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Canine Microwear in Relation to Diet in Sumatran Primates and African Great Apes

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Canine Microwear in Relation to Diet in Sumatran Primates and African Great Apes

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Abstract

This thesis considers canine microwear in relation to diet in five Sumatran primates (*Pongo abelii, Hylobates lar, Hylobates agilis, Presbytis thomasi,* and *Macaca fascicularis*) and two African great apes (*Pan paniscus* and *Pan troglodytes schweinfurthii*) using both microwear texture analysis and microwear feature analysis techniques. Statistical results for texture analysis show that there are significant differences in scale of maximum and heterogeneity. This indicates that some species have large pits on their canine surfaces, having these dominated by deep features at coarse scale yet have a slight microwear heterogeneity. For feature analysis, all variables show statistically significant variation. Variance in average width and number of scratches, for example between *Po. abelii* and *H. agilis*, can be related to food choice, canine use for food processing and/or to their distinctive canine morphologies.

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Dedication

      This thesis is dedicated to my beloved deceased father. Thank you for accompanying me for 24 years of my life. Thank you for all life lessons. I know that you wanted to see me graduate. I want to tell you "I did it." I hope you are proud of me. It is still tearing me apart because you cannot see me walking down on commencement. Nevertheless, I know you are watching me from the best place you could deserve along with your parents and brother. See you when I see you.

Contents

List of Tables

List of Figures

Introduction

Diet has been identified as the main driver of differences in an animal's ecology, physiology, and behavior (Moreno-Black, 1978; Ungar *et al.,* 2008). However, research on diet is mainly conducted through phenology or animal studies in the wild, which only give information about the type, availability, and quantity of food consumed (Moreno-Black, 1978, Nakagawa, 2009). Nowadays, the study of feeding behavior is not merely about food, but it also involves the teeth that help animals extract the edible parts associated with their dietary niche and their evolutionary adaptations (Strait, 1997; Ungar, 1998). Tooth shape evolved to overcome difficulties in breaking down different types of food (Lucas *et al*, 2004), therefore increasing chewing efficiency (Teaford, 1994). Teeth also provide information about patterns of diets and functional adaptations of fossil species, including extinct primates (Wood and Zuckerman, 1981).

It is challenging to study feeding behaviors of primates compared with those of many other mammals because of their catholic diets; they rely on up to several hundred plant species to fulfill their energy needs (Hardus *et al.,* 2012, Coiner-Collier *et al.* 2016). Other factors making the study of primate feeding ecology difficult include their long-life histories, low reproductive rates, inadequate sample sizes for statistical analyses, restrictions on using wild primates in experimental settings and frequent change in diets due to resource depletion associated with rapid anthropogenic changes of their habitats (Maestripiari, 2009; Serckx *et al.* 2015). However, primate feeding ecology has continued to be a major area of interest in primatological studies because of the large diversity of niches individual species occupy, its influence on social behavior, and the fact that a knowledge of diet and its responses to environmental change helps enlighten the understanding of human evolution and behavior (Hohmann *et al.* 2012).

It is recognized that each food type has different material and abrasive properties; thus, it should leave a distinctive pattern of marks or scratches on tooth surfaces that could be used to distinguish dietary differences (Ungar *et al.* 2008, Teaford and Runestad, 1992). Dental microwear therefore presents a promising approach to assess dietary patterns in living primates; so, it holds the potential to give a new perspective on diets (Percher *et al.,* 2017), and to provide direct evidence of food eaten in the past, offering a precious glimpse at feeding behavior and food choices of extinct primates (Gordon, 1982; Walker, 1984; Ryan and Johanson, 1989; Scott *et al.* 2005; Ungar, 2018). Covert and Kay (1981) describe two main foci of dental microwear: first, the distinguishing of specific wear patterns which link to specific diets, potentially allowing the reconstruction of diets of extinct species, and second, the identification of the geometry of wear, which can be used to infer masticatory dynamics and chewing directions.

Scott *et al.* (2012) have identified two challenges for the study of dental microwear and primate diets: first, the dietary pattern of extant primates is complex, flexible, and variable, and second, dental microwear exhibits intrinsic hurdles associated with quantification of surface patterns. Furthermore, some other factors might significantly influence dental microwear patterns: salivary flow, applied force, sex, age, hardness of food, extrinsic mineral dust on the food surface, phytoliths and exogenous grit (Teaford and Oyen, 1989; Ungar et al. 1995; Gordon, 1982; Kinzey and Norconk, 1990, Xia *et al.* 2015; Hua *et al.* 2020; Winkler *et al.* 2020).

Ungar (1994b) characterizes six techniques in food ingestion based on how the anterior teeth are used: 1) no usage of anterior teeth; 2) nipping is when the item is held between the incisors or lips, then pulled outward with hand or head; 3) incising is when anterior teeth penetrate the food, removing sections of it; 4) crushing is when pressure is applied to open a food item positioned between the incisors without penetrating it; 5) scraping is when the incisor labial face scrapes a

hard surface, removing softer tissues; and 6) stripping is when stems or rachises are pulled between anterior teeth or upper and lower lips, removing attached items (usually young leaves).

Molars and incisors are the two main tooth types typically used in dental microwear research (Ungar and Teaford, 1996). Microwear on molars can be described as pits and scratches. Pits are microwear attributes typically defined by a ratio of length-to-width of less than four to one (Ryan, 1979; Grine, 1986). Pits are formed during food crushing when particles in or on the food cause compression ruptures on occlusal surfaces during the power stroke (Maas, 1994). Scratches are defined as linear microwear features with a ratio of length-to-width of more than four to one. The difference between pit and scratch formation is related to the direction from which opposing cusps come together (Schmidt 2009). Diets that create scratches have cusps that slide onto each other with less direct opposition. Hence, a diet of relatively soft, tough food requiring shearing will leave scratches (Schmidt 1998; Organ *et al.* 2005). Thus frugivorous anthropoids, such as in African apes *Pan* and *Papio*, have flat molars and more pitting on their Phase II molar facets (Kay, 1975; Hylander, *et al* 1978; Teaford and Walker, 1984), while folivores and grass-blade eaters, such as in *Gorilla* and *Theropithecus,* exhibit more striae, longer cheek teeth crests and more sloping occlusal surfaces that are adapted for shearing rigid cell walls, (Hiiemae and Crompton, 1985, Ungar, 2019).

Microwear on incisors, on the other hand, is related to ingestive behavior and possibly reflects feeding height in the canopy (Delezene *et al.* 2016; Kelley, 1990). Studies of incisor microwear have proven valuable for inferring aspects of feeding behavior and diet in anthropoids too (Ungar, 1994a; Ungar and Spencer, 1999) because incisors are often used for food preparation, such as opening fruit skin, biting, and ingestion processes (Lucas and Luke, 1984). For example, according to Ryan's (1981) study, the incisors of gorillas exhibit a broad area of polish, small pits,

and labiolingually oriented wear striae, presumably connected to the leaf stripping and pith consumption.

Ryan (1981), using qualitative examination of SEM imagery, likewise associated fine wear striae on chimpanzee incisors to extraction of the pith of *Aframomum*, while he related small pits and damage on the proximal end to fruit husking. Moreover, he noted that baboon incisal microwear exhibits extensive border damage, including a group of large pits and micro-flakes; he attributed these features to use on hard foods, such as seeds, roots, and rhizomes (Ryan, 1981). The front teeth of primates are involved principally in food acquisition (taking, holding, seizing, and/or grasping food) and initial processing (e.g., opening fruit skin) (Hiiemae and Crompton 1985; Beauchemin, 1991; Hiiemae and Kay, 1972; Lucas and Luke, 1984). Ingestive behaviors assist in the oral processing of solid food items, facilitating a faster rate of digestion as required by a shortened primate gut (Lucas and Luke, 1984).

While studies of molar and incisor microwear have a long history, research on the relationships between canine microwear and diet in primates is far from well-documented. The primary research on primate canines has focused on tooth size and tooth-size dimorphism, and it is widely accepted that canines serve as weapons for intraspecific combat, display and as a defense against predators (Plavcan and Ruff, 2008). Canine dimorphism of both sexes is influenced by sexual selection, access to females, body weight, predation, diet, phylogenetic inertia and competition for limited resources (Walker, 1984; Kay *et al*. 1988; Leutenegger and Kelly, 1977; Harvey *et al.* 1978; Plavcan and van Schaik, 1992; Manning and Chamberlain, 1993; Weston *et al*. 2004). And primates exhibit significant variability in shape and size of canines among species, both within and between sexes (Smith, 1969; Smith, 1980; Plavcan, 1993; Schwartz *et al.* 2005). Some work on canine microwear was recently published by Delezene *et al*. (2016) on pitheciids

and *Ateles*, however there has yet to be any quantitative analysis of canine microwear published for Old World primates to the best of my knowledge. This is despite the fact that Ryan (1981) hypothesized that canine tooth use differences will probably exhibit different types of microwear, and Harvey *et al*. (2009) hypothesized that canines also have a role in food preparation.

Animal review

This study considers canine microwear in five genera of primates representing seven species. Five species are from Sumatra: *Pongo abelii, Presbytis thomasi, Hylobates lar, Hylobates agilis,* and *Macaca fascicularis*, which are known to have differences in diet and ingestive behavior (Ungar 1994). The other two species, the African great apes *Pan troglodytes schweinfurthii* and *Pan paniscus*, have both been demonstrated to differ subtly in diet in a manner that might be reflected in canine use and microwear patterning. The selection of species allows for comparison of closely related species with similar canine form (*Pan* spp. and *Pongo*), and contrast with gibbons (also frugivores but with very different canine form) and Old-World monkeys (both frugivore-insectivore macaques and folivore-frugivore langurs). The Sumatran primates were selected because their incisor microwear has been documented and can be compared with that on their canines (Ungar 1995).

The Sumatran Primates

Macaca fascicularis

Macaca fascicularis is found throughout much of Southeast Asia, including Sumatra and other Indonesian Sunda shelf islands. The long-tailed macaque is the smallest monkey in the Sundaland area (approximately 3 – 4 kg in body mass) (Lucas and Corlett, 1991). This species is cosmopolitan and opportunistic in its feeding behavior, with marked dietary plasticity. Although

M. fascicularis is a versatile and massively dispersed species, Eudey *et al.* (2021) state that the conservation status of the long-tailed macaque is now listed as vulnerable due to excessive hunting and anthropogenic disturbance in its home range. Long-tailed macaques occupy a broad range of habitats throughout much of Southeast Asia, except high-latitude forests (Caldecott, 1986, Chivers and Hladik, 1986, Brotcorne, 2014).

Wild macaques are primarily selective frugivores, their diet consists of fruits (23% - 32%), and anthropogenic foods (27%) together with leaves (15% - 19%) and other food such as insects, seeds or small animals (Yeager, 1996; Ruslin *et al.* 2018). Research that was conducted by Ungar (1994) states that long-tailed macaques prefer small fleshy fruits and were recorded to exhibit little food preparation, although sometimes they also eat larger fruits that demand more complex ingestive processes. Long-tailed macaques live in a dynamic multi-male group consisting of several males, several females, and offspring, forming fission-fusion subgroups during the daytime to increase efficiency in searching for food (van Schaik *et al*., 1983a). In such highly dynamic groups, obtaining food while avoiding aggression with high-ranking females is difficult. The low-ranking females usually wait for the dominant individuals to leave and eat the remaining food, which usually has low quality (Koenig *et al.* 1998; Koenig, 2002). Therefore, it opens the possibility that the dental microwear of alpha females be different from that of non-alpha females.

