruits), and less low-quality foods (bark, leaves) compared to their Bornean counterparts (Rijksen and Meijaard 1999; Delgado and van Schaik 2000; Russon et al. 2009). In Sumatran habitats where fruit has become scarce, such as anthropogenically degraded landscapes, Sumatran orangutans similarly

spend more time eating bark than their conspecifics in more pristine environments (Campbell-Smith et al. 2011).

Dental occlusal microwear (hereafter ‘microwear’) has been used to infer the diet and ecology of primates, past and present (e.g., Teaford 1985, 1988; Teaford and Glander 1991; Teaford and Runestad 1992; Teaford et al. 1996; Ungar and Teaford 1996; Ungar et al. 2004), including shedding light on modern and fossil pongines (e.g. Teaford and Walker, 1984; King et al. 1999; Ungar, 1994; Merceron et al. 2005, 2006; Scott et al. 2012). Dental microwear provides information pertaining to the most recent diet of an individual, prior to its death, i.e., ‘the last supper effect’ (Grine, 1986; Teaford & Oyen 1989). Prior studies comparing orangutans with other Primates, as well as examining orangutans themselves, helped shed light on notable similarities and differences between species. Orangutans were found to have large numbers of microwear features as well as frequency of pits that were associated with hard or unripe fruit consumption and the processing of hard husked objects (King et al. 1999). While some studies found some effect of sex in orangutan microwear variables (Ungar, 1994; King et al. 1999), more recent studies have found no significant differences between the sexes (Merceron et al. 2005). In comparisons with other apes, orangutan microwear consistently compared most favorably with those of the chimpanzee (Teaford, 1988; King et al. 1999; Merceron et al. 2005). Early studies such as some of these, however, used a light or scanning electron microscope to count individual features (e.g., pits and scratches; Walker et al. 1978; Teaford and Walker 1984; Grine et al. 2002). While revealing, variability between human counters can pose challenges (Gordon 1988; Grine et al. 2002; Galbany et al., 2005; Scott et al. 2006; Schmidt 2010). Dental Microwear Texture Analysis (DMTA) analyzes dental microwear surfaces in three-dimensions using a scanning white light confocal microscope and scale sensitive fractal analysis (Ungar et al., 2003; Scott et al. 2005,

2006). Wear surfaces are quantified in an automatic manner and textural attributes of a given surface are calculated the same, regardless of the observer.

In this study we examine the dental microwear of fossil orangutans from West Sumatra (Figure 1), comparing them to modern Bornean orangutans, as well as all other great apes, in order to infer dietary habitats of fossil orangutans. These sites are thought to represent rainforest habitats based on their faunal compositions (de Vos 1983; Louys and Meijaard, 2010; Westaway et al. 2017; Smith et al. this volume). We expect that lower quality diets associated with orangutans living in dipterocarp forests, and thus subject to mast fruit availability, will be higher in tougher foods such as bark that will be reflected by higher anisotropy values. We explore whether differences in the microwear variables present in teeth from well-dated Sumatran sites existed, and what this might indicate regarding ecological and environmental changes in Sumatra over the late Pleistocene.

## **2. Materials and Methods**

### **2.1 Specimens**

Specimens of extant (n=12) wild *Pongo pygmaeus* from the American Museum of Natural History (AMNH; New York City, NY, USA) and the Lee Kong Chian Natural History Museum (ZRC; Singapore) were sampled. Modern specimens are wild caught specimens from Borneo. More specific locality information was available for microwear analyses for four specimens: ZRC4742, ZRC4746L, and ZRC4750L are from Pontianak, west Kalimantan, and AMNH140426 is from Sandakan, Sabah. The taxonomic status of fossil orangutans is complicated and will be addressed more fully in a subsequent publication; for the purposes of this study all fossil orangutans are referred as *Pongo* sp. Fossil specimens (n=29) of *Pongo* sp. are from Lida Ajer (LA; n=6), Ngalau

Gupin (NG; n=22), and Ngalau Sampit (NS; n=1), representing a minimum of 2, 4, and 1 individuals for each site, respectively (Table 1). Fossils from each site were initially screened for microwear analysis by eye and hand lens, with only the best-preserved teeth examined. This resulted in 3 teeth (33%) discarded from Lida Ajer, and 30 teeth (54%) from Ngalau Gupin. Casts were further assessed for quality, with an additional 4 molds (9%) from Ngalau Gupin taken but not used in the final analysis. All fossils are housed in the Geology and Palaeontology collections of the Institut of Teknologi Bandung (Indonesia), and molds in the DREAM lab of Vanderbilt University (USA).

The fossils from Lida Ajer were collected from the sinkhole at the rear of the cave and are presumed to have been reworked from cemented breccias chronologically constrained to 62-72 ka (Westaway et al. 2017) by Bayesian modelling derived from a combination of various numerical dating methods (U-series, Red TL, pIRIR, combined U-series/ESR). *Sus* and *Rhinoceros* teeth from Ngalau Gupin have been directly dated to ~130 ka using combined U-series/ESR method (Smith et al. in prep.), and the orangutan specimens from this site are considered coeval with these fossils. The specimen from Ngalau Sampit was collected from a breccia with a capping flowstone providing a minimum U-series age of ~90 ka (Louys et al. 2017). Data generated from extant specimens were added to and compared with published great ape and macaque data (Scott et al. 2012). The confocal microscopes used to generate both the published data and new specimen data are directly comparable (microscopes "Connie" and "Dolly", respectively; Arman et al., 2016, see Table 5 within this reference).

## **2.2 Dental Microwear Texture Analysis (DMTA)**

DMTA has been used to distinguish diets in a broad range of extant taxa (e.g. ungulates,



carnivorans, marsupials, and xenarthrans; Scott 2012, Jones and DeSantis, 2016, DeSantis et al. 2017a, 2017b, Haupt et al. 2013) including primates (e.g. Scott et al. 2005, 2006, 2012; Percher et al. 2018; Ungar et al. 2008, 2012). DMTA is also better able to distinguish dietary behavior as compared to 2D feature based methods (DeSantis et al. 2013). Primates that eat hard/brittle foods (e.g., fruit with hard pits, seeds) have higher complexity (*Asfc*), while animals that eat tougher foods (e.g., grass, tough leaves) have higher anisotropy (*epLsar*; Ungar et al., 2003, 2007; Scott et al., 2005, 2006; DeSantis 2016). Texture fill volume (*Tfv*) is also useful for quantifying the size of features by comparing the volume filled by large (10  $\mu\text{m}$  diameter) and small (2  $\mu\text{m}$  diameter) square cuboids, with high *Tfv* values indicating potentially deeper and/or larger features (Scott et al 2006). *Tfv* typically parallels complexity, with the highest values occurring in taxa that also have higher complexity values; however, it does not yield significant differences between the great apes *Gorilla* and *Pan* (Scott et al. 2012). *HAsfc*<sub>81</sub> is another attribute that compares the complexity of one area of the surface to subdivided surfaces (i.e., a given surface is divided into 9x9 sub-surfaces, a total of 81 sub-surfaces, respectively), comparing individual sub-surfaces to the surface as a whole—potentially indicative of the size and variability in wear-causing particles (e.g., Scott et al., 2006, 2012; DeSantis, 2016).

“Phase II” facets (e.g. 9, x, 10n; Kay, 1977) were molded and analyzed to assess dietary behavior in the great apes examined (Table 1), standardizing the same position as best as possible among sampled teeth (based on wear). Teeth were cleaned with cotton swabs and acetone, after which a polyvinylsiloxane dental impression material (President’s Jet, Coltene-Whaledent Corp., Alstatten, Switzerland) was applied to their occlusal surfaces. The molds were subsequently cast using a high-resolution epoxy (Epotek 301, Epoxy Technologies Corp., Billerica, MA, USA). Casts were scanned with Sensofar PLu neox optical profiler (Solarius Development, Inc.,

Sunnyvale, CA) using a 100× objective lens at Vanderbilt University. These data were compared to extant primate data from this study (scanned on the confocal noted above at Vanderbilt) and published data (i.e., Scott et al., 2012) that were scanned on a Sensofar Plu white-light scanning confocal profiler (Solarius Development, Inc., Sunnyvale, CA) using a 100× objective lens at the University of Arkansas. While it is important to consider differences in DMTA attribute values between microscopes, all new analyses were performed on "Dolly" (at Vanderbilt University); however, DMTA attributes are indistinguishable between "Dolly" and "Connie" (at the University of Arkansas; see Arman et al., 2016 and Table 5 within). Further, the same exact areas and methods were used for all analyses here conducted and referenced.

A total area of 204x276  $\mu\text{m}^2$  was scanned, a 2x2 grid (a total of four scans); the median attribute value of all four scans is reported for each specimen (per Ungar et al. 2003, Scott et al. 2005, 2006). All tooth surfaces underwent scale-sensitive fractal analysis (SSFA) via analysis of tooth surfaces using both toothfrax and Sfrax (Surfract Corp., <http://www.surfract.com/>) software; the median value of the four scans was used to represent a given specimen. The scans were analyzed for complexity ( $Asfc$ ), anisotropy ( $epLsar$ ), textural fill volume ( $Tfv$ ), and heterogeneity ( $HAsfc_{81}$ ). Examples of microwear attributes are displayed in Figure 2.