Ungar (1994b) described ingestive behavior of macaques in detail. He stated that macaques also consume young leaves; they nip smaller insects and arachnids using their anterior teeth or put them in their mouth during grooming or foraging. Fruits such as *Laportea sinuata, Carallia brachiata, Turpinia sphaerocarpa* were usually nipped with the incisors or placed in the mouth with the hand. Moderate-size-thick skin fruit such as *Tinomiscium phytocrenoides, Lansium domesticum* need complex initial processing: they have to be incised and peeled back, with the

pericarp being scraped off the pits with the anterior teeth. Fruit such as *Aglaia* spp. are crushed between their upper and lower anterior teeth, squeezing their inner part, while for *Mallotus sphaerocarpus* and *Pyonarrhena cauliflora*, the macaques usually extract the seeds and juice. Larger fruits such as *Cyranthocalyx sumatrana* and *Gnetum cf. latifollum* are often incised to extract their inner part although their seeds are usually larger than fig seeds.

Presbytis thomasi

Presbytis thomasi, or Thomas' langur, is a specialized folivore/seed-predator endemic to Aceh Province, North Sumatra (Wich *et al.,* 2007; Setiawan and Traeholt, 2020). Thomas' langurs live in highly dynamic one-male multi-female groups (Steenbeek and van Schaik, 2001; van Schaik *et al.,* 1983a). Both males and females emigrate from their natal groups, and infanticide is common (Steenbeek, 1999). *Presbytis thomasi* generally lives in undisturbed primary evergreen lowland alluvial rainforest, though it can be found at altitude in montane (1500 to 2400 m) (Wich and Sterck, 2010; Staler, 2016), and in secondary forest within the margins of rubber plantations (Wich and de Vries, 2006). It is listed as a vulnerable species (IUCN Red List). The Thomas' langur is a medium-sized monkey, weighing around 7.5 to 8 kg (van Schaik *et al.,* 1983b) with no sexual dimorphism either in body size or weight when they reach adulthood (Sterck, 1995 in Wich and Sterck, 2010). It has been noted that males may have larger canines than females despite the lack of body size dimorphism (Sterck, unpublished data in Wich and Sterck, 2010).

Like other colobine species, *Pr. thomasi* has enlarged salivary glands to lubricate food and an enlarged multichambered stomach capable of digesting young leaves, which can make up as much as 83% of their diet. Other foods eaten include fruit seeds, flowers, and, lianas (Steenbeek and van Schaik, 2001; Wich and Sterck, 2010; Kirkpatrick, 2017). As a colobine, *Pr. thomasi* has dentition distinct from macaques and other cercopithecine monkeys, and relatively large molars

with long crests for shearing tough foods to extract the required nutrients from the nonreproductive parts of trees and other plants (Wright and Willis, 2012). This species also has relatively small incisors and often uses them to pierce through thick bunches of leaves or hard fruit husks. (Ungar, 1994a; Ungar 1996)

Ungar (1994b) stated that *Pr. thomasi* use their incisor frequently for fruit ingestion, the evidence is shown in the comparison of fruit and leaf consumption, with more than two third (20% of total feeding time) for fruit incision and 82% for leaf incision (40% of total daily feeding time). Ungar (1992) states that langurs rarely ate smaller fruits, however, when they did, the food was either nipped directly from the branch (e.g., *Sapium baccatum, Picrasma javanica*) or put in the mouth with their hand (e.g., *Micromelum pubescens, Turpinia sphaerocarpa).* When they eat fruits with edible skin and hard pits, such as *Terminalia bellerica, Baccaurea sp*, the langurs usually scrape them with their incisors, and will use their front teeth to crush soft skinned fruits such as *Aglaia odoratissim*a and *Mallotus sphaerocarpus.* or incised *Ficus schwarzii* fruit to remove seeds and pulp. *Pr. thomasi* prefers medium-sized young leaves such as those from Euphorbiaceae family. They nip small young leaves and incise the petioles of *Hodgsonia macrocarpa* from leaf blades and eat it as a whole.

Pongo abelii

Pongo abelii, the Sumatran orangutan, is a semi-solitary great ape, although individuals occasionally form groups. Orangutans are predominately arboreal and can be found in the forests of Sumatra and Borneo (Indonesia and Malaysia). The Sumatran orangutan species considered in this study (*Pongo abelii*) occupies alluvial, montane, and peat swamp forests (van Schaik, 1996). It has a life expectancy of up to 58 years for males and 53 years for females (Wich *et al.* 2004). This species is predicted to have only approximately 6500 to 6600 individuals left and is classified

as a Critically Endangered species on IUCN Red List (Wich *et al.,* 2008; Nater *et al.,* 2012; Wich *et al.,* 2016).

The Sumatran orangutan usually consumes soft pulpy ripe fruit, especially figs, when available, and depends on other vegetation such as leaves and bark during low fruit season, although not as much as the Bornean orangutan *Pongo pygmaeus* (Wich *et al.,* 2004; Taylor, 2006; Vogel *et al.* 2013). Wich *et al.* (2006) state that the Sumatran orangutan has a more consistent and invariant diet than the Bornean orangutan by maintaining fruit intake even during non-mast seasons. This anomaly occurs because their habitat at sites such as Ketambe has high fruit productivity and supplies enough food year-round. This might explain why the Sumatran orangutan has a lower jaw load resistance than its Bornean congener (Taylor, 2006).

The orangutans are known to use their anterior teeth and lips heavily compared with other primates, as recorded in more than 90% of all feeding scans by Ungar (1994b). They usually nip small to medium-sized fruits such as *Ficus benjamina, Tetrastigma hookeri, Turpinia sphaerocarpa* with their lips and anterior teeth. The softer medium-sized fruits such as *Aglaia odoratissima* and *Mallotus sphaerocarpus* which require heavy initial processing are usually positioned over the incisors by prehensile lips and crushed or incised open for *Garcinia spp., Canangium odorata.* Hard-skin fruits, such as *Gnetum cf. latifollum, Quercus s.,* are usually cracked open with their incisors and molars. Large fruit with edible skin, such as *Artocarpus elasticus, Cyranthocalyx sumatranu*, are usually incised and seeds of larger figs such as *Ficus drupace ,*and *F. stupenda* are usually spit out. Orangutans nip small flowers and leaves from the branches and use their lips and anterior teeth to pick off ants or termites from their nests. They often nip or strip larger mature leaves from the branches, and they usually use an elaborate scraping

technique that includes both canine and incisor use to extract woody stems or bark for consumption.

Hylobates spp.

Hylobates spp. is classified as the lesser ape with relatively small body size (5 to 11 kg), no sexual dimorphism and a wide dispersal in Asia. Sexual monomorphism is predicted due to a high degree of social equality between male and female gibbons, although sometimes females can be "codominant" (Leighton, 2008). Both sexes have long, curved, dagger-like canines (Fleagle, 2013) and both defend their territories against conspecifics. Gibbons are small arboreal apes that form family units of 2 adults and dependent offspring (Ellefson, 1968; O'Brien and Kinnaird, 2011). Gibbon foods are dominated by small fruits, which comprise between 50 and 71% of the diet. They also consume flowers, young leaves, and insects on occasion. Gibbons prefer juicy-soft pulp, medium-sized yellow fruits (6 to 30 grams) with thin skin, and large crops (McConkey *et al.,* 2002). The preference for smaller fruits lacking husks is probably due to limited availability of hands to manipulate food over the incisors given the need for efficient suspensory foraging (Ungar, 1995). And this has important implications for ingestive behavior. There are two *Hylobates* species used in the current study.

Hylobates agilis, the agile Gibbon, is found in Sumatra, peninsular Malaysia, and Thailand, and is classified as endangered species based on the IUCN Red List (Geissmann *et al.,* 2020). *Hylobates agilis* has various coat colorations, yet males tend to have white cheeks (Bartlett, 2007) and occupy a vast range of habitats from swamp lowland forest to montane forest. Nevertheless, the highest population densities are found in dipterocarp forests (Yanuar, 2009). *Hylobates Lar,* the lar gibbon, is found in Indonesia, Laos, Peninsular Malaysia, Thailand and Myanmar, predominantly occupying lowland evergreen, semi-evergreen and mixed evergreen-deciduous

forests (Brokelman and Geissman, 2020). This species is classified as endangered in the IUCN Red List. *Hylobates lar* is an asexually dichromatic species which means both sexes are either black or buff (Bartlett, 2007; Bartlett and Light, 2017).

Gibbons are reported to rarely use their anterior teeth during feeding. *Hylobates lar* individuals in particular use their anterior teeth in a small proportion of feeding scans to incise particular food items. *Hylobates lar* exhibits nipping as its common behavior and occasionally incises and crushes multifarious food items (Ungar, 1994b). In contrast to the other species observed in Ungar's (1994b) study, gibbons use their incisors less than half of their total feeding time; for example, *Hylobates lar* choose small, ripe, soft-skinned fruit with fleshy pericarps. They prefer fruits such as *Bischoffia javanica, Turpinia sphaerocarpa,* and *Ficus sumatrana,* which do not require incisal preparation. Larger fruits such as *Ficus drupacea,* and *F. annulate* are reported as the less often taken fruits and were eaten as a whole. Some hard-skinned fruits such as *Aglaia korthalsii, Garcinia dioica* and *Gnetum cf. latifollum* required incisal processing to open up the flesh or seed prior to consumption. Frequently, gibbons crush *Aglaia odoratissima, Cissus nodosa* and *Mallotus sphaerocarpus* between their cheek teeth to extract juices and seeds. In terms of leaves, gibbons prefer small to medium-sized young leaves and exhibit incising or they pop them into their mouths without incisor use.

The African great apes

Pan spp.

The two studied *Pan* species are the pygmy chimpanzee (*Pan paniscus*) or bonobo, and the common chimpanzee (*Pan troglodytes* – I used the *Pa. t. schweinfurthii* subspecies). Bonobos were "discovered" in the late 1920s and separated from common chimpanzees due to some features

11

that distinguish the congeners. The main feature that distinguishes the two species is average adult size (although the degree of difference and overlap are still debatable) (Shea, 1984). However, it is suggested that the differences in morphology between the species may be size-related, or allometric (Shea, 1984). In terms of their dentition, based on literature reviewed by McHenry and Corruccini (1981) *Pa. paniscus* has smaller canine and less canine dimorphism than the chimpanzee. Hylander (1975) states that chimpanzees are marked by their massive incisors relative to the body mass and their dental microwear has been linked to heavy incisal processing of large and resistant fruits.

Shea and Coolidge Jr (1988) state that, when considering cranial variation, all subspecies of *Pa. troglodytes* more closely resemble one another than *Pa. paniscus*. Both species are highly frugivorous and evince a fission-fusion social organization (Plumptre *et al.,* 2016). For those individuals that inhabit the savanna, the food scarcity hypothesis may more significantly affect their behavior – and subsequently their social organization – than conspecifics in more forested environments (Pruetz, 2006).

Pan troglodytes schweinfurthii, the eastern chimpanzee, is listed as endangered in the IUCN Red List. It is found in southeastern Central African Republic and the Democratic Republic of Congo, Burundi, Rwanda, western Uganda and Western Tanzania. These chimpanzees occupy lowland to savanna woodlands and have maximum densities at 1000 to 2000 m above sea level. Their diets vary between seasons and populations, yet consist predominantly of ripe fruit, fibrous pith and leaves during non-mast season. (McLennan, 2013; Plumptre *et al.,* 2016).

Nishida and Uehara (1983) described chimpanzee feeding techniques for extracting plants; for leaves and blossoms, they hold the leafy or blossomy branch with one hand and strip off the young leaves or the blossoms with one head stroke or strip the leaves with their fingers and put

them into their mouth. Several times, they recorded that, instead of stripping off the leaves or blossoms directly from the branch, chimpanzees pick the leaves or blossoms, gather them in their hand or in their mouth and chew them altogether. However, some blossom species such as *Erytltrina abyssinica, Sterculia tragacantha* need to be broken off first. For seeds, chimpanzees prefer fallen seeds of *Parkia fillicoidea* and other dry fruits with sticky pulp such as *Canthium crassum, Parinari curatelhfolia, Uapaca kirkiana,* seeds of *Piliostignla thonningii*. Chimpanzees are reported to commonly look for and pick up fallen ripe fruits. Hard-skinned fruits such as from the Apocynaceae (*Saba florida*) or Loganiaceae (*Strychnos innocua*) are incised with their anterior teeth. *Landolphtia owariensis* is a woody vine species whose pits are eaten by the chimpanzees of Mahale. To extract the innards of the 1 mm of diameter pits, the chimpanzees use their teeth and fingers. Although roots consumed are not identified to plant species in the literature, chimpanzees eat a few species of emerging woody roots, which they cut with their incisors and chew with cheek teeth.

Pan paniscus is also listed as an endangered species on the IUCN Red List. Like many other primates, male bonobos have larger canines than females (Johanson, 1974). The distribution of bonobos is limited to the central part of the Democratic Republic of the Congo. Terada *et al* (2015) stated that the bonobo is relatively less studied due to difficulty accessing their remote locations and so details regarding their ecology are less well documented. The bonobo inhabits various habitats, from forest-savannah mosaic to moist tropical forest, however their exact distribution, how frequent they occupy each type of habitat, and ecological niche remain poorly understood (Fruth *et al.* 2016; Terada *et al.* 2015). Studies published to date indicate that their diet consists of more than 50% leaves of herbaceous food, regardless of mast season, supplemented by

bark, flowers, and fungus (Badrian and Malenky, 1984; Malenky and Wrangham, 1994; Fruth *et al.,* 2013) but none clearly describe their feeding behavior and food processing techniques.

Kano and Mulavwa (1984) noted that the pygmy chimpanzees usually use their fingers to pick fruit from branches, however young individuals occasionally use their mouths to pick the fruit directly from the branches. They sometimes put their food between their lower lip and lower anterior teeth. Primatologists suspect that bonobos, like their sister taxon, the chimpanzee, exhibit tool-use to extract food or non-fruit. However, Neufuss *et al* (2017) hypothesized the lack of recorded data may be due to their small number in the wild and limited number of already-habituated individuals.

Hypotheses

While there has been extensive research on dental microwear of molars and incisors as related to diet and tooth use, and exhaustive studies of canine dimorphism as related to socioecology, there is much less study of microwear on canines as related to diet. While these teeth certainly play an important role (perhaps even their primary role) in agonistic behavior, they are also used, even if only on occasion, in food acquisition and processing. Nevertheless, with the notable exception of the work of Delezene *et al*. (2016) on pitheciids and *Ateles*, there have been no quantitative analyses of canine microwear as it relates to feeding behavior in primates. Ryan (1981) stated that canine tooth use differences likely exhibit different types of microwear, and Harvey *et al*. (2009) state that canines also have a role in food preparation; thus, we can expect relationships between diet and microwear found on canines.

Unfortunately, however, unlike studies of molar microwear, studies of the anterior teeth require documentation of ingestive behaviors to interpret microwear patterning. And while there

have been a few such studies of ingestive behaviors in wild primates (e.g., Ungar, 1990, 1994), these have been focused on incisor use rather than canines. Nevertheless, it is of value to determine whether species with documented differences in diet and ingestive behaviors (even those focused on incisor use) differ in canine microwear patterning as well. This is a first step toward determining the potential value of canine microwear for inferring details about feeding behavior in fossil primates. Therefore, this thesis aims to explore the use of canine dental microwear to track the feeding patterns of Sumatran primates and African apes – both with documented differences in diet and at least some reports of variation in ingestive behavior in the literature.

Based on the aforementioned background and what we know about each of the studied primates' ingestive behavior, this thesis proposes several hypotheses, as follows:

1. Based on what we already know about the four sympatric Sumatran primates' initial food processing and their food choice, I predict that both *Hylobates* species will have much less canine microwear compared to other studied species. This prediction is due to the following reasons. *Hylobates* do not do heavy initial processing, their preferred foods are usually small-sized and fleshy fruit, and they tend to exhibit less hand usage to hold food to be incised due to their heavy use for brachiating. This is also due to morphological barriers such as size of mouth and the canine shape (small and prone to breakage if they process hard-skin fruit). Meanwhile, *Pongo abelii* is predicted to have the highest number of canine microwear due to their heavy incisors use.

2. Significant variation between frugivorous primates in canine microwear patterning is expected. For example, chimpanzees (*Pa. troglodytes schweinfurthii*), one of the frugivorous primates in this study, are known to occupy a large variety of habitats, from evergreen rainforest to woodland-savanna, and consume a large variety of food, from ripe

fleshy fruit to seeds and insects (Goodall, 1986 in Aliaga-Martinez *et al.* 2017). Their closest relative, the Bonobos (*Pa. paniscus*) occupies dry forest, swamp and disturbed forest more often. Bonobos consume herbaceous plants (*Uapaca* spp.) and are recorded to frequently eat mushrooms in swamp forest (Hashimoto *et al.* 1998; Terada *et al.* 2015). Therefore, I expect frugivorous primates to exhibit differences in microwear texture complexity and heterogeneity related to diet and tooth use (Scott *et al.* 2012).

3. The studied species rely on heavy initial food processing before consumption and have dietary diversity predicted to exhibit canines with higher values for complexity (*Asfc*), anisotropy (*epLsar*), and heterogeneity (*HAsfc*) for dental microwear texture analysis, and larger values for average width (*Min*), average length (*Maj*), number of tallies (*n*), and orientation (*r*) for microwear feature analysis. *Pongo abelii* (the Sumatran orangutan) is predicted to have the most wear on its canines among Sumatran primates. It has been well documented that the orangutan exhibits fruit husking activity and relies on hard food items, such as bark, and occasionally the meat of slow loris during the non-mast season (Utami Atmoko and van Hooff 1997; Hardus et al. 2012). Therefore, to process hard-object food items, orangutans might use their canines during initial processing.

4. Significant differences are predicted to occur between the other Sumatran primates (*H. lar, H. agilis, Pr. thomasi,* and *M. fascicularis*) and orangutans (*Po. abelii*). This prediction is based on the amount of initial fruit processing and differences in food choices among the species. Therefore, two terrestrial great apes from Africa, which are closely living relatives of the orangutan, the bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes schweinfurthii*), are used as comparisons. It is more difficult to interpret variation between the African apes given the lack of documented ingestive behaviors of these species. Some

differences in canine microwear are expected, though, given habitat and presumed diet differences. Likewise, some differences are expected between the Asian and African apes given habitat and presumed diet differences. Chimpanzees occupy a wide range of habitats, from open mosaic environments to continuous tropical forests. Bonobos mainly occupy continuous forest areas (Pennec et al. 2020), while orangutans occupy continuous tropical forests and is the only arboreal great ape. However, these apes do exhibit some dietary similarities, with feeding patterns reliant on fallback food during the dry season (Malenky and Stiles, 1991; Malenky and Wrangham, 1994).

Materials and Methods

Samples and Casting Procedures

The microwear canine replicas used in this study were generated from the original dental specimens of primates taken by Peter Ungar, Lucas Delezene and Mark Teaford in the Sumatran and African primates' collection of the American Museum of Natural History, National Museum of Natural History, Senkenberg Naturmuseum Frankfurt, and Musee Royal de l'Afrique. Sumatran primate samples are n = 13 *M. fascicularis* (long-tailed macaque), n = 11 *Hylobates lar* (lar gibbon), n = 13 *Hylobates agilis* (agile gibbon), n = 8 *Presbytis thomasi* (Thomas's langur), and n = 24 *Pongo abelii* (Sumatran orangutan), while African apes are n = 39 *Pan troglodytes* (common chimpanzee) and n = 21 *Pan paniscus* (bonobo). Teeth were cleaned with acetyl alcohol-soaked cotton swabs, and molds were prepared with President's Jet regular body polyvinylsiloxane dental impression material (Coltene-Whaledent Corp. Mawah, NJ) (Peterson et al., 2017).

Replicas were made from high-resolution epoxy (Epotek 501, Epoxy Technologies Corp.) following convention. The molds were poured with epoxy and spun in a centrifuge to remove air

bubbles. In order to add the remaining material to the mold, a pipette was used to diminish the chance of creating air bubbles. The molds were set for twenty-four hours before the casts were removed for study (Scott *et al.* 2006; Peterson, 2017).

While all available molds were poured and casts prepared, only specimens that preserved unequivocal unobstructed antemortem microwear were used in this study (e,g., see Teaford, 1988 for criteria of inclusion). Of 260 specimens examined, useable microwear was found on canines of 128 individuals.

Dental Microwear Texture Analysis Scanning Protocol

All replicas were scanned using a Sensofar PLu Neox white-light confocal optical profiler (Solarious Development Inc.) using a 100x objective lens. The area size was 127 µm x 96 µm, with 0.17 µm lateral point spacing, 0.2 µm vertical step, and vertical resolution (as reported by the manufacturer) of < 1 nm (Ungar et al., 2017). Scanning preference was for the distolingual-incisal facet of the maxillary canine (Figure 1). The preference for this surface is for consistency of analysis and to reduce the possibility of interference of the honing mechanism in the microwear.
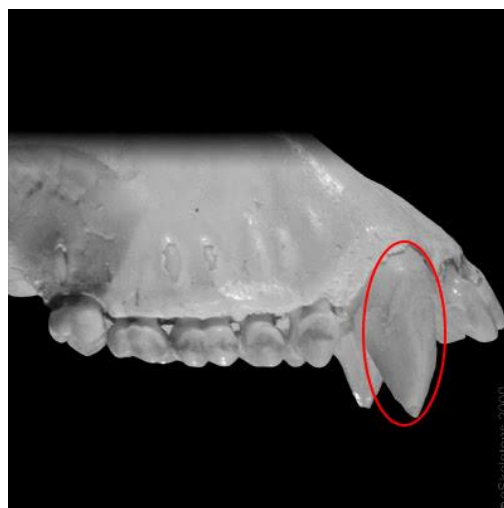
Figure 1. Distolingual facet of labial surface of canine (circled)

The occlusal surface was placed on the confocal profiler stage and leveled parallel to the base plane. Only areas free from casting defects or surface damage (e.g., chipping) were selected. The scanned areas were saved as *.plu files and then opened in SensoMap Premium Software (Mountains Map 8, Digital Surf Corp). Data were processed by leveling and thresholding with the lowest and highest threshold margins set to 0.1% and 99.9%, to eliminate data spikes. Any minor defects on the scanned surface were erased digitally using Mountains Map software and the area was subsequently filled using the nearest-neighbor algorithm following usual protocols (Peterson et al, 2017).

Microwear feature analysis (Ungar 1995; Ungar *et al.*, 1991) and microwear texture analysis (Ungar et al, 2003, et seq.) were employed in this study, following Ungar *et al.*'s (2021) recommendation for anterior teeth. The reason for using these two approaches together is to improve the characterization of microwear on canine surfaces that lack flat facets. The two analysis methods are described below.