### 2.3 Statistical analysis

DMTA values were primarily non-normally distributed (Table 2), non-parametric tests were used for most comparisons, as other studies in occlusal microtexture (e.g. Scott et al. 2005, 2012). *Pongo pygmaeus* and fossil *Pongo* sp. were compared using Mann-Whitney U-tests (non-parametric); additionally,  $Asfc$  values were also compared using parametric t-tests as these data were normally distributed. We used Kruskal-Wallis tests and Dunn's procedure to compare all

extant taxa to each other and to *Pongo* sp.; and to compare modern *Pongo* with *Pongo* sp. from Ngalau Gupin and Lida Ajer, with differences between groups assessed via *post-hoc* Mann-Whitney U comparisons. Further, *Pongo* sp. from Ngalau Gupin and Lida Ajer were also directly compared via Mann-Whitney U-tests. Significance was evaluated at  $\alpha=0.05$ .

### 3. Results

Dental microwear data for *Pongo pygmaeus* analysed in the present work and fossil specimens of *Pongo* sp. (in addition to relevant great ape data) included in Supplemental Table 1, are summarized in Table 2 and graphically represented in Figure 3, with detailed specimen data noted in Table 1. Published data (Scott et al. 2012) used in these analyses are also summarized in Table 2 and noted in Supplemental Table 1.

As both prior comparison and our comparisons (which includes additional *Pongo pygmaeus* data) of the two species of *Gorilla* (i.e., *Gorilla beringei* and *Gorilla gorilla*) with *Pan troglodytes* and *Pongo pygmaeus* are indistinguishable from comparisons at the genus level (Scott et al., 2012), both species of *Gorilla* were combined in subsequent comparisons of modern and fossil taxa. All extant great apes (*Gorilla*, *Pan*, and *Pongo*) are indistinguishable in *Asfc* and *Tfv* values ( $p>0.1$ ; Fig. 3A). *Pan* has significantly lower *epLsar* than both *Gorilla* ( $p=0.034$ ) and *Pongo* ( $p=0.008$ ; Fig. 3A). *Pan* also has significantly higher *HAsfc*<sub>81</sub> than both *Gorilla* ( $p=0.032$ ) and *Pongo* ( $p=0.013$ ). For completeness, *Pongo pygmaeus* was also compared to the crab-eating macaque *Macaca fascicularis* (from Scott et al. 2012) as they occupy similar habitats. These taxa are indistinguishable in *Asfc*, *epLsar*, and *HAsfc*<sub>81</sub> values ( $p>0.05$  for all; Fig. 3B). *Pongo pygmaeus* has significantly lower *Tfv* than *Macaca fascicularis* ( $p=0.029$ ); though caution should be taken when comparing these taxa due to differences in tooth morphology.

Fossil specimens of *Pongo* (i.e. *Pongo* sp.) are indistinguishable in *Asfc* from all extant apes examined here (*Gorilla*, *Pan*, and *Pongo*) including both parametric and non-parametric comparisons with just *Pongo pygmaeus* ( $p > 0.1$ ; Fig. 3C). *Pongo* sp. has significantly lower *epLsar* than modern *Pongo pygmaeus* ( $p = 0.015$ ; and,  $p = 0.022$  when only compared to *Pongo pygmaeus*), significantly lower *Tfv* than *Gorilla* ( $p = 0.048$ ), and significantly lower *HAsfc*<sub>81</sub> than all extant taxa ( $p < 0.0001$  for *Gorilla*, *Pan*, and *Pongo pygmaeus* when comparing only *Pongo pygmaeus* and *Pongo* sp.;  $p = 0.0002$  for *Pongo pygmaeus* when comparing all taxa here examined). When separating out *Pongo* sp. from Ngalau Gupin and Lida Ajer, compared to *Pongo pygmaeus*, no significant differences were found for *Asfc* or *Tfv* ( $p \geq 0.2$ ). Differences for *epLsar* exceeded  $\alpha = 0.05$  ( $p = 0.086$ ), with *post-hoc* tests revealing significantly lower values in Ngalau Gupin *Pongo* sp. than *Pongo pygmaeus* ( $p = 0.033$ ). Both Lida Ajer and Ngalau Gupin *Pongo* sp. have significantly lower *HAsfc*<sub>81</sub> values than *Pongo pygmaeus* ( $p = 0.003$  and  $p < 0.001$ , respectively). There are no significant differences in any DMTA attribute (*Asfc*, *epLsar*, *Tfv*, *HAsfc*<sub>81</sub>) between *Pongo* sp. from Ngalau Gupin and Lida Ajer localities (though low sample size at Lida Ajer reduces statistical power). Proportions of complex (*Asfc* > 2) and anisotropic values (*epLsar* > 0.005) for specimens of each taxon are note in Fig. 3D.

#### 4. Discussion

Our results suggest that the West Sumatran fossil orangutans ate more fruit than extant orangutans from Borneo, consistent with differences in diets observed between *P. pygmaeus* and *P. abelii*. Soft fruit eaters have lower *HAsfc*<sub>81</sub> values and lower *epLsar* values (Scott et al., 2012), which the fossil orangutans display, and that may be explained by a heavier reliance on higher-quality foods. In this, they are similar to values recorded for *Pan* (for both *Asfc* and *epLsar*, but not *Tfv* and

*HAsfc*), who preferentially seek out soft fruits when foraging (Scott et al. 2012; Wrangham *et al.* 1997). Higher *epLsar* values in *Pongo pygmaeus* are likely the result of higher intake of tougher foods such as the inner cambium layer of bark and leaves, fallback foods commonly ingested between masting events (Vogel et al. 2009). Confirmation of this requires a comparative microwear sample of modern Sumatran and Tapanuli orangutans. The differences in *HAsfc*<sub>81</sub> observed between modern and fossil orangutans could also be related to the presence of dipterocarp forests and irregular fruit masting events today. We found no significant differences in either *Asfc* or *Tfv* between fossil and modern Bornean orangutans, suggesting that the degree of hard object feeding was similar between extinct and modern Bornean taxa. Taken together, our results suggest that fossil Sumatran orangutan diets may have included more fruit than Bornean orangutans, similar to that observed in modern Sumatran species (*Pongo abelii*; Taylor 2006; Wich et al. 2006; Morrogh-Bernard et al. 2009).

Ngalau Gupin is the older site examined here, with the fossils from this cave likely dating to the end of Marine Isotope Stage (MIS) 6 or the beginning of MIS5 (~130 ka; Lisiecki and Raymo 2005). Lida Ajer on the other hand, likely dates to the end of MIS5 to the beginning of MIS4 (~71 ka; Lisiecki and Raymo 2005). Thus, these fossils bracket MIS5, a period of warm and wet climate and vegetation. Ngalau Sampit dates to MIS5 (~100 ka; Lisiecki and Raymo 2005), but only a single orangutan fossil is reported from this site so far. Despite fossil specimens originating from sites occurring during times characterized by disparate climatic regimes, the diets of fossil *Pongo* sp. from these sites were likely similar (based on indistinguishable DMTA attribute values,  $p \geq 0.37$ ). While the Lida Ajer orangutan sample was restricted to six individuals, and hence sample size may be a challenge, there is no indication of distinct diets in these individuals compared to earlier orangutans living in the Padang Highlands. Thus, the habitats available to

orangutans in the Padang Highlands inferred from microwear data remained unchanged through at least one glacial/interglacial cycle of the Pleistocene. This contrasts with most of Southeast Asia, where numerous lines of evidence suggest savannah environments replaced rainforests throughout the region during glacials, but especially in the proposed ‘central savannah corridor’ of Sundaland (Heaney 1991; Bird et al. 2005; Louys and Meijaard 2010; Wurster et al. 2010, 2019; Bacon et al. 2018; Suraprasit et al. 2019). Such environmental fluctuations have long been suspected as detrimental to rainforest taxa (e.g. Louys et al. 2007, Louys 2008), with rainforest margins in Borneo and Sumatra potentially acting as refugia for orangutans during glacial periods. However, a recent re-evaluation of orangutan palaeoecology and distributions suggest that these apes may have been more resilient to environmental changes than previously appreciated (Spehar et al. 2018). The factors involved in the orangutan extirpation or extinction of orangutans from western Sumatra remain unresolved.

If the modern Bornean orangutan diets are similarly unchanged since the Pleistocene, then our results suggest that the modern dietary differences observed between Sumatran and Bornean orangutans has a long geological history. However, given that modern Sumatran orangutans ingest tougher foods and less fruits in habitats negatively impacted by people (Campbell-Smith et al. 2011), all species of orangutans are likely flexible foragers in the face of environmental or habitat changes. This finding suggests that it is fruit availability, not species identity, that determines the dominant microwear signal in orangutan teeth, and gives us confidence that the microwear signal preserved in our fossil specimens accurately reflects local environmental conditions, even if we cannot yet confidently allocate our specimens to any particular species of orangutan. Dietary information is a key component to comprehending how ecological conditions affect orangutan distributions, social structures, and behavior (Russon et al. 2009). Thus, further examination of

fossil orangutan diets may provide greater insights into the evolutionary history of these apes. With a broad distribution across much of Southeast Asia, examining microwear of fossil orangutans may also provide insights into past environments in the region more broadly, with differences in anisotropy a potential marker for reconstructing the history and distribution of fruit mastication in the tropics.