Microwear feature analysis

For microwear feature analysis, a digital photo simulation of each surface was generated in MountainsMap 8 and outputted in *.bmp format. Microware 4.02 software was used to identify major and minor axe edges of each wear feature, and tallies (*n*), average length (*Maj*), breadth (*Min*), and length of the mean vector of long-axis orientation (*r*) were calculated (Ungar *et al.* 2021). Grine *et al.* (2002) state that Microware 4.02 tends to have an intraobserver error of around 7% and an interobserver error of around 9%; therefore, to minimize measurement error, each surface was measured three times, at different times, and averages were used in analyses.

Microwear texture analysis

Five scale-sensitive fractal analysis (SSFA) variables were analyzed using the MountainsMap Scale-Sensitive Analysis module. First, area-scale fractal complexity (*Asfc*) is used to characterize microwear surface texture complexity, which has been associated with food hardness (Scott *et al.,* 2012). *Asfc* estimates the slope of the steepest portion of the curve fit to a log-log plot of a relative area over the extent of scales multiplied by -1000. Surfaces dominated by features of varying sizes and shapes tend to have higher complexity values (Scott et al. 2005). Second, the scale of maximum complexity (*Smfc*) was calculated. *Smfc* represents the scale at which the complexity slope described above begins to tail off. Lower values are associated with surfaces that have more features at finer scales (Scott *et al.* 2005). Third, the exact proportion length-scale anisotropy of relief (*epLsar*) is used to measure the surface texture orientation. A surface with high anisotropy has a preferred texture orientation, such as when there are highly aligned scratches. On the other hand, a surface with lower anisotropy lacks this directionality (Scott et al., 2006; Peterson, 2017). The final attributes examined are measures of heterogeneity of area-scale fractal complexity across a given surface, calculated in 3 x 3 and 9 x 9 grids, *HAsfc9* and *HAsfc81* respectively. Each is calculated as the median absolute deviation of *Asfc* divided by the median of *Asfc* (Scott *et al.,* 2006; Krueger and Ungar, 2012; Peterson *et al*., 2017). A high *HAfsc* value indicates substantive variation across a given surface.

Statistical Protocol

Microwear feature and texture data were analyzed using a general linear model scheme to compare species following microwear analysis conventions. First, all data were rank transformed to mitigate violation of assumptions inherent to parametric statistical analyses (Conover and Iman, 1981).

Multivariate analyses of variance (MANOVAs) were used to determine overall significance in the models, considering the feature and texture datasets separately. All microwear attributes were used as the dependent variables and species was the factor used in Wilks's Lambda, Pillai Trace test, and Lawley-Hotelling Trace tests. Wilks's lambda is the most common MANOVA test statistic, being used to test the independence of the variables and when their exact distribution is unknown (Grilo and Coelho, 2010), Hotelling-Lawley Trace test is used to trace if the heterogeneity is due to a slight covariance inequality across the group, while Pillai-Barlett Trace is used when the number of sample sizes of each group is extremely unequal (Beasley and Sheehan, 1994).

Once significance in the MANOVA was established, single-classification ANOVAs were used to compare species for individual microwear attributes to determine the sources of significant variation. Finally, sources of significant variation in individual ANOVAs were assessed using pairwise comparisons: Tukey's Honestly-Significant-Difference (HSD) and Fisher's Least-Significant-Difference (LSD) tests. These were used to determine which species differed significantly for a given significant attribute. The main idea of Tukey's HSD is to calculate the genuine significant difference between two means. Tukey's HSD detects the exact distribution of the largest difference between a set of means from the same population, which makes this test conservative (Abdi and Williams, 2010). Unlike Tukey's HSD, Fisher's Least-Significant-Difference (LSD) calculates the smallest significant differences between two means; therefore, Fisher's LSD is more liberal than Tukey's HSD (Williams and Abdi 2010). Both tests were used to balance risks of Type I and Type II error (following Cook and Farewell, 1996). In cases where Fisher's LSD but not Tukey's HSD test presented significant results ($p < 0.05$), these should be interpreted as "suggestive" or of marginal significance.

Results

Representative photosimulations of canine microwear surfaces are illustrated in Figure 1.
Descriptive statistics and analytical statistical analyses are presented in Tables 1 to 5.
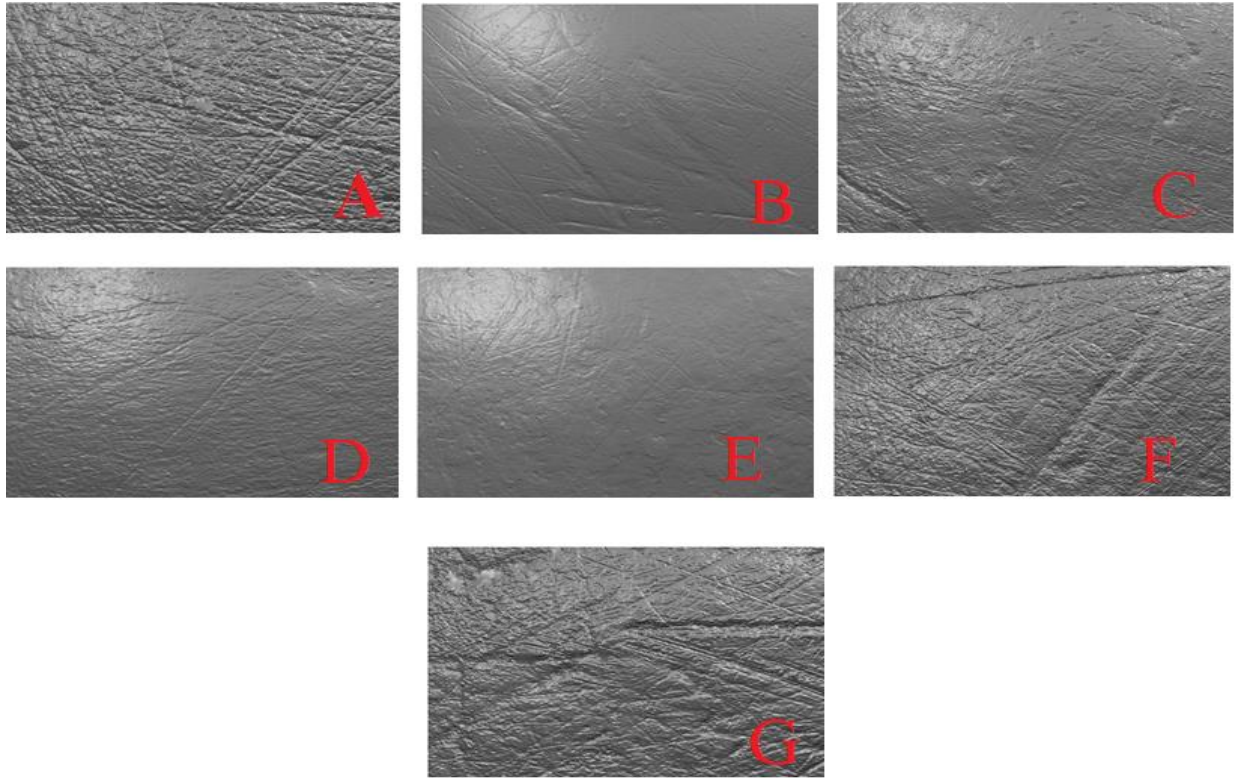
*Figure 2: Canine microwear of studied species with size of field of view 127 µm x 96 µm. A)
Pongo abelii (ZMA 01058), B) Presbytis thomasi (FSNM 3225), C) Macaca fascicularis (ZMA
14241), D) Hylobates agilis (NMNH 144089), E) Hylobates lar (RMNH 42074).*

Table 1. Descriptive statistics

	Po. abelii	Pr. thomasi	H. lar	H.agilis	M. fascicularis	Pa. t. schweinfurthii	Pa. paniscus
n	24	8	10	13	13	39	21
Smfc							
mean	0.896	0.835	0.555	0.711	0.898	1.078	0.918
s.d	0.264	0.223	0.233	0.125	0.368	0.666	0.447
HAsfc$_9$							
Mean	0.254	0.449	0.566	0.417	0.392	0.360	0.250
s.d	0.131	0.188	0.652	0.282	0.329	0.177	0.148
HAsfc$_{81}$							
Mean	0.516	0.614	0.782	0.657	0.866	0.588	0.422
s.d	0.444	0.174	0.678	0.384	1.106	0.261	0.174
Asfc							
Mean	4.175	2.842	6.690	4.882	5.742	3.466	3.655
s.d	1.965	1.449	8.451	4.908	4.645	1.570	1.718
epLsar							
Mean	0.004	0.004	0.004	0.004	0.003	0.003	0.003
s.d	0.002	0.002	0.002	0.002	0.001	0.001	0.001
Maj							
Mean	211.450	149.268	196.561	196.561	181.852	184.293	173.456
s.d	38.978	31.794	60.554	60.554	58.838	36.490	30.527
Majsd							
Mean	146.946	97.547	127.598	127.326	113.095	118.933	116.674
s.d	31.822	33.360	39.133	70.839	54.779	36.509	27.815
Min							
Mean	4.103	3.131	3.444	3.518	3.624	3.702	3.361
s.d.	0.347	0.520	0.425	0.599	0.323	0.577	0.519
Minsd							
Mean	1.541	1.145	1.335	1.301	1.374	1.212	1.116
s.d	0.360	0.207	0.179	0.204	0.290	0.364	0.150
r							
Mean	0.426	0.464	0.659	0.535	0.517	0.595	0.553
s.d	0.138	0.126	0.235	0.205	0.151	0.194	0.133
n							
Mean	61.000	64	15.700	24.385	39.000	36.487	37.429
s.d	28.067	54.240	10.258	16.616	26.966	28.608	21.579

The results of the statistical analyses are presented in Tables 2 to 5 respectively.

Table 2. MANOVA Microwear feature and texture analysis

Feature analysis	Value	F-Ratio	*df	p-Value
Wilks's Lambda	0.403	3.272	36, 512	**< 0.001**
Pillai Trace	0.770	2.967	36, 726	**< 0.001**
Hotelling-Lawley Trace	1.094	3.473	36, 686	**< 0.001**
Texture analysis				
Wilks's Lambda	0.488	3.079	30, 470	**< 0.001**
Pillai Trace	0.613	2.818	30, 605	**< 0.001**
Hotelling-Lawley Trace	0.856	3.291	30, 577	**< 0.001**

As predicted, MANOVA results for both microwear feature and texture analysis revealed significant variation among the species, in feature analysis (Wilks's Λ = 0.403, F-Ratio = 3.272, p-value = < 0.001; Pillai Test = 0.770, F-Ratio = 2.967, p-value < 0.001; Hotelling-Lawley Trace = 1.094, F-Ratio = 3.473, p-value < 0.001), and texture analysis (Wilks's Λ = 0.488, F-Ratio = 3.079, p-value = < 0.001; Pillai Test = 0.613, F-Ratio = 2.818, p-value < 0.001; Hotelling-Lawley Trace = 0.856, F-Ratio = 3.291, p-value < 0.001). The ANOVA test results to determine sources of that variation are presented in Table 3.

Table 3. ANOVA: univariate F-Test

	Type III SS	df	Mean Squares	F-Ratio	p-Value
epLsar	6601.929	6	1100.322	0.792	0.578
Smfc	58955.254	6	9825.880	10.665	**< 0.001**
HAsfc$_9$	21404.561	6	3567.430	2.815	**0.013**
HAsfc$_{81}$	20471.191	6	3411.870	2.676	**0.018**
Asfc	8786.980	6	1464.500	1.068	0.386
Maj	27900.330	6	4650.060	3.831	**0.002**
Majsd	21572.930	6	3587.990	2.883	**0.013**
Min	48549.200	6	8091.530	7.759	**< 0.001**
Minsd	48486.410	6	8081.070	7.746	**< 0.001**
r	25285.080	6	4214.180	3.412	**0.004**
n	40 628.040	6	6771.340	6.114	**< 0.001**

Individual ANOVA tests on each variable shows that microwear of studied species varies significantly different for scratch density (*n*), orientation of wears (*r*), average length (*Maj*), average width (*Min*), scale of maximum complexity (*Smfc*) and heterogeneity of area-scale fractal complexity (*HAsfc*) with p-value ≤ 0.05.

Post hoc or pairwise tests were employed to determine the sources of significant variation (e.g., which pairs of species differed) for the variables that showed significant ANOVA results. Tukey's Honestly-Significant-Difference and Fisher's Least-Significant-Difference were used, and the results are presented in Table 4 and Table 5.

Table 4. Summary of Microwear Feature Analysis: Tukey's HSD and Fisher's LSD with *p < 0.05 for Fisher's LSD test, **p < 0.05 for both Tukey's HSD and Fisher's LSD tests (shown in bold).

Pairwise comparison		Maj	Majsd	Min	Minsd	r	n
H. agilis	*Pa. t. schweinfurthii*	10.359	2.795	-8.987	10.192	-11.397	-15.692
H. agilis	*H. lar*	-4.769	4.554	9.331	-1.012	-25.104	15.541
H. agilis	*M. fascicularis*	19.462	11.769	-0.769	-0.192	0.874	-22.385
H. agilis	*Po. abelii*	-14.269	-24.404*	**-38.123****	-26.265*	22.304	**-48.676****
H. agilis	*Pa. paniscus*	19.993	4.513	15.612	**34.919****	-5.773	-21.813
H. agilis	*Pr. thomasi*	40.981*	23.846	30.481*	27.726	13.159	-37.260*
Pa. t. schweinfurthii	*H. lar*	14.487	7.349	-18.318	11.204	13.706	-31.108*
Pa. t. schweinfurthii	*M. fascicularis*	-9.744	-8.974	-8.128	10.385	-13.590	6.692
Pa. t. schweinfurthii	*Po. abelii*	23.987*	**27.199****	**29.136****	**36.487****	**-33.702****	**32.984****
Pa. t. schweinfurthii	*Pa. paniscus*	-10.275	-1.718	-24.599*	**-24.272****	-5.625	6.121
Pa. t. schweinfurthii	*Pr. thomasi*	-31.263*	-21.051	**-39.468****	-17.534	-24.556	21.567
H. lar	*M. fascicularis*	24.231	16.323	-10.100	0.819	27.296	-37.800*
H. lar	*Po. abelii*	-9.5	-19.850	**-47.454****	-25.283*	**47.408****	**-64.092****
H. lar	*Pa. paniscus*	14.487	9.067	6.281	35.931*	19.331	-37.229*
H. lar	*Pr. thomasi*	45.750*	28.400	21.150	28.273	38.262*	**-52.675****
M. fascicularis	*Po. abelii*	-33.731*	**-36.173****	**-37.354****	-26.103*	20.112	-26.292*
M. fascicularis	*Pa. paniscus*	-7.256	-7.139	16.381	**35.112****	-7.695	0.571
M. fascicularis	*Pr. thomasi*	21.519	12.077	31.250*	27.918	10.966	-14.875
Po. abelii	*Pa. paniscus*	**34.262****	28.917*	**53.735****	**61.214****	-28.077*	26.863*
Po. abelii	*Pr. thomasi*	**55.250****	**48.250****	**68.604****	**54.021****	-9.146	11.417
Pa. paniscus	*Pr. thomasi*	20.988	19.33	14.869	-17.534	18.932	-15.446

Two pairs of species, *Po. abelii* with *Pa. paniscus* and *Po. abelii* with *Pr. thomasi* are significantly different in average length (*Maj*) both in Tukey's HSD and Fisher's LSD. Other pairs like *H. agilis* with *Pr. thomasi; Pa. t. schweinfurthii* with *Po. abelii; Pa. t. schweinfurthii* with *Pr. thomasi; H. lar* with *Pr. thomasi* are significant on Fisher's LSD, which means there are only slight differences among them. Meanwhile, significant differences in *Majsd* (standard deviation of the

average length of microwear) in both Tukey's HSD and Fisher's LSD are found for pairs of *Pa. t. schweinfurthii* with *Po. abelii; Po. abelii* with *Pr. thomasi;* and *M. fascicularis* with *Po. abelii.* This indicates there is a difference in value of average length variation. Meanwhile, the pairs of *H. agilis* with *Po. abelii* and *Po. abelii* with *Pa. paniscus* only have a slight variation in their *Majsd* variable.

For average width (*Min*), significant variation is found between several pairs of species (in both Tukey's HSD and Fisher's LSD), including *H. agilis* with *Po. abelii; Pa. t. schweinfurthii* with *Po. abelii; Pa. t. schweinfurthii* with *Pr. thomasi; H. lar* with *Po. abelii; M. fascicularis* with *Po. abelii; Po. abelii* with *Pa. paniscus* and *Po. abelii* with *Pr. thomasi.* Most of the significant pairs are the species that were paired with *Po. abelii.* Other pairs, such as *H. agilis* and *Pr. thomasi, Pa. t. schweinfurthii* and *Pa. paniscus,* and *M. fascicularis* and *Pr. thomasi,* are significant by Fisher's LSD, meaning they only exhibit small differences that only Fisher's LSD can recognize. For *Minsd* (standard deviation of the average width of microwear) significant pairs (in both Tukey's HSD and Fisher's LSD) are *H. agilis* and *Pa. paniscus, Pa. t. schweinfurthii* and *Po. abelii, Pa. t. schweinfurthii* and *Pa. paniscus, M. fascicularis* and *Pa. paniscus, Po. abelii* and *Pa. paniscus* and *Po. abelii* and *Pr. thomasi.* Meanwhile, significant differences in Fisher's LSD are in *H, agilis* and *Po. abelii, H. lar* and *Po. abelii* and *M. fascicularis* and *Po. abelii*

For *r* (orientation of homogeneity) only two pairs show significant variation in both Tukey's HSD and Fisher's LSD: *H. lar* with *Po. abelii* and *Po. abelii* with *Pa. t. schweinfurthii.* The microwear orientation can be seen on Figure 1 and the mean value for *r* can be seen in Table 1. Meanwhile, the pairs of *H. lar* with *Pr. thomasi* and *Po. abelii* with *Pa. paniscus* exhibit significant differences only by Fisher's LSD.

For *n* (microwear density) significant pairs (in both Tukey's HSD and Fisher's LSD) are *H. agilis* with *Po. abelii*, *Pa. t. schweinfurthii* with *Po. abelii*, *H. lar* with *Po. abelii* and *H. lar* with *Pr. thomasi*. Pairwise comparisons of *H. agilis* with *Pr. thomasi*, *Pa. t. schweinfurthii* with *H. lar*, *H. lar* with *M. fascicularis*, *H. lar* with *Pa. paniscus*, *M. fascicularis* with *Po. abelii* and *Po. abelii* with *Pa. paniscus* are significant in Fisher's LSD tests only, implying the differences are of marginal significance.

Table 5. Summary of Microwear Texture Analysis: Tukey's HSD and Fisher's LSD with *p < 0.05 for Fisher's LSD test, **p < 0.05 for both Tukey's HSD and Fisher's LSD tests (shown in bold).

Pairwise Comparison		Smfc	HAsfc9	HAsfc81
H. agilis	*H. lar*	13.727	-2.188	-2.677
H. agilis	*M. fascicularis*	-21.769	8.423	1.269
H. agilis	*Po. abelii*	-28.006*	22.337	22.548
H. agilis	*Pa. t. schweinfurthii*	**-54.744****	0.628	0.628
H. agilis	*Pa. paniscus*	**-40.685****	25.247*	28.161*
H. agilis	*Pr. thomasi*	-18.861	-19.913	-8.577
H. lar	*M. fascicularis*	-35.469*	10.612	3.946
H. lar	*Po. abelii*	**-41.733****	24.525	25.225
H. lar	*Pa. t. schweinfurthii*	**-68.471****	2.817	3.305
H. lar	*Pa. paniscus*	**-54.412****	27.436*	30.838*
H. lar	*Pr. thomasi*	-32.587*	-17.725	-5.900
M. fascicularis	*Po. abelii*	-6.237	13.913	21.279
M. fascicularis	*Pa. t. schweinfurthii*	**-32.974****	-7.795	-0.641
M. fascicularis	*Pa. paniscus*	-18.916	16.824	26.892*
M. fascicularis	*Pr. thomasi*	2.909	-28.337	-9.864
Po. abelii	*Pa. t. schweinfurthii*	**-26.737****	-21.708*	-21.920*
Po. abelii	*Pa. paniscus*	-12.679	2.911	5.613
Po. abelii	*Pr. thomasi*	9.146	-42.250*	-31.125*
Pa. t. schweinfurthii	*Pa. paniscus*	-14.059	-24.619*	-27.533*
Pa. t. schweinfurthii	*Pr. thomasi*	**-35.883****	20.542	9.205
Pa. paniscus	*Pr. thomasi*	21.824	**-45.161****	-36.738*

For texture analysis, only three variables showed significant variation: *Smfc, HAsfc$_9$* and *Hasfc$_{81}$*. *Smfc* varied by Tukey's HSD and Fisher's LSD for the following pairs of species: *Pa. t. schweinfurthii* with *H. agilis; H. agilis* with *Pa. paniscus; H. lar* with *Po. abelii; H. lar* with *Pa. t. schweinfurthii; H. lar* with *Pa. paniscus; M. fascicularis* with *Pa. t. schweinfurthii; Pa. t. schweinfurthii* with *Po. abelii* and *Pa. t. schweinfurthii* with *Pr. thomasi.* Most significant pairing include Hylobatidae species, which have the lowest *Smfc* values among the studied species (Table 1). Since *Smfc* represents the maximum scale of the complexity of the slope, the significant pairs have differences in microwear features at the finer scale (Scott *et al.* 2005). Meanwhile, *HAsfc$_9$* has only one significant pair in both Tukey's HSD and Fisher's LSD. For *HAsfc$_{81}$*, *Pa. paniscus* and *Pr. thomasi* differ significantly only for Fisher's HSD.

Microwear feature and texture analysis data is plotted in boxplots in Figures 3 and 4.