## **5. Conclusions**

Understanding orangutan diets today and in the past is an important first step in reconstructing orangutan adaptations to different environmental conditions. We demonstrate that fossil orangutans from the Padang Highlands consumed foods that were less tough than that consumed by extant modern orangutans from Borneo. This is comparable to dietary differences observed between *Pongo pygmaeus* on Borneo and *Pongo abelii* from Sumatra. Differences in diets between modern and fossil orangutans suggest the environment differences between Sumatra and Borneo present today also existed during the Pleistocene. No dietary changes were observed in our fossil samples throughout the Pleistocene, and insights into the cause of extinction of orangutan populations in the Padang Highlands remain elusive. Addressing this latter question will require further data and more well-dated sites from the region, particularly those following human arrival on the island, as well as further investigations into orangutan fossil taxonomy to resolve the species identity of fossil specimens. Nevertheless, our study provides an important insight into ancient orangutan diets, filling a key gap in understanding their evolutionary history.

## **6. Acknowledgments**

We would like to thank Eleanor Hoeger, Robert Voss (American Museum of Natural History, New York), and Lim Kok Peng (Lee Kong Chian Natural History Museum, Singapore) for access to museum specimens. Holly Smith and Jerry Drawhorn are thanked for their assistance during fieldwork, and HS for photos of specimens. Funding was provided by an Australian Research Council Future Fellowship FT160100450 (to Louys), and EAR grant 1053839 and funding from Vanderbilt University (to DeSantis). Two anonymous reviewers and the editor provided valuable feedback that helped improve this manuscript.

## 7. References

- Arman, S.D., Ungar, P.S., Brown, C.A., DeSantis, L.R.G., Schmidt, C., Prideaux, G.J., 2016. Minimizing inter-microscope variability in dental microwear texture analysis. *Surf. Topogr.: Metrol. Prop.* 4, 024007. <https://doi.org/10.1088/2051-672X/4/2/024007>
- Ashton, P.S., Givnish, T.J., Appanah, S., 1988. Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. *Am. Nat.*, 132, 44-66.
- Bacon, A.M., Durringer, P., Westaway, K., Joannes-Boyau, R., Zhao, J.X., Bourgon, N., Dufour, E., Pheng, S., Tep, S., Ponche, J.L. and Barnes, L., 2018. Testing the savannah corridor hypothesis during MIS2: The Boh Dambang hyena site in southern Cambodia. *Quat. Int.* 464, 417-439.
- Bird, M.I., Taylor, D., Hunt, C., 2005. Palaeoenvironments of insular Southeast Asia during the Last Glacial Period: a savanna corridor in Sundaland?. *Quat. Sci. Rev.*, 24, 2228-2242.
- Campbell-Smith, G., Campbell-Smith, M., Singleton, I. and Linkie, M., 2011. Raiders of the lost bark: Orangutan foraging strategies in a degraded landscape. *PLoS one*, 6(6). <https://doi.org/10.1371/journal.pone.0020962>
- Delgado Jr, R.A., Van Schaik, C.P., 2000. The behavioral ecology and conservation of the orangutan (*Pongo pygmaeus*): a tale of two islands. *Evol. Anthropol.: Issues, News, Rev.*, 9, 201-218. [https://doi.org/10.1002/1520-6505\(2000\)9:5<201::AID-EVAN2>3.0.CO;2-Y](https://doi.org/10.1002/1520-6505(2000)9:5<201::AID-EVAN2>3.0.CO;2-Y)
- DeSantis, L.R.G., 2016. Dental microwear textures: reconstructing diets of fossil mammals. *Surf. Topogr.: Metrol. Prop.* 4, 023002. <https://doi.org/10.1088/2051-672X/4/2/023002>
- DeSantis, L.R.G., Scott, J.R., Schubert, B.W., Donohue, S.L., McCray, B.M., Van Stolk, C.A., Winburn, A.A., Greshko, M.A., O'Hara, M.C., 2013. Direct comparisons of 2D and 3D dental microwear proxies in extant herbivorous and carnivorous mammals. *PLoS ONE* 8, e71428. <https://doi.org/10.1371/journal.pone.0071428>
- DeSantis, L.R.G., Schubert, B.W., Schmitt-Linville, E., Ungar, P.S., Donohue, S.L., Haupt, R.J., 2015. Dental microwear textures of carnivores from the La Brea Tar Pits, California, and potential extinction implications. In: Harris, J.M. (Ed.), *La Brea and Beyond: The Paleontology of Asphalt-Preserved Biotas*, Science Series. Natural History Museum of Los Angeles County, pp. 37-52.
- DeSantis, L.R.G., Tseng, Z.J., Liu, J., Hurst, A., Schubert, B.W., Jiangzuo, Q., 2017a. Assessing niche conservatism using a multiproxy approach: dietary ecology of extinct and extant spotted hyenas. *Paleobiol.* 43, 286-303. <https://doi.org/10.1017/pab.2016.45>
- DeSantis, L.R.G., Field, J.H., Wroe, S., Dodson, J.R., 2017b. Dietary responses of Sahul (Pleistocene Australia-New Guinea) megafauna to climate and environmental change. *Paleobiol.* 43, 181-195. <https://doi.org/10.1017/pab.2016.50>
- De Vos, J., 1983. The *Pongo* faunas from Java and Sumatra and their significance for biostratigraphical and paleo-ecological interpretations. *Proc. Koninklijke Nederlandse Akademie van Wetenschappen Ser. B.* 86, 417-425.