29
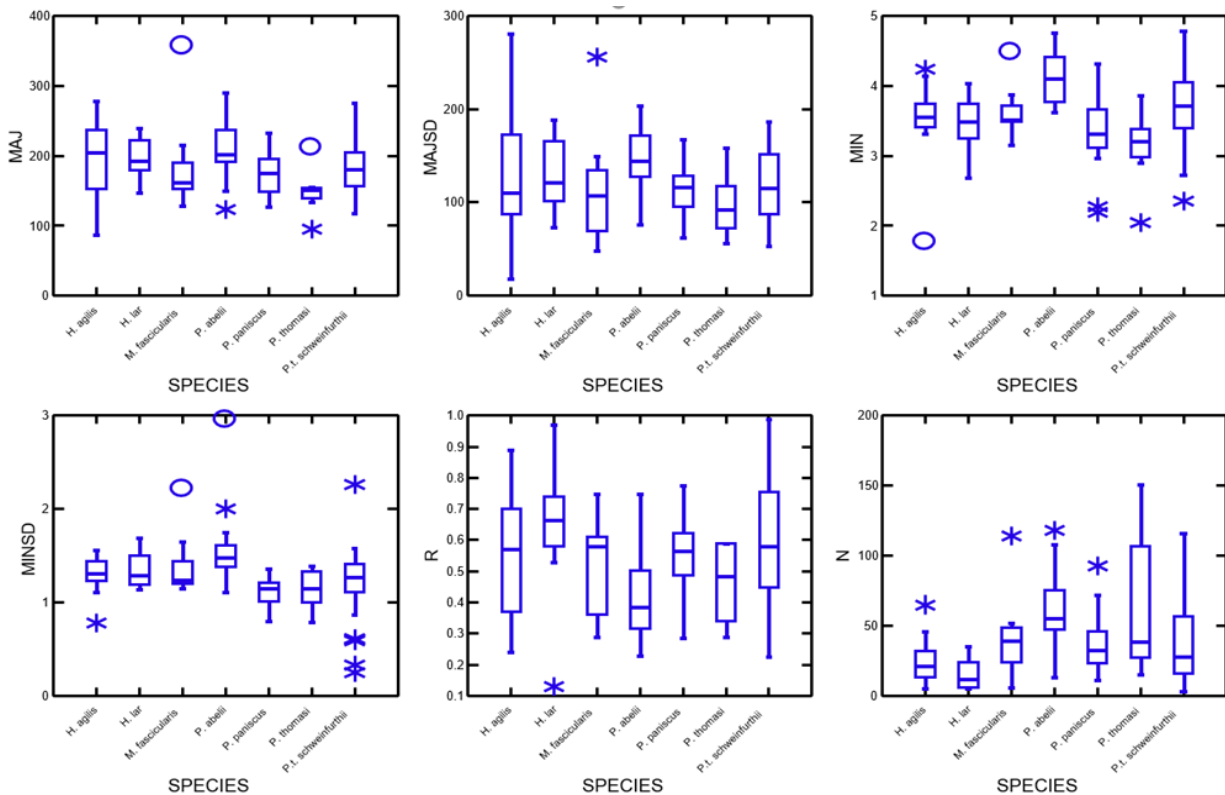
Figure 3. Box and whiskers plots for microwear feature analysis. Boxes indicate the 25-50th and 50-75th percentile ranges, whiskers indicate 0-25th and 75-100th percentile ranges excluding outliers (o) and extreme values (*)
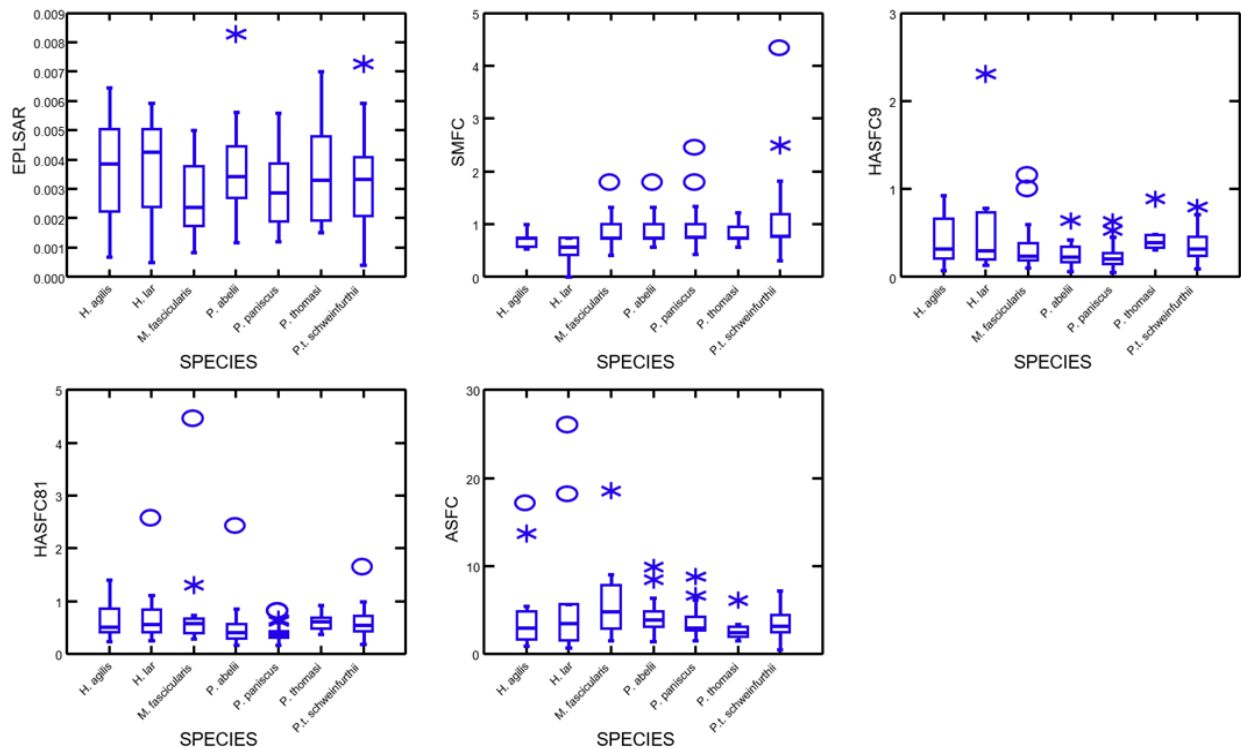
Figure 4. Box and whiskers plots for microwear texture analysis. Boxes indicate the 25-50th and 50-75th percentile ranges, whiskers indicate 0-25th and 75-100th percentile ranges excluding outliers (o) and extreme values (*)

The box and whiskers plot helps visualize the data dispersal of all species for each examined variable. Figure 3 shows data dispersal for microwear feature analysis; it shows that *Min* and *Minsd* have the most outliers and *r* has relatively the longest boxplot compared with the rest of the variables indicating variable *r* has the greatest interquartile range. Meanwhile, Figure 4 shows data dispersal for microwear texture analysis; it shows that *Asfc* has the highest number of outliers and *HAsfc81* has a relatively short boxplot compared with the rest of the variables, indicating that canines show low values for *HAsfc81.*

Discussion

The measurement of central tendency shows that between both Hylobatidae species, the microwear on *H. lar* canines tends to be heterogenous and have more features at various sizes in the finer scale, with homogenously oriented wears and the lowest scratch density. *Macaca fascicularis* has heterogenous features at the 9 x 9 scale, and *Pr. thomasi* shows the narrowest width yet the longest average length of microwear. *Presbytis thomasi* has less variety of microwear features, yet the highest scratch density, which probably is due to a wide range of data points. *Pongo abelii* is more uniform with the longest and widest scratches but they are not oriented to a similar direction. *Pan t. schweinfurthii* has the largest features on coarse scale among all studied species, while *Pa. paniscus* has homogenous microwear at a 9 x 9 scale.

MANOVA tests had significant results for both texture and feature analysis. However, the ANOVA univariate F-test, particularly for texture analysis, rejects half of the second hypotheses due to *Asfc* and *epLsar* not being statistically significant (though *HAsfc* and *Smfc* were both significant). This suggests that *HAsfc* and *Smfc* may be the best variables for separating taxa by microwear texture analysis. *Asfc* and *epLsar* are two attributes that reflect species' dietary diversity, but this holds only for molar studies where tough foods are sheared and hard foods are crushed between opposing cheek teeth (Ragni *et al.* 2017; Schubert *et al.* 2010). *HAsfc* may be related to causative factors such as the size and variability of wear-causing particles and canine use behaviors (Scott *et al.* 2006; Krueger *et al.,* 2008; Ungar *et al.* 2008). Meanwhile, *Smfc* relates to the sizes of features on the surface (e.g., presence or absence of small features). A low *Smfc* value indicates that before the species' death, their diet may have varied with no consistent pattern of consumption of food that were especially hard or tough (Pontzer *et al.* 2011).

Half of the second hypothesis is supported by significant values of *HAsfc* in *Po. abelii* when compared to *H. lar* and *Pa. t. schweinfurthii*. *Pa. paniscus* exhibits significant differences compared to *Pr. thomasi* (Tukey's HSD and Fisher's LSD)*, H. agilis, H. lar,* and *Pa. t. schweinfurthii*, although the rest of differences were found only in Fisher's LSD. *Smfc* is statistically significant in both Tukey's HSD and Fisher's LSD in Hyobatidae spp. when compared to all great apes, and *Pa. t. schweinfurthii* when compared to *M. fascicularis, Po. abelii* and *Pr. thomasi.* Pairwise comparison for feature analysis shows *Po. abelii* is statistically significant (in Tukey's HSD and/or Fisher's LSD) in all feature analysis variables in comparison to *Pa. paniscus, Pa. t. schweinfurthii* and *M. fascicularis*; only not significant in feature orientation and number of scratches with *Pr. thomasi.*

The microwear patterns seen for Hylobatidae species are probably caused by three factors. First, the lack of canines in processing hard, brittle food, results in almost no large pits. Second, the shape of the *Hylobates* spp. canine is the most distinct with a prominent long, more end-curved, dagger-like shape (Fleagle, 2013). Third, morphological barriers, such as the size of the mouth and need for free hands not engaged in ingestion, leads these species to prefer to eat small ripe fleshy fruit and young leaves requiring little ingestive behavior (Palombit, 1997). Although they might switch to fallback food during scarcity, their choice of small-sized, mostly less challenging unripe or immature fruit (Vogel *et al.* 2009) means less pressure on their canines for food processing. Additional causes to consider are adhesive wear, which is caused by tough, woody seeds and seed pods, leading to an increased tooth on tooth contact, and dust accumulation on food surfaces which unintentionally forms light wears on them (Ungar *et al.* 1995).

Macaca fascicularis, Pr. thomasi, and *Po. abelii* show significant differences compared with *Pa. t. schweinfurthii*. For *Macaca fascicularis,* Aliaga-Martinez *et al.* (2017) hypothesize that

the cheek pouch plays a key role in food-to-tooth contact on the enamel surface, which would accentuate microwear features due to the abrasiveness of food particles. However, there is no report that *Pa. t. schweinfurthii* relies on foods that require huge jaw loads such as barks, like *Po. abelii* does. Instead, *Pa. t. schweinfurthii* consumes herbaceous vegetation such as *Triumfetta cordifolia, Ipomoea involcurata, Aneilema aequinoctiale* and *Pteridium aquilinum* (Matthews *et al.,*2011), small flowery fruit such as *Musanga leo-errerae* (Furuichi *et al.,* 2001), honeybees and ants (Yamagiwa and Basabose, 2009), while pith and stems have a minor contribution to the diet and don't act as fallback (Watts *et al.* 2011).

In sum, some of the hypotheses generated for this thesis – e.g., that orangutans would have the most canine microwear with the largest and deepest features and that gibbon would have the least microwear – were confirmed. This shows us that canine microwear holds the potential to reveal important differences in tooth use between species. On the other hand, other differences observed, such as between frugivorous species, remain unexplained. More work is needed to document canine use in the wild and to explain these differences in the future.

These differences may be due to dietary variation. *Pongo abelii* is primarily frugivorous while *Pr. thomasi* is more folivorous – though how food size corresponds to canine microwear feature length is yet to be determined. The comparison between *Pa. paniscus* and *Po. abelii* shows significant differences possibly due to *Pa. paniscus* consuming more than 50% of herbaceous plants (Badrian and Malenky, 1984; Malenky and Wrangham, 1994; Fruth *et al.,* 2013) and a consumption of pith and dispersed ground vines as reported by Wrangham and White (1988). However, this result needs further investigation given the lack of information on associated differences in canine use. *Po. abelii* is reported to exhibit a great amount of initial processing, which is consistent with its high striation density compared to other species. *Pongo abelii*

microwear likely has heterogeneous striation orientation due to its feeding pattern and food choice that differs from its pairs. As reported, *Po. abelii* must change their diet during non-mast season from fleshy fruit to leaves, barks, insects, etc. Ingestion, particularly for barks, requires high effort and technique, therefore *Po. abelii* will apply initial processing forces in every direction possible to extract the edible part.

Although almost all *Po. abelii* pairs are frugivores, the variances were predicted due to dietary diversity in terms of food properties. *Pongo abelii* is the only fully arboreal great ape and feeds mostly on food that requires initial processing, such as incising and puncturing, which probably has different consistency and texture from food that are consumed by *Pa. t. schweinfurthii, Pa. paniscus* and *Pr. thomasi.*

Conclusion

The conclusions that can be drawn are listed below

1. Each of the studied species has a unique pattern of microwear on its canine. Measures of central tendency show *H. lar* and *H. agilis* have the narrowest microwear features and frugivorous great apes such as *Po. abelii* have the longest and widest scratches.

2. ANOVA univariate F-test indicates that all variables in the feature analysis vary significantly while two in the microwear texture variables, *HAsfc* and *Smfc*, separated these species.

3. Pairwise comparison for feature analysis shows that *Po. Abelii* differs most from the other species in microwear features and textures. This is consistent with extreme use of its canines in food processing compared with the other species considered here. The very

densities of canine microwear in *Hylobates* spp. is consistent with previous observations that gibbons do not use their front teeth often in ingestive behavior.

4. Canine microwear analysis holds potential to reveal differences in tooth use between species but understanding those differences and determining the limits of resolution for canine microwear interpretation will require documentation of canine use in the wild, particularly for species with feeding ecology that differs in ways more subtle than broad diet category designation.

5. The results indicate that there are likely other things that canine microwear can tell us. However, the interpretation will have to wait until other detailed research on canine use in these species is done.

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Appendix

Statistical summary of Pairwise comparisons for MAJORX

Post Hoc Test of MAJORX					
Tukey's Honestly-Significant-Difference Test					
SPECIES	SPECIES	Difference	p-Value	95% Confidence Interval	
				Lower	Upper
H. agilis	*H. lar*	-4.769	1	-47.972	38.434
H. agilis	*M. fascicularis*	19.462	0.789	-20.825	59.749
H. agilis	*Po. abelii*	-14.269	0.898	-49.64	21.102
H. agilis	*Pa. paniscus*	19.993	0.665	-16.255	56.24
H. agilis	*Pr. thomasi*	40.981	0.121	-5.174	87.135
H. agilis	*Pa. t. schweinfurthii*	9.718	0.977	-23.176	42.612
H. lar	*M. fascicularis*	24.231	0.647	-18.972	67.434
H. lar	*Po. abelii*	-9.5	0.991	-48.159	29.159
H. lar	*Pa. paniscus*	24.762	0.514	-14.701	64.225
H. lar	*Pr. thomasi*	45.75	0.082	-2.971	94.471
H. lar	*Pa. t. schweinfurthii*	14.487	0.904	-21.92	50.894
M. fascicularis	*Po. abelii*	-33.731	0.073	-69.102	1.64
M. fascicularis	*Pa. paniscus*	0.531	1	-35.717	36.779
M. fascicularis	*Pr. thomasi*	21.519	0.816	-24.635	67.674
M. fascicularis	*Pa. t. schweinfurthii*	-9.744	0.977	-42.638	23.151
Po. abelii	*Pa. paniscus*	34.262	0.017	3.571	64.953
Po. abelii	*Pr. thomasi*	55.25	0.002	13.318	97.182
Po. abelii	*Pa. t. schweinfurthii*	23.987	0.11	-2.66	50.635
Pa. paniscus	*Pr. thomasi*	20.988	0.774	-21.686	63.662
Pa. paniscus	*Pa. t. schweinfurthii*	-10.275	0.931	-38.075	17.526
Pr. thomasi	*Pa. t. schweinfurthii*	-31.263	0.238	-71.128	8.602

Statistical summary of Pairwise comparisons for MAJORX (Cont.)

Fisher's Least-Significant-Difference Test

SPECIES$(i)	SPECIES$(j)	Difference	p-Value	95% Confidence Interval	
				Lower	Upper
H. agilis	*H. lar*	-4.769	0.745	-33.78	24.241
H. agilis	*M. fascicularis*	19.462	0.157	-7.591	46.514
H. agilis	*Po. abelii*	-14.269	0.237	-38.02	9.482
H. agilis	*Pa. paniscus*	19.993	0.107	-4.347	44.333
H. agilis	*Pr. thomasi*	40.981	0.01	9.989	71.973
H. agilis	*Pa. t. schweinfurthii*	9.718	0.385	-12.37	31.806
H. lar	*M. fascicularis*	24.231	0.101	-4.78	53.241
H. lar	*Po. abelii*	-9.5	0.47	-35.459	16.459
H. lar	*Pa. paniscus*	24.762	0.067	-1.737	51.261
H. lar	*Pr. thomasi*	45.75	0.007	13.035	78.465
H. lar	*Pa. t. schweinfurthii*	14.487	0.243	-9.96	38.934
M. fascicularis	*Po. abelii*	-33.731	0.006	-57.482	-9.98
M. fascicularis	*Pa. paniscus*	0.531	0.966	-23.809	24.871
M. fascicularis	*Pr. thomasi*	21.519	0.172	-9.473	52.511
M. fascicularis	*Pa. t. schweinfurthii*	-9.744	0.384	-31.832	12.344
Po. abelii	*Pa. paniscus*	34.262	0.001	13.653	54.871
Po. abelii	*Pr. thomasi*	55.25	0	27.093	83.407
Po. abelii	*Pa. t. schweinfurthii*	23.987	0.009	6.094	41.881
Pa. paniscus	*Pr. thomasi*	20.988	0.15	-7.667	49.643
Pa. paniscus	*Pa. t. schweinfurthii*	-10.275	0.278	-28.943	8.393
Pr. thomasi	*Pa. t. schweinfurthii*	-31.263	0.022	-58.032	-4.494

Statistical summary of Pairwise comparisons for MAJORSD

SPECIES$(i)	SPECIES$(j)	Difference	p-Value	95% Confidence Interval	
				Lower	Upper
H. agilis	*H. lar*	-4.554	1	-48.684	39.577
H. agilis	*M. fascicularis*	11.769	0.98	-29.383	52.921
H. agilis	*Po. abelii*	-24.404	0.42	-60.534	11.726
H. agilis	*Pa. paniscus*	4.513	1	-32.513	41.539
H. agilis	*Pr. thomasi*	23.846	0.75	-23.299	70.991
H. agilis	*Pa. t. schweinfurthii*	2.795	1	-30.805	36.395
H. lar	*M. fascicularis*	16.323	0.931	-27.807	60.453
H. lar	*Po. abelii*	-19.85	0.756	-59.339	19.639
H. lar	*Pa. paniscus*	9.067	0.995	-31.244	49.377
H. lar	*Pr. thomasi*	28.4	0.628	-21.366	78.166
H. lar	*Pa. t. schweinfurthii*	7.349	0.997	-29.84	44.537
M. fascicularis	*Po. abelii*	-36.173	0.049	-72.303	-0.043
M. fascicularis	*Pa. paniscus*	-7.256	0.997	-44.282	29.769
M. fascicularis	*Pr. thomasi*	12.077	0.989	-35.068	59.222
M. fascicularis	*Pa. t. schweinfurthii*	-8.974	0.986	-42.575	24.626
Po. abelii	*Pa. paniscus*	28.917	0.093	-2.433	60.267
Po. abelii	*Pr. thomasi*	48.25	0.016	5.418	91.082
Po. abelii	*Pa. t. schweinfurthii*	27.199	0.05	-0.021	54.418
Pa. paniscus	*Pr. thomasi*	19.333	0.849	-24.257	62.924
Pa. paniscus	*Pa. t. schweinfurthii*	-1.718	1	-30.115	26.679
Pr. thomasi	*Pa. t. schweinfurthii*	-21.051	0.73	-61.772	19.67

Post Hoc Test of MAJORSD
Tukey's Honestly-Significant-Difference Test

Statistical summary of Pairwise comparisons for MAJORSD (Cont.)

Fisher's Least-Significant-Difference Test

SPECIES$(i)	SPECIES$(j)	Difference	p-Value	95% Confidence Interval	
				Lower	Upper
H. agilis	*H. lar*	-4.554	0.761	-34.187	25.079
H. agilis	*M. fascicularis*	11.769	0.401	-15.864	39.402
H. agilis	*Po. abelii*	-24.404	0.049	-48.665	-0.143
H. agilis	*Pa. paniscus*	4.513	0.72	-20.349	29.375
H. agilis	*Pr. thomasi*	23.846	0.138	-7.811	55.504
H. agilis	*Pa. t. schweinfurthii*	2.795	0.807	-19.767	25.357
H. lar	*M. fascicularis*	16.323	0.278	-13.31	45.956
H. lar	*Po. abelii*	-19.85	0.141	-46.367	6.667
H. lar	*Pa. paniscus*	9.067	0.509	-18.001	36.135
H. lar	*Pr. thomasi*	28.4	0.095	-5.018	61.818
H. lar	*Pa. t. schweinfurthii*	7.349	0.561	-17.623	32.32
M. fascicularis	*Po. abelii*	-36.173	0.004	-60.434	-11.912
M. fascicularis	*Pa. paniscus*	-7.256	0.564	-32.119	17.606
M. fascicularis	*Pr. thomasi*	12.077	0.452	-19.581	43.734
M. fascicularis	*Pa. t. schweinfurthii*	-8.974	0.433	-31.537	13.588
Po. abelii	*Pa. paniscus*	28.917	0.008	7.866	49.968
Po. abelii	*Pr. thomasi*	48.25	0.001	19.489	77.011
Po. abelii	*Pa. t. schweinfurthii*	27.199	0.004	8.921	45.476
Pa. paniscus	*Pr. thomasi*	19.333	0.193	-9.937	48.604
Pa. paniscus	*Pa. t. schweinfurthii*	-1.718	0.859	-20.786	17.351
Pr. thomasi	*Pa. t. schweinfurthii*	-21.051	0.13	-48.395	6.292

Statistical summary of Pairwise comparisons for MINORX

Post Hoc Test of MINORX					
Tukey's Honestly-Significant-Difference Test					
SPECIES$(i)	SPECIES$(j)	Difference	p-Value	95% Confidence Interval	
				Lower	Upper
H. agilis	*H. lar*	9.331	0.993	-30.716	49.378
H. agilis	*M. fascicularis*	-0.769	1	-38.113	36.575
H. agilis	*Po. abelii*	-38.123	0.011	-70.91	-5.337
H. agilis	*Pa. paniscus*	15.612	0.818	-17.988	49.211
H. agilis	*Pr. thomasi*	30.481	0.352	-12.302	73.263
H. agilis	*Pa. t. schweinfurthii*	-8.987	0.977	-39.478	21.504
H. lar	*M. fascicularis*	-10.1	0.99	-50.147	29.947
H. lar	*Po. abelii*	-47.454	0.002	-83.289	-11.61
H. lar	*Pa. paniscus*	6.281	0.999	-30.299	42.861
H. lar	*Pr. thomasi*	21.15	0.812	-24.011	66.311
H. lar	*Pa. t. schweinfurthii*	-18.318	0.682	-52.065	15.429
M. fascicularis	*Po. abelii*	-37.354	0.014	-70.141	-4.567
M. fascicularis	*Pa. paniscus*	16.381	0.782	-17.219	49.98
M. fascicularis	*Pr. thomasi*	31.25	0.321	-11.533	74.033
M. fascicularis	*Pa. t. schweinfurthii*	-8.218	0.986	-38.709	22.273
Po. abelii	*Pa. paniscus*	53.735	0	25.286	82.184
Po. abelii	*Pr. thomasi*	68.604	0	29.736	107.47
Po. abelii	*Pa. t. schweinfurthii*	29.136	0.009	4.436	53.837
Pa. paniscus	*Pr. thomasi*	14.869	0.926	-24.688	54.426
Pa. paniscus	*Pa. t. schweinfurthii*	-24.599	0.073	-50.369	1.171
Pr. thomasi	*Pa. t. schweinfurthii*	-39.468	0.027	-76.421	-2.515

Statistical summary of Pairwise comparisons for MINORX (Cont.)