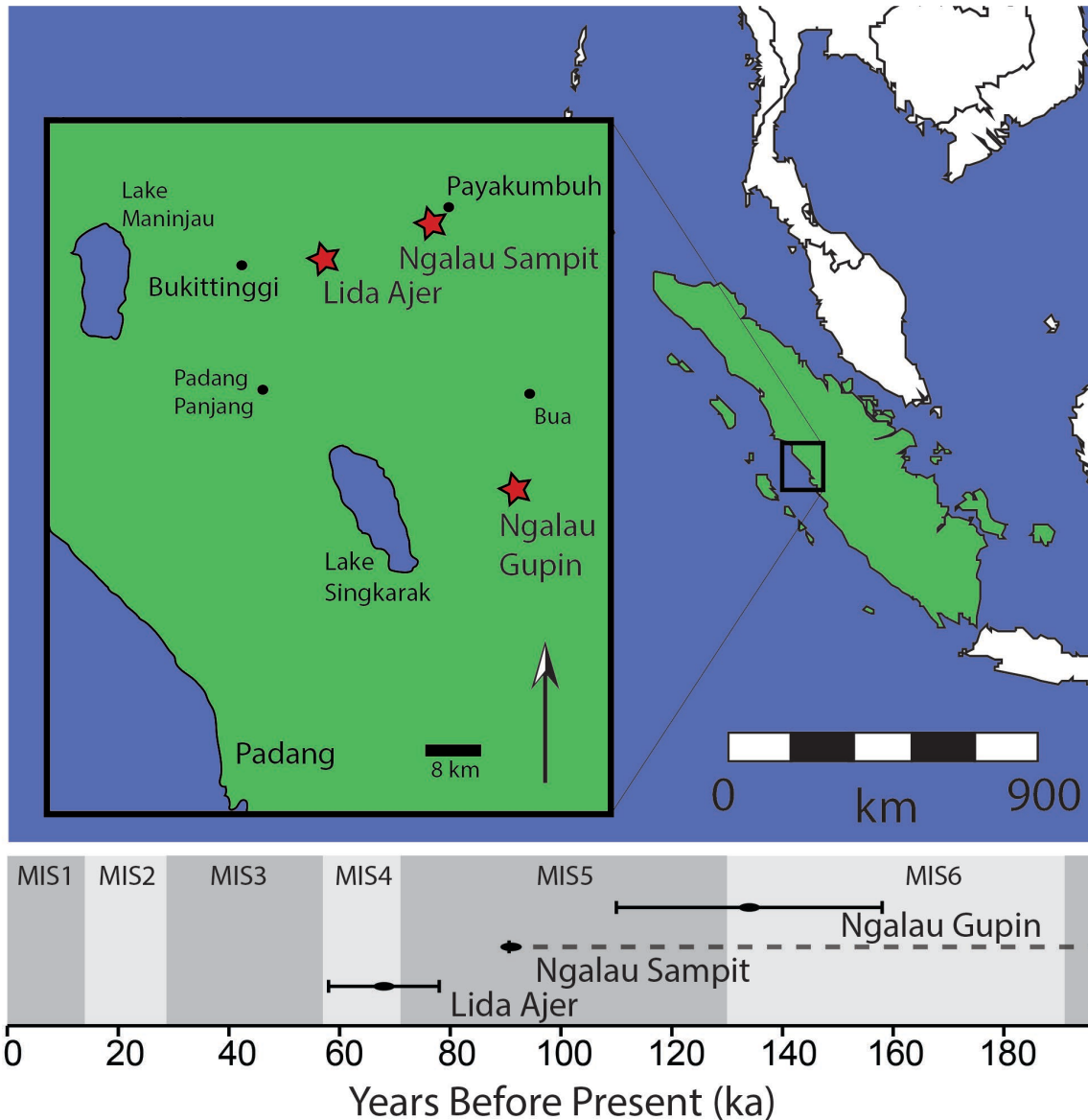


- Djojosedharmo, S., van Schaik, C.P., 1992. Why are orangutans so rare in the highlands. *Trop Biodivers*, 1, 11-22.
- Drawhorn, G. M., 1994 *The Systematics and Paleodemography of Fossil Orangutans*. PhD Thesis, Univ. California, Davis.
- Dubois, E., 1891 Voorlopig bericht omtrent het onderzoek naar de Pleistocene en Tertiaire vertebraten-fauna van Sumatra en Java, gedurende het jaar 1890. *Nat. Tijdschr. Ned. Indië* 51, 93-100
- Finarelli, J.A. and Clyde, W.C., 2004. Reassessing hominoid phylogeny: evaluating congruence in the morphological and temporal data. *Paleobiology*, 30(4), 614-651.
- Galbany, J., Martínez, L.M., López - Amor, H.M., Espurz, V., Hiraldo, O., Romero, A., Juan, J. de, Pérez - Pérez, A., 2005. Error rates in buccal-dental microwear quantification using scanning electron microscopy. *Scanning* 27, 23-29. <https://doi.org/10.1002/sca.4950270105>
- Galdikas, B.M., 1988. Orangutan diet, range, and activity at Tanjung Puting, Central Borneo. *Int. J. Primatol.*, 9, 1-35. <https://doi.org/10.1007/BF02740195>
- Gordon, K.D., 1988. A review of methodology and quantification in dental microwear analysis. *Scanning Microsc.* 2, 1139-1147.
- Grine, F. E. 1986. Dental evidence for dietary differences in *Australopithecus* and *Paranthropus*: a quantitative analysis of permanent molar microwear. *J. Hum. Evol.* 15, 783-822.
- Grine, F.E., Ungar, P.S., Teaford, M.F., 2002. Error rates in dental microwear quantification using scanning electron microscopy. *Scanning* 24, 144-153. <https://doi.org/10.1002/sca.4950240307>
- Gruwier, B.J., 2017. The large vertebrate remains from Binjai Tamieng (Sumatra, Indonesia). *J. Indo-Pacific Archaeol.*, 41, 22-29. <https://doi.org/10.7152/jipa.v41i0.15027>
- Hardus, M.E., Lameira, A.R., Zulfa, A., Atmoko, S.S.U., de Vries, H. and Wich, S.A., 2012. Behavioral, ecological, and evolutionary aspects of meat-eating by Sumatran orangutans (*Pongo abelii*). *Int. J. Primatol.*, 33, 287-304. <https://doi.org/10.1007/s10764-011-9574-z>
- Haupt, R.J., DeSantis, L.R.G., Green, J.L., Ungar, P.S., 2013. Dental microwear texture as a proxy for diet in xenarthrans. *J. Mammal.* 94, 856-866. <https://doi.org/10.1644/12-MAMM-A-204.1>
- Heaney, L.R., 1991. A synopsis of climatic and vegetational change in Southeast Asia. In *Tropical Forests and Climate* (pp. 53-61). Springer, Dordrecht.
- Hooijer, D. A., 1948 Prehistoric teeth of man and of the orang-utan from central Sumatra, with notes on the fossil orang-utan from Java and Southern China. *Zool. Meded.* 29, 175-301.
- Jablonski, N.G., Whitfort, M.J., 1999. Environmental change during the Quaternary in East Asia and its consequences for mammals. *Rec. West. Aust. Mus.*, 57, 307-315.
- Jones, D.B., Desantis, L.R.G., 2016. Dietary ecology of the extinct cave bear: evidence of omnivory as inferred from dental microwear textures. *Acta Palaeontol. Pol.* 61, 735-741. <https://doi.org/10.4202/app.00253.2016>
- Jones, D.B., Desantis, L.R.G., 2017. Dietary ecology of ungulates from the La Brea tar pits in southern California: a multi-proxy approach. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 466, 110-127. <https://doi.org/10.1016/j.palaeo.2016.11.019>
- Karriger, W.M., Schmidt, C.W., 2016. Dental microwear texture analysis of Croatian Neandertal molars. *PaleoAnthropol.* 172-184.
- Kay, R.F., 1977. The evolution of molar occlusion in the Cercopithecidae and early catarrhines. *Am. J. Phys. Anthropol.* 46, 327-352. <https://doi.org/10.1002/ajpa.1330460213>
- King, T., Aiello, L.C. and Andrews, P., 1999. Dental microwear of *Griphopithecus alpani*. *J. Hum. Evol.* 36(1), 3-31.
- Knott, C.D., 1998. Changes in orangutan caloric intake, energy balance, and ketones in response to fluctuating fruit availability. *Int. J. of Primatol.*, 19, 1061-1079. <https://doi.org/10.1023/A:1020330404983>
- Leighton, M., 1993. Modeling dietary selectivity by Bornean orangutans: evidence for integration of multiple criteria in fruit selection. *Int. J. of Primatol.*, 14, 257-313. <https://doi.org/10.1007/BF02192635>
- Lisiecki, L. E. and Raymo, M. E., 2005. A Pliocene-Pleistocene stack of 57 globally distributed benthic  $d^{18}O$  records. *Paleoceanogr.* 20, PA1003, doi:10.1029/2004PA001071
- Louys, J., 2008. Quaternary extinctions in southeast Asia. In *Mass extinction* (pp. 159-189). Springer, Berlin, Heidelberg.
- Louys, J. and Meijaard, E., 2010. Palaeoecology of Southeast Asian megafauna - bearing sites from the Pleistocene and a review of environmental changes in the region. *J. Biogeogr.* 37(8), 1432-1449.
- Louys, J., Curnoe, D., Tong, H., 2007. Characteristics of Pleistocene megafauna extinctions in Southeast Asia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 243, 152-173. <https://doi.org/10.1016/j.palaeo.2006.07.011>
- Louys, J., Kealy, S., O'Connor, S., Price, G.J., Hawkins, S., Aplin, K., Rizal, Y., Zaim, J., Mahirta, Tanudirjo, D.A., Santoso, W.D., Hidayah, A.R., Trihascaryo, A., Wood, R., Bevitt, J., Clark, T., 2017. Differential

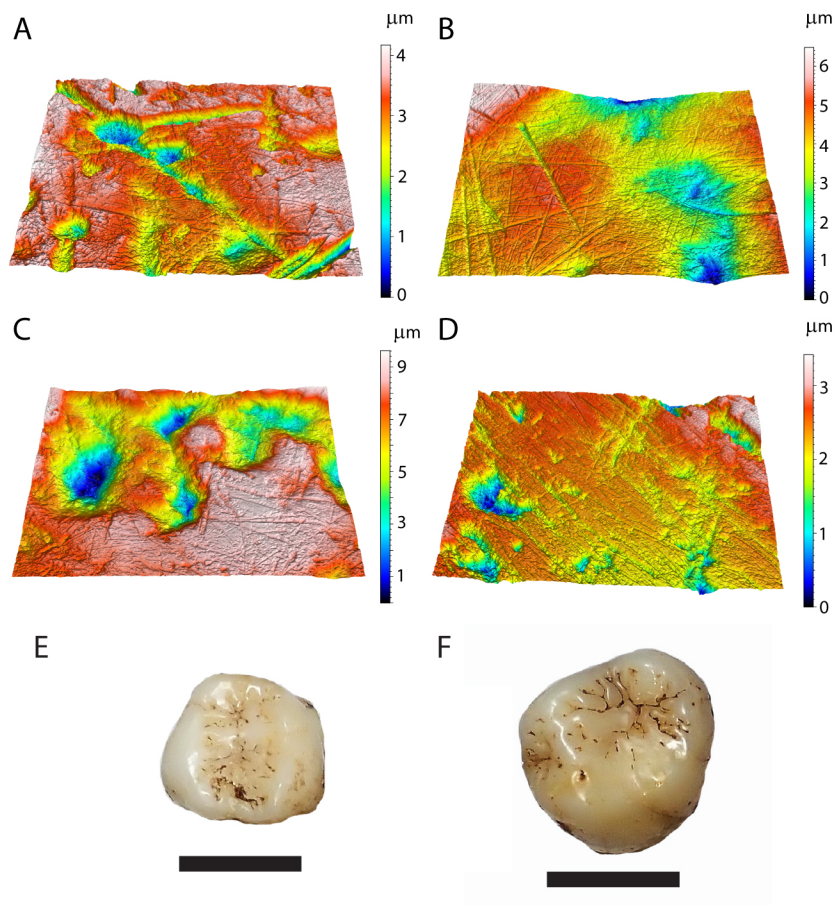
- preservation of vertebrates in Southeast Asian caves. *Int. J. Speleol.* 46: 379–408.  
<https://doi.org/10.5038/1827-806X.46.3.2131>
- MacKinnon, J., 1974. The behaviour and ecology of wild orang-utans (*Pongo pygmaeus*). *Anim. Behav.*, 22, 3-74.  
[https://doi.org/10.1016/S0003-3472\(74\)80054-0](https://doi.org/10.1016/S0003-3472(74)80054-0)
- Merceron, G., Blondel, C., Bonis, L.D., Koufos, G.D., Viriot, L., 2005. A new method of dental microwear analysis: application to extant primates and *Ouranopithecus macedoniensis* (Late Miocene of Greece). *Palaios* 20, 551–561. <https://doi.org/10.2110/palo.2004.p04-17>
- Merceron, G., Taylor, S., Scott, R., Chaimanee, Y. and Jaeger, J.J., 2006. Dietary characterization of the hominoid *Khoratpithecus* (Miocene of Thailand): evidence from dental topographic and microwear texture analyses. *Naturwissenschaften*, 93(7), 329-333.
- Morrogh-Bernard, H.C., Husson, S.J., Knott, C.D., Wich, S.A., van Schaik, C.P., van Noordwijk, M.A., Lackman-Ancrenaz, I., Marshall, A.J., Kanamori, T., Kuze, N. and bin Sakong, R., 2009. Orangutan activity budgets and diet. In: Wich, S.A., Setia, T.M. and van Schaik, C.P. eds. *Orangutans: geographic variation in behavioral ecology and conservation*. OUP Oxford, pp.119-133.
- Nater, A., Mattle-Greminger, M.P., Nurcahyo, A., Nowak, M.G., De Manuel, M., Desai, T., Groves, C., Pybus, M., Sonay, T.B., Roos, C., Lameira, A.R., 2017. Morphometric, behavioral, and genomic evidence for a new orangutan species. *Curr. Biol.*, 27, 3487-3498. <https://doi.org/10.1016/j.cub.2017.09.047>
- Newbery, D.M., Chuyong, G.B., Zimmermann, L., 2006. Mast fruiting of large ectomycorrhizal African rain forest trees: importance of dry season intensity, and the resource-limitation hypothesis. *New Phytol.*, 170, 561-579. <https://doi.org/10.1111/j.1469-8137.2006.01691.x>
- Percher, A.M., Merceron, G., Nsi Akoue, G., Galbany, J., Romero, A. and Charpentier, M.J., 2018. Dental microwear textural analysis as an analytical tool to depict individual traits and reconstruct the diet of a primate. *Am. J. Phys. Anthropol.* 165(1), 123-138.
- Piper, P.J., Rabett, R.J., 2009. Hunting in a tropical rainforest: evidence from the Terminal Pleistocene at Lobang Hangu, Niah Caves, Sarawak. *Int. J. Osteoarchaeol.*, 19(4), 551-565. <https://doi.org/10.1002/oa.1046>
- Rijksen, H.D., Meijaard, E., 1999. *Our vanishing relative: the status of wild orang-utans at the close of the twentieth century*. Dordrecht: Kluwer Academic Publishers.
- Russon, A.E., Wich, S.A., Ancrenaz, M., Kanamori, T., Knott, C.D., Kuze, N., Morrogh-Bernard, H.C., Pratje, P., Ramlee, H., Rodman, P., Sawang, A., 2009. Geographic variation in orangutan diets. In: Wich, S.A., Setia, T.M. and van Schaik, C.P. eds. *Orangutans: geographic variation in behavioral ecology and conservation*. OUP Oxford, pp.135-156.
- Sanson, G.D., Miller, W.A., 1979. Mechanism of molar progression in macropods. *Anat. Rec.* 193, 674.
- Schmidt, C.W., 2010. On the relationship of dental microwear to dental macrowear. *Am. J. Phys. Anthropol.* 142, 67–73. <https://doi.org/10.1002/ajpa.21197>
- Scott, J.R., 2012. Dental microwear texture analysis of extant African Bovidae. *Mammalia* 76, 157–174.
- Scott, R.S., Ungar, P.S., Bergstrom, T.S., Brown, C.A., Grine, F.E., Teaford, M.F., Walker, A., 2005. Dental microwear texture analysis shows within-species diet variability in fossil hominins. *Nature* 436, 693–695. <https://doi.org/10.1038/nature03822>
- Scott, R.S., Ungar, P.S., Bergstrom, T.S., Brown, C.A., Childs, B.E., Teaford, M.F., Walker, A., 2006. Dental microwear texture analysis: technical considerations. *J. Hum. Evol.* 51, 339–349. <https://doi.org/10.1016/j.jhevol.2006.04.006>
- Scott, R.S., Teaford, M.F., Ungar, P.S., 2012. Dental microwear texture and anthropoid diets. *Am. J. Phys. Anthropol.* 147, 551–579. <https://doi.org/10.1002/ajpa.22007>
- Smith, T.M., Bacon, A.M., Demeter, F., Kullmer, O., Nguyen, K.T., de Vos, J., Wei, W., Zermeno, J.P., Zhao, L., 2011. Dental tissue proportions in fossil orangutans from mainland Asia and Indonesia. *Hum. Orig. Res.*, 1, e1-e1. <https://doi.org/10.4081/hor.2011.3>
- Spehar, S.N., Sheil, D., Harrison, T., Louys, J., Ancrenaz, M., Marshall, A.J., Wich, S.A., Bruford, M.W., Meijaard, E., 2018. Orangutans venture out of the rainforest and into the Anthropocene. *Sci. Adv.*, 4, e1701422. <https://doi.org/10.1126/sciadv.1701422>
- Suraprasit, K., Jongautcharyakul, S., Yamee, C., Pothichaiya, C. and Bocherens, H., 2019. New fossil and isotope evidence for the Pleistocene zoogeographic transition and hypothesized savanna corridor in peninsular Thailand. *Quatern. Sci. Rev.* 221, 105861
- Taylor, A.B., 2006. Feeding behavior, diet, and the functional consequences of jaw form in orangutans, with implications for the evolution of *Pongo*. *J. Hum. Evol.* 50, 377–393. <https://doi.org/10.1016/j.jhevol.2005.10.006>

- Teaford, M.F., 1985. Molar microwear and diet in the genus *Cebus*. *Am. J. Phys. Anthropol.* 66, 363–370. <https://doi.org/10.1002/ajpa.1330660403>
- Teaford, M.F., 1988. A review of dental microwear and diet in modern mammals. *Scanning Microsc.* 2, 1149–1166.
- Teaford M.F. and Oyen, O.J., 1989. In vivo and in vitro turnover in dental microwear. *Am. J. Phys. Anthropol.* 80(4), 447–60.
- Teaford, M.F. and Walker, A., 1984. Quantitative differences in dental microwear between primate species with different diets and a comment on the presumed diet of *Sivapithecus*. *Am. J. Phys. Anthropol.* 64(2), 191–200.
- Teaford, M.F., Glander, K.E., 1991. Dental microwear in live, wild-trapped *Alouatta palliata* from Costa Rica. *Am. J. Phys. Anthropol.* 85, 313–319. <https://doi.org/10.1002/ajpa.1330850310>
- Teaford, M.F., Runestad, J.A., 1992. Dental microwear and diet in Venezuelan primates. *Am. J. Phys. Anthropol.* 88, 347–364. <https://doi.org/10.1002/ajpa.1330880308>
- Teaford, M.F., Walker, A., 1984. Quantitative differences in dental microwear between primate species with different diets and a comment on the presumed diet of *Sivapithecus*. *Am. J. Phys. Anthropol.* 64, 191–200. <https://doi.org/10.1002/ajpa.1330640213>
- Teaford, M.F., Maas, M.C., Simons, E.L., 1996. Dental microwear and microstructure in early Oligocene primates from the Fayum, Egypt: implications for diet. *Am. J. Phys. Anthropol.* 101, 527–543. [https://doi.org/10.1002/\(SICI\)1096-8644\(199612\)101:4<527::AID-AJPA7>3.0.CO;2-S](https://doi.org/10.1002/(SICI)1096-8644(199612)101:4<527::AID-AJPA7>3.0.CO;2-S)
- Ungar, P.S., 1994. Incisor microwear of Sumatran anthropoid primates. *Am. J. Phys. Anthropol.* 94(3), 339–363.
- Ungar, P., Teaford, M., Kay, R., 2004. Molar microwear and shearing crest development in Miocene catarrhines. *Anthropol.* 42, 21–35.
- Ungar, P.S., Teaford, M.F., 1996. Preliminary examination of non-occlusal dental microwear in anthropoids: implications for the study of fossil primates. *Am. J. Phys. Anthropol.* 100, 101–113. [https://doi.org/10.1002/\(SICI\)1096-8644\(199605\)100:1<101::AID-AJPA10>3.0.CO;2-4](https://doi.org/10.1002/(SICI)1096-8644(199605)100:1<101::AID-AJPA10>3.0.CO;2-4)
- Ungar, P.S., Brown, C.A., Bergstrom, T.S., Walker, A., 2003. quantification of dental microwear by tandem scanning confocal microscopy and scale-sensitive fractal analyses. *Scanning* 25, 185–193. <https://doi.org/10.1002/sca.4950250405>
- Ungar, P.S., Merceron, G., Scott, R.S., 2007. Dental microwear texture analysis of Varswater bovids and Early Pliocene paleoenvironments of Langebaanweg, Western Cape Province, South Africa. *J. Mammal. Evol.* 14, 163–181. <https://doi.org/10.1007/s10914-007-9050-x>
- Ungar, P.S., Grine, F.E., Teaford, M.F., 2008. Dental microwear and diet of the Plio-Pleistocene hominin *Paranthropus boisei*. *PLoS ONE* 3, e2044. <https://doi.org/10.1371/journal.pone.0002044>
- Ungar, P.S., Krueger, K.L., Blumenschine, R.J., Njau, J., Scott, R.S., 2012. Dental microwear texture analysis of hominins recovered by the Olduvai Landscape Paleanthropology Project, 1995–2007. *J. Hum. Evol.* 63, 429–437. <https://doi.org/10.1016/j.jhevol.2011.04.006>
- Vogel, E.R., Haag, L., Mitra-Setia, T., Van Schaik, C.P., Dominy, N. J., 2009. Foraging and ranging behavior during a fallback episode: *Hylobates albibarbis* and *Pongo pygmaeus wurmbii* compared. *Am. J. Phys. Anthropol.* 140, 716–726. <https://doi.org/10.1002/ajpa.21119>
- Walker, A., Hoeck, H.N., Perez, L., 1978. Microwear of mammalian teeth as an indicator of diet. *Science (New York, N.Y.)* 201, 908–910. <https://doi.org/10.1126/science.684415>
- Welker, F., Ramos-Madriral, J., Kuhlwilm, M., Liao, W., Gutenbrunner, P., de Manuel, M., Samodova, D., Mackie, M., Allentoft, M.E., Bacon, A.M. and Collins, M.J., 2019. Enamel proteome shows that Gigantopithecus was an early diverging pongine. *Nature*, 576(7786), 262–265.
- Westaway, K.E., Louys, J., Due Awe, R., Morwood, M.J., Price, G.J., Zhao, J.-x., Aubert, M., Joannes-Boyau, R., Smith, T., Skinner, M.M., Compton, T., Bailey, R.M., van den Bergh, G.D., de Vos, J., Pike, A.W.G, Stringer, C., Saptomo, E.W., Rizal, Y., Zaim, J., Santoso, W.D., Trihasaryo, A., Kinsley, L., Sulistyanto, B., 2017. An early modern human presence in Sumatra 73,000–63,000 years ago. *Nature*, 548, 322–325. <https://doi.org/10.1038/nature23452>
- Wich, S.A., Van Schaik, C.V., 2000. The impact of El Nino on mast fruiting in Sumatra and elsewhere in Malesia. *J. Trop. Ecol.*, 16, 563–577. <https://doi.org/10.1017/S0266467400001577>
- Wich, S.A., Utami-Atmoko, S.S., Setia, T.M., Djoyosudharmo, S., Geurts, M.L., 2006. Dietary and energetic responses of *Pongo abelii* to fruit availability fluctuations. *Int. J. Primatol.*, 27, 1535–1550. <https://doi.org/10.1007/s10764-006-9093-5>
- Wrangham, R.W., Conklin-Brittain, N.L., Hunt, K.D., 1998. Dietary response of chimpanzees and Cercopithecines to seasonal variation in fruit abundance. I. Antifeedants. *Int. J. Primatol.*, 19, 949–970. <https://doi.org/10.1023/A:1020318102257>

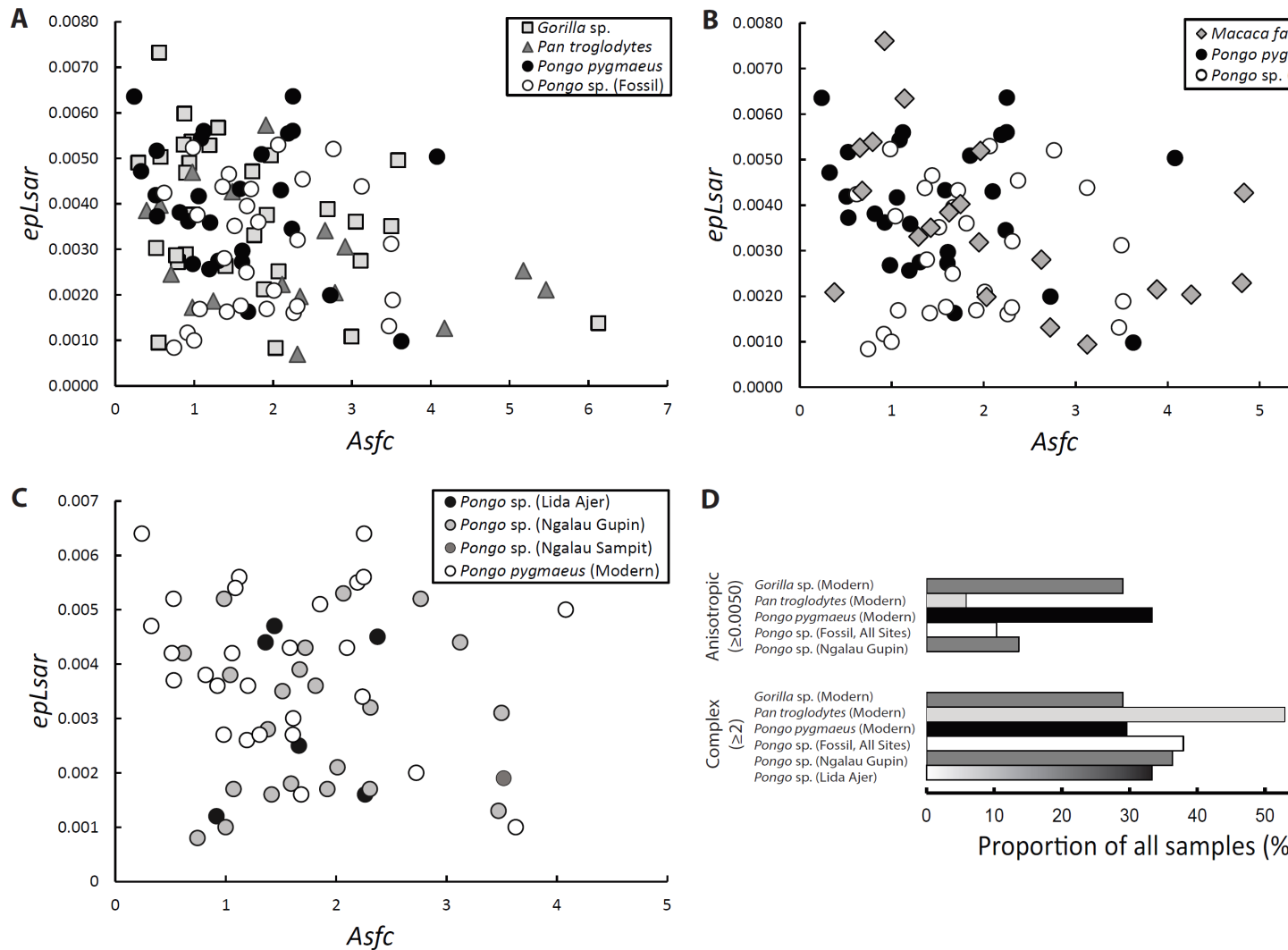
- Wurster, C.M., Bird, M.I., Bull, I.D., Creed, F., Bryant, C., Dungait, J.A. and Paz, V., 2010. Forest contraction in north equatorial Southeast Asia during the Last Glacial Period. *Proc. Natl. Acad. Sci.* 107(35), 15508-15511.
- Wurster, C.M., Rifai, H., Zhou, B., Haig, J. and Bird, M.I., 2019. Savanna in equatorial Borneo during the late Pleistocene. *Sci. Rep.* 9(1), 1-7.
- Wycherley, P. R. 1973. The phenology of plants in the humid tropics. *Micronesia* 9, 75–96.



**Figure 1.** Map of fossil localities yielding orangutan fossils examined in this study, shown relative to major towns and cities in the Padang Highlands. Ages of the sites are illustrated at  $2\sigma$  confidence level (Louys et al. 2017; Westaway et al. 2017; Smith et al. this volume). Ngalau Sampit only has a minimum age (shown via dashed line) although this is considered close to the true age of the deposit. Marine Isotope Stages (Lisiecki and Raymo, 2005) are indicated by the shaded sections of the timeline, MIS1-6 are shown in full. For a list of geographical coordinates see Louys et al. (2017).



**Figure 2.** Occlusal surfaces of fossil *Pongo* from western Sumatra and modern Bornean orangutans. (A)-(D) 3D surface models displaying microwear features of fossil *Pongo* sp. (A) LA 31, (B) NG 11.44, (C) NS 15.1, and modern *Pongo pygmaeus* (D) AMNH 146612; (E)-(F) occlusal surfaces of fossil orangutans (E) NG11.17 and (F) NG11.14; scale bar = 1 cm.



**Figure 3.** Plot of anisotropy and complexity of all great apes and/or geographically co-occurring taxa compared (including data from Scott et al. 2012) and all fossil and modern specimens of *Pongo* sp. Bivariate plot of anisotropy and complexity of all great apes examined (A), geographically overlapping orangutans and *Macaca fascicularis* (B), modern and fossil *Pongo* specimens examined (C), and a bar graph of the proportion of anisotropic and complex microwear specimens (D). Note, zero specimens of *Pongo* sp. from Lida Ajer had anisotropic values ( $\geq 0.005$ ).

**Table 1.** List of fossil orangutan specimens examined. Lowercase letters in the Tooth column refer to mandibular teeth, uppercase to maxillary.

<b>Specimen ID</b>	<b>Site</b>	<b>Tooth</b>
LA15.5	Lida Ajer	?Lm1
LA15.8	Lida Ajer	Rm1
LA30	Lida Ajer	Lm1
LA31	Lida Ajer	Rp3
LA32	Lida Ajer	Rm1
LA33	Lida Ajer	Lm1
NG11.10	Ngalau Gupin	Lm1
NG11.11	Ngalau Gupin	RM1
NG11.12	Ngalau Gupin	Rm2
NG11.14	Ngalau Gupin	Lm3
NG11.17	Ngalau Gupin	RM2
NG11.18	Ngalau Gupin	Rp4
NG11.21	Ngalau Gupin	RM3
NG11.22	Ngalau Gupin	P3
NG11.23	Ngalau Gupin	Rp3
NG11.24	Ngalau Gupin	LM2
NG11.25	Ngalau Gupin	Rp3
NG11.26	Ngalau Gupin	Lm2



NG11.27	Ngalau Gupin	Lp3
NG11.34	Ngalau Gupin	RM2
NG11.36	Ngalau Gupin	RP3
NG11.42	Ngalau Gupin	p4
NG11.44	Ngalau Gupin	RM1
NG11.45	Ngalau Gupin	Lp4
NG11.46	Ngalau Gupin	Rp4
NG11.47	Ngalau Gupin	Rp3
NG11.48	Ngalau Gupin	Rp3
NG15.13	Ngalau Gupin	?LM2
NS15.1	Ngalau Sampit	?m3

**Table 2.** DMTA attribute values for all specimens examined or included in statistical comparisons.

<b>Taxon</b>	<b>N</b>	<b>Attribute</b>	<b>Min.</b>	<b>Max.</b>	<b>Range</b>	<b>Median</b>	<b>Mean</b>	<b>SD (n-1)</b>	<b>Normality</b>
<i>Gorilla beringei</i>	16	<i>Asfc</i>	0.518	6.124	5.606	1.182	1.711	1.455	<b>0.001</b>
		<i>epLsar</i>	0.0010	0.0060	0.0050	0.0035	0.0036	0.0015	0.499
		<i>Tfv</i>	0.000	19247.120	19247.120	8997.756	9083.769	5652.455	0.862
		<i>HAsfc81</i>	0.393	7.927	7.534	0.885	1.302	1.796	<b>&lt;0.0001</b>
<i>Gorilla gorilla</i>	15	<i>Asfc</i>	0.290	3.499	3.208	1.303	1.694	1.045	0.133
		<i>epLsar</i>	0.0008	0.0073	0.0065	0.0038	0.0039	0.0017	0.874
		<i>Tfv</i>	2091.280	22837.300	20746.019	11806.023	9816.945	5834.257	0.274
		<i>HAsfc81</i>	0.522	2.114	1.593	0.853	0.943	0.415	<b>0.009</b>
<i>Pan troglodytes</i>	17	<i>Asfc</i>	0.395	5.461	5.067	2.114	2.246	1.523	0.087
		<i>epLsar</i>	0.0007	0.0057	0.0050	0.0025	0.0028	0.0013	0.583
		<i>Tfv</i>	2209.088	17398.047	15188.959	9160.731	9428.853	4664.934	0.726
		<i>HAsfc81</i>	0.505	3.535	3.030	1.210	1.339	0.719	<b>0.008</b>
<i>Pongo pygmaeus</i>	27	<i>Asfc</i>	0.240	4.080	3.840	1.308	1.542	0.940	0.053
		<i>epLsar</i>	0.0010	0.0064	0.0054	0.0042	0.0040	0.0014	0.734
		<i>Tfv</i>	0.000	16947.125	16947.125	8598.145	7160.075	5808.400	<b>0.006</b>
		<i>HAsfc81</i>	0.402	2.170	1.768	0.782	0.902	0.437	<b>0.001</b>
<i>Pongo sp.</i>	29	<i>Asfc</i>	0.620	3.517	2.897	1.670	1.848	0.823	0.073
		<i>epLsar</i>	0.0008	0.0053	0.0045	0.0031	0.0030	0.0014	0.105
		<i>Tfv</i>	0.000	13718.140	13718.140	6501.660	6630.863	4663.229	0.641
		<i>HAsfc81</i>	0.295	1.000	0.705	0.481	0.540	0.216	0.220

N, number of specimens sampled; Taxon, species examined; Min., minimum; Max., maximum; Range, total range; SD, standard deviation (n-1); Normality, Shapiro-Wilk, with bold values indicate non-normally distributed data,  $p < 0.05$ .

**Supplemental Table 1.** DMTA attribute values for all specimens here examined or included in statistical comparisons.

Status	Species	Museum	Specimen #	<i>Asfc</i>	<i>epLsar</i>	<i>Tfv</i>	<i>HAsfc81</i>	
Modern	<i>Gorilla beringei</i>	NMNH	239883	0.518	0.0030	8746.916	0.393	Sc
Modern	<i>Gorilla beringei</i>	NMNH	395636	0.968	0.0054	12259.155	1.276	Sc
Modern	<i>Gorilla beringei</i>	NMNH	396934	0.573	0.0050	2179.473	1.172	Sc
Modern	<i>Gorilla beringei</i>	NMNH	396935	0.894	0.0029	0.000	0.844	Sc
Modern	<i>Gorilla beringei</i>	NMNH	396936	6.124	0.0014	9176.526	7.927	Sc
Modern	<i>Gorilla beringei</i>	NMNH	397351	0.790	0.0027	12211.581	0.926	Sc
Modern	<i>Gorilla beringei</i>	NMNH	397358	1.884	0.0021	15793.107	0.482	Sc
Modern	<i>Gorilla beringei</i>	NMNH	545027	0.876	0.0060	11501.098	0.694	Sc
Modern	<i>Gorilla beringei</i>	NMNH	545028	1.920	0.0038	19247.120	1.166	Sc
Modern	<i>Gorilla beringei</i>	NMNH	545030	0.548	0.0010	5384.083	0.431	Sc
Modern	<i>Gorilla beringei</i>	NMNH	545031	3.585	0.0050	15457.481	0.960	Sc
Modern	<i>Gorilla beringei</i>	NMNH	545032	1.763	0.0033	13374.805	1.514	Sc
Modern	<i>Gorilla beringei</i>	NMNH	545034	1.973	0.0051	5986.510	0.682	Sc
Modern	<i>Gorilla beringei</i>	NMNH	545035	0.866	0.0053	539.299	1.104	Sc
Modern	<i>Gorilla beringei</i>	NMNH	545036	1.397	0.0026	4664.171	0.623	Sc
Modern	<i>Gorilla beringei</i>	NMNH	545037	2.689	0.0039	8818.985	0.629	Sc
Modern	<i>Gorilla gorilla</i>	AMNH	167325	2.068	0.0025	6437.311	0.577	Sc
Modern	<i>Gorilla gorilla</i>	AMNH	167327	3.499	0.0035	15301.801	0.853	Sc
Modern	<i>Gorilla gorilla</i>	AMNH	167330	2.030	0.0008	2640.854	0.522	Sc
Modern	<i>Gorilla gorilla</i>	AMNH	167332	1.736	0.0047	3813.055	0.644	Sc
Modern	<i>Gorilla gorilla</i>	AMNH	167334	3.109	0.0027	7864.378	0.901	Sc
Modern	<i>Gorilla gorilla</i>	AMNH	167339	1.303	0.0057	14611.653	0.770	Sc
Modern	<i>Gorilla gorilla</i>	AMNH	170362	3.047	0.0036	13268.739	1.254	Sc
Modern	<i>Gorilla gorilla</i>	AMNH	200501	0.981	0.0038	22837.300	0.799	Sc
Modern	<i>Gorilla gorilla</i>	CMNH	B1075	0.555	0.0073	12127.773	0.733	Sc
Modern	<i>Gorilla gorilla</i>	CMNH	B1076	1.192	0.0053	2091.280	0.880	Sc
Modern	<i>Gorilla gorilla</i>	CMNH	B1181	0.937	0.0049	13166.423	0.578	Sc
Modern	<i>Gorilla gorilla</i>	CMNH	B1410	0.895	0.0047	3878.580	0.979	Sc
Modern	<i>Gorilla gorilla</i>	CMNH	B1419	2.994	0.0011	11806.023	2.114	Sc
Modern	<i>Gorilla gorilla</i>	CMNH	B1899	0.290	0.0049	5440.732	1.476	Sc
Modern	<i>Gorilla gorilla</i>	CMNH	B1908	0.771	0.0029	11968.269	1.062	Sc
Modern	<i>Macaca fascicularis</i>	NMNH	13169	3.125	0.0009	14459.474	0.616	Sc
Modern	<i>Macaca fascicularis</i>	NMNH	114410	2.722	0.0013	14535.539	1.154	Sc
Modern	<i>Macaca fascicularis</i>	NMNH	125102	2.031	0.0020	10539.273	1.167	Sc
Modern	<i>Macaca fascicularis</i>	NMNH	121803	4.255	0.0020	10337.286	3.976	Sc
Modern	<i>Macaca fascicularis</i>	NMNH	198300	0.377	0.0021	8241.357	1.244	Sc
Modern	<i>Macaca fascicularis</i>	NMNH	141145	3.883	0.0022	13739.876	1.852	Sc
Modern	<i>Macaca fascicularis</i>	NMNH	144505	4.806	0.0023	12926.521	0.684	Sc

Modern	<i>Macaca fascicularis</i>	NMNH	114411	2.626	0.0028	10398.090	0.977	Sc
Modern	<i>Macaca fascicularis</i>	NMNH	196815	1.948	0.0032	13014.691	0.670	Sc
Modern	<i>Macaca fascicularis</i>	NMNH	317191	1.289	0.0033	14835.882	0.686	Sc
Modern	<i>Macaca fascicularis</i>	NMNH	175896	1.424	0.0035	7542.977	0.642	Sc
Modern	<i>Macaca fascicularis</i>	NMNH	292555	1.624	0.0038	15017.728	0.839	Sc
Modern	<i>Macaca fascicularis</i>	NMNH	143583	1.747	0.0040	13611.024	0.967	Sc
Modern	<i>Macaca fascicularis</i>	NMNH	83944	4.830	0.0043	15299.894	1.462	Sc
Modern	<i>Macaca fascicularis</i>	NMNH	198301	0.679	0.0043	850.585	0.887	Sc
Modern	<i>Macaca fascicularis</i>	NMNH	121802	1.964	0.0052	8853.760	1.915	Sc
Modern	<i>Macaca fascicularis</i>	NMNH	196827	0.653	0.0053	7594.230	0.504	Sc
Modern	<i>Macaca fascicularis</i>	NMNH	34913/19192	0.793	0.0054	1626.060	0.839	Sc
Modern	<i>Macaca fascicularis</i>	NMNH	144419	1.139	0.0063	14831.804	0.947	Sc
Modern	<i>Macaca fascicularis</i>	NMNH	34914	0.923	0.0076	11253.216	1.415	Sc
Modern	<i>Pan troglodytes</i>	CMNH	B1722upper	0.977	0.0017	7343.722	0.505	Sc
Modern	<i>Pan troglodytes</i>	CMNH	B1903upper	2.659	0.0034	4096.568	1.457	Sc
Modern	<i>Pan troglodytes</i>	CMNH	B1956upper	2.308	0.0007	6762.212	1.172	Sc
Modern	<i>Pan troglodytes</i>	CMNH	B2027upper	2.341	0.0020	9245.959	1.956	Sc
Modern	<i>Pan troglodytes</i>	CMNH	B2033lower	0.566	0.0040	6147.559	0.764	Sc
Modern	<i>Pan troglodytes</i>	CMNH	B2034upper	4.174	0.0013	9160.731	1.488	Sc
Modern	<i>Pan troglodytes</i>	CMNH	B2756upper	2.114	0.0022	12601.933	0.937	Sc
Modern	<i>Pan troglodytes</i>	CMNH	B2771	0.395	0.0039	4569.624	1.513	Sc
Modern	<i>Pan troglodytes</i>	CMNH	B3398upper	1.242	0.0019	17398.047	0.541	Sc
Modern	<i>Pan troglodytes</i>	CMNH	B3412	2.785	0.0020	3276.291	1.525	Sc
Modern	<i>Pan troglodytes</i>	CMNH	B3413upper	1.484	0.0043	15167.619	0.828	Sc
Modern	<i>Pan troglodytes</i>	CMNH	B3418upper	0.707	0.0025	11257.337	1.202	Sc
Modern	<i>Pan troglodytes</i>	CMNH	B3434	5.461	0.0021	16422.856	3.535	Sc
Modern	<i>Pan troglodytes</i>	CMNH	B3437	5.174	0.0025	13897.522	1.210	Sc
Modern	<i>Pan troglodytes</i>	CMNH	B3537upper	0.977	0.0047	2209.088	1.377	Sc
Modern	<i>Pan troglodytes</i>	CMNH	B3538upper	2.914	0.0031	9075.805	2.017	Sc
Modern	<i>Pan troglodytes</i>	CMNH	B3553upper	1.908	0.0057	11657.619	0.739	Sc
Modern	<i>Pongo pygmaeus</i>	SAPM	1981103	0.326	0.0047	2093.714	0.782	Sc
Modern	<i>Pongo pygmaeus</i>	SAPM	1981106	3.627	0.0010	8713.198	2.170	Sc
Modern	<i>Pongo pygmaeus</i>	SAPM	1981111	0.240	0.0064	1886.291	0.590	Sc
Modern	<i>Pongo pygmaeus</i>	SAPM	1981113	1.192	0.0026	12544.071	1.611	Sc
Modern	<i>Pongo pygmaeus</i>	SAPM	1981145	1.122	0.0056	13093.951	0.662	Sc
Modern	<i>Pongo pygmaeus</i>	SAPM	1981147	0.530	0.0037	16015.377	0.896	Sc
Modern	<i>Pongo pygmaeus</i>	SAPM	198159	2.726	0.0020	8174.687	1.990	Sc
Modern	<i>Pongo pygmaeus</i>	SAPM	198162	0.818	0.0038	27.923	0.701	Sc
Modern	<i>Pongo pygmaeus</i>	SAPM	198174	2.193	0.0055	1818.750	0.964	Sc
Modern	<i>Pongo pygmaeus</i>	SAPM	198178	1.854	0.0051	8598.145	0.927	Sc
Modern	<i>Pongo pygmaeus</i>	SAPM	198188	0.925	0.0036	2066.095	0.622	Sc
Modern	<i>Pongo pygmaeus</i>	SAPM	198190	1.683	0.0016	546.325	1.281	Sc

Modern	<i>Pongo pygmaeus</i>	SAPM	198196	0.982	0.0027	16947.125	0.655	Sc
Modern	<i>Pongo pygmaeus</i>	SAPM	198197	1.608	0.0027	10877.960	1.145	Sc
Modern	<i>Pongo pygmaeus</i>	SAPM	198199	0.512	0.0042	637.181	0.918	Sc
Modern	<i>Pongo pygmaeus</i>	AMNH	140426	1.308	0.0027	14984.061	0.629	
Modern	<i>Pongo pygmaeus</i>	AMNH	146612	1.582	0.0043	642.274	0.569	
Modern	<i>Pongo pygmaeus</i>	AMNH	18010	1.087	0.0054	10273.562	0.519	
Modern	<i>Pongo pygmaeus</i>	AMNH	200898	1.202	0.0036	1562.249	1.093	
Modern	<i>Pongo pygmaeus</i>	AMNH	200900	1.611	0.0030	11219.461	0.518	
Modern	<i>Pongo pygmaeus</i>	AMNH	28252	0.527	0.0052	0.000	0.836	
Modern	<i>Pongo pygmaeus</i>	AMNH	28253	1.058	0.0042	3661.846	1.055	
Modern	<i>Pongo pygmaeus</i>	ZRC	4742	2.250	0.0056	65.563	0.624	
Modern	<i>Pongo pygmaeus</i>	ZRC	4746L	2.099	0.0043	8679.812	0.775	
Modern	<i>Pongo pygmaeus</i>	ZRC	4750L	2.239	0.0034	13355.620	0.428	
Modern	<i>Pongo pygmaeus</i>	ZRC	4754L	2.253	0.0064	13701.007	0.402	
Modern	<i>Pongo pygmaeus</i>	ZRC	4755L	4.080	0.0050	11135.791	0.981	
Fossil	<i>Pongo</i> sp.	Fossils	LA15.5	1.441	0.0047	11061.775	0.478	
Fossil	<i>Pongo</i> sp.	Fossils	LA15.8	0.916	0.0012	5539.440	0.315	
Fossil	<i>Pongo</i> sp.	Fossil	LA30	1.361	0.0044	1344.109	0.410	
Fossil	<i>Pongo</i> sp.	Fossil	LA31	2.375	0.0045	2453.754	0.809	
Fossil	<i>Pongo</i> sp.	Fossil	LA32	1.663	0.0025	7731.573	0.387	
Fossil	<i>Pongo</i> sp.	Fossil	LA33	2.263	0.0016	27.925	0.398	
Fossil	<i>Pongo</i> sp.	Fossil	NG11.10	1.921	0.0017	2442.613	0.314	
Fossil	<i>Pongo</i> sp.	Fossil	NG11.11	1.721	0.0043	12496.907	0.498	
Fossil	<i>Pongo</i> sp.	Fossil	NG11.12	1.041	0.0038	0.000	0.688	
Fossil	<i>Pongo</i> sp.	Fossil	NG11.14	1.382	0.0028	5259.057	0.481	
Fossil	<i>Pongo</i> sp.	Fossil	NG11.17	1.670	0.0039	11255.521	0.387	
Fossil	<i>Pongo</i> sp.	Fossil	NG11.18	0.985	0.0052	877.815	0.602	
Fossil	<i>Pongo</i> sp.	Fossil	NG11.21	2.066	0.0053	13718.140	0.564	
Fossil	<i>Pongo</i> sp.	Fossil	NG11.22	2.766	0.0052	10043.602	0.952	
Fossil	<i>Pongo</i> sp.	Fossil	NG11.23	2.311	0.0032	5786.197	0.947	
Fossil	<i>Pongo</i> sp.	Fossil	NG11.24	1.814	0.0036	6924.177	0.467	
Fossil	<i>Pongo</i> sp.	Fossil	NG11.25	3.498	0.0031	7190.850	0.988	
Fossil	<i>Pongo</i> sp.	Fossil	NG11.26	3.471	0.0013	11365.749	0.483	
Fossil	<i>Pongo</i> sp.	Fossil	NG11.27	0.744	0.0008	6501.660	0.357	
Fossil	<i>Pongo</i> sp.	Fossil	NG11.34	0.999	0.0010	13106.521	0.386	
Fossil	<i>Pongo</i> sp.	Fossil	NG11.36	1.592	0.0018	5270.534	0.515	
Fossil	<i>Pongo</i> sp.	Fossil	NG11.42	1.415	0.0016	167.550	0.401	
Fossil	<i>Pongo</i> sp.	Fossil	NG11.44	2.306	0.0017	10752.185	0.295	
Fossil	<i>Pongo</i> sp.	Fossil	NG11.45	0.620	0.0042	418.372	0.300	
Fossil	<i>Pongo</i> sp.	Fossil	NG11.46	1.514	0.0035	5293.602	0.754	
Fossil	<i>Pongo</i> sp.	Fossil	NG11.47	3.124	0.0044	7851.160	0.569	
Fossil	<i>Pongo</i> sp.	Fossil	NG11.48	2.012	0.0021	13526.722	0.433	

Fossil	<i>Pongo</i> sp.	Fossils	NG15.13	1.071	0.0017	1114.121	0.494	
Fossil	<i>Pongo</i> sp.	Fossils	NS15.1	3.517	0.0019	12773.406	1.000	