Fisher's Least-Significant-Difference Test

SPECIES$(i)	SPECIES$(j)	Difference	p-Value	95% Confidence Interval	
				Lower	Upper
H. agilis	*H. lar*	9.331	0.493	-17.56	36.222
H. agilis	*M. fascicularis*	-0.769	0.952	-25.845	24.307
H. agilis	*Po. abelii*	-38.123	0.001	-60.139	-16.10
H. agilis	*Pa. paniscus*	15.612	0.173	-6.95	38.173
H. agilis	*Pr. thomasi*	30.481	0.038	1.753	59.209
H. agilis	*Pa. t. schweinfurthii*	-8.987	0.387	-29.462	11.487
H. lar	*M. fascicularis*	-10.1	0.459	-36.991	16.791
H. lar	*Po. abelii*	-47.454	0	-71.517	-23.39
H. lar	*Pa. paniscus*	6.281	0.614	-18.282	30.844
H. lar	*Pr. thomasi*	21.15	0.17	-9.175	51.475
H. lar	*Pa. t. schweinfurthii*	-18.318	0.112	-40.979	4.343
M. fascicularis	*Po. abelii*	-37.354	0.001	-59.37	-15.33
M. fascicularis	*Pa. paniscus*	16.381	0.153	-6.181	38.943
M. fascicularis	*Pr. thomasi*	31.25	0.033	2.522	59.978
M. fascicularis	*Pa. t. schweinfurthii*	-8.218	0.428	-28.692	12.256
Po. abelii	*Pa. paniscus*	53.735	0	34.632	72.838
Po. abelii	*Pr. thomasi*	68.604	0	42.504	94.704
Po. abelii	*Pa. t. schweinfurthii*	29.136	0.001	12.55	45.722
Pa. paniscus	*Pr. thomasi*	14.869	0.27	-11.693	41.431
Pa. paniscus	*Pa. t. schweinfurthii*	-24.599	0.006	-41.903	-7.295
Pr. thomasi	*Pa. t. schweinfurthii*	-39.468	0.002	-64.281	-14.65

Statistical summary of Pairwise comparisons for MINORSD

Post Hoc Test of MINORSD
Tukey's Honestly-Significant-Difference Test

SPECIES$(i)	SPECIES$(j)	Difference	p-Value	95% Confidence Interval	
				Lower	Upper
H. agilis	*H. lar*	-1.012	1	-41.068	39.045
H. agilis	*M. fascicularis*	-0.192	1	-37.545	37.161
H. agilis	*Po. abelii*	-26.295	0.214	-59.09	6.5
H. agilis	*Pa. paniscus*	34.919	0.036	1.312	68.527
H. agilis	*Pr. thomasi*	27.726	0.473	-15.067	70.519
H. agilis	*Pa. t. schweinfurthii*	10.192	0.957	-20.306	40.691
H. lar	*M. fascicularis*	0.819	1	-39.237	40.876
H. lar	*Po. abelii*	-25.283	0.365	-61.127	10.561
H. lar	*Pa. paniscus*	35.931	0.058	-0.658	72.52
H. lar	*Pr. thomasi*	28.737	0.497	-16.435	73.91
H. lar	*Pa. t. schweinfurthii*	11.204	0.959	-22.552	44.96
M. fascicularis	*Po. abelii*	-26.103	0.222	-58.897	6.692
M. fascicularis	*Pa. paniscus*	35.112	0.034	1.504	68.72
M. fascicularis	*Pr. thomasi*	27.918	0.465	-14.875	70.711
M. fascicularis	*Pa. t. schweinfurthii*	10.385	0.953	-20.114	40.883
Po. abelii	*Pa. paniscus*	61.214	0	32.758	89.67
Po. abelii	*Pr. thomasi*	54.021	0.001	15.143	92.899
Po. abelii	*Pa. t. schweinfurthii*	36.487	0	11.78	61.194
Pa. paniscus	*Pr. thomasi*	-7.193	0.998	-46.76	32.373
Pa. paniscus	*Pa. t. schweinfurthii*	-24.727	0.07	-50.503	1.049
Pr. thomasi	*Pa. t. schweinfurthii*	-17.534	0.803	-54.496	19.428

Statistical summary of Pairwise comparisons for MINORSD (Cont.)

Fisher's Least-Significant-Difference Test

SPECIES$(i)	SPECIES$(j)	Difference	p-Value	95% Confidence Interval	
				Lower	Upper
H. agilis	*H. lar*	-1.012	0.941	-27.909	25.886
H. agilis	*M. fascicularis*	-0.192	0.988	-25.274	24.89
H. agilis	*Po. abelii*	-26.295	0.02	-48.316	-4.274
H. agilis	*Pa. paniscus*	34.919	0.003	12.352	57.487
H. agilis	*Pr. thomasi*	27.726	0.058	-1.009	56.461
H. agilis	*Pa. t. schweinfurthii*	10.192	0.326	-10.287	30.672
H. lar	*M. fascicularis*	0.819	0.952	-26.078	27.717
H. lar	*Po. abelii*	-25.283	0.04	-49.352	-1.215
H. lar	*Pa. paniscus*	35.931	0.004	11.362	60.5
H. lar	*Pr. thomasi*	28.737	0.063	-1.595	59.07
H. lar	*Pa. t. schweinfurthii*	11.204	0.33	-11.463	33.87
M. fascicularis	*Po. abelii*	-26.103	0.021	-48.124	-4.081
M. fascicularis	*Pa. paniscus*	35.112	0.003	12.544	57.679
M. fascicularis	*Pr. thomasi*	27.918	0.057	-0.817	56.653
M. fascicularis	*Pa. t. schweinfurthii*	10.385	0.317	-10.095	30.864
Po. abelii	*Pa. paniscus*	61.214	0	42.106	80.322
Po. abelii	*Pr. thomasi*	54.021	0	27.915	80.127
Po. abelii	*Pa. t. schweinfurthii*	36.487	0	19.897	53.077
Pa. paniscus	*Pr. thomasi*	-7.193	0.593	-33.762	19.375
Pa. paniscus	*Pa. t. schweinfurthii*	-24.727	0.005	-42.035	-7.419
Pr. thomasi	*Pa. t. schweinfurthii*	-17.534	0.164	-42.353	7.286

Statistical summary of Pairwise comparisons for R

Post Hoc Test of R
Tukey's Honestly-Significant-Difference Test

SPECIES$(i)	SPECIES$(j)	Difference	p-Value	95% Confidence Interval	
				Lower	Upper
H. agilis	*H. lar*	-25.104	0.617	-68.685	18.477
H. agilis	*M. fascicularis*	2.192	1	-38.447	42.832
H. agilis	*Po. abelii*	22.304	0.519	-13.376	57.985
H. agilis	*Pa. paniscus*	-5.773	0.999	-42.337	30.792
H. agilis	*Pr. thomasi*	13.159	0.982	-33.399	59.717
H. agilis	*Pa. t. schweinfurthii*	-11.397	0.951	-44.579	21.784
H. lar	*M. fascicularis*	27.296	0.516	-16.285	70.877
H. lar	*Po. abelii*	47.408	0.006	8.411	86.406
H. lar	*Pa. paniscus*	19.331	0.785	-20.477	59.139
H. lar	*Pr. thomasi*	38.262	0.246	-10.884	87.409
H. lar	*Pa. t. schweinfurthii*	13.706	0.928	-23.019	50.432
M. fascicularis	*Po. abelii*	20.112	0.642	-15.568	55.792
M. fascicularis	*Pa. paniscus*	-7.965	0.995	-44.53	28.599
M. fascicularis	*Pr. thomasi*	10.966	0.993	-35.592	57.524
M. fascicularis	*Pa. t. schweinfurthii*	-13.59	0.892	-46.772	19.592
Po. abelii	*Pa. paniscus*	-28.077	0.105	-59.037	2.882
Po. abelii	*Pr. thomasi*	-9.146	0.996	-51.445	33.153
Po. abelii	*Pa. t. schweinfurthii*	-33.702	0.004	-60.582	-6.822
Pa. paniscus	*Pr. thomasi*	18.932	0.854	-24.116	61.979
Pa. paniscus	*Pa. t. schweinfurthii*	-5.625	0.997	-33.668	22.419
Pr. thomasi	*Pa. t. schweinfurthii*	-24.556	0.548	-64.77	15.658

Statistical summary of Pairwise comparisons for R (Cont.)

Fisher's Least-Significant-Difference Test					
SPECIES$(i)	SPECIES$(j)	Difference	p-Value	95% Confidence Interval	
				Lower	Upper
H. agilis	*H. lar*	-25.104	0.092	-54.368	4.16
H. agilis	*M. fascicularis*	2.192	0.874	-25.096	29.481
H. agilis	*Po. abelii*	22.304	0.068	-1.654	46.263
H. agilis	*Pa. paniscus*	-5.773	0.642	-30.326	18.78
H. agilis	*Pr. thomasi*	13.159	0.406	-18.105	44.422
H. agilis	*Pa. t. schweinfurthii*	-11.397	0.313	-33.679	10.884
H. lar	*M. fascicularis*	27.296	0.067	-1.968	56.56
H. lar	*Po. abelii*	47.408	0	21.222	73.595
H. lar	*Pa. paniscus*	19.331	0.155	-7.4	46.062
H. lar	*Pr. thomasi*	38.262	0.023	5.261	71.264
H. lar	*Pa. t. schweinfurthii*	13.706	0.273	-10.954	38.367
M. fascicularis	*Po. abelii*	20.112	0.099	-3.847	44.071
M. fascicularis	*Pa. paniscus*	-7.965	0.522	-32.518	16.587
M. fascicularis	*Pr. thomasi*	10.966	0.489	-20.297	42.23
M. fascicularis	*Pa. t. schweinfurthii*	-13.59	0.23	-35.871	8.691
Po. abelii	*Pa. paniscus*	-28.077	0.009	-48.866	-7.288
Po. abelii	*Pr. thomasi*	-9.146	0.525	-37.549	19.257
Po. abelii	*Pa. t. schweinfurthii*	-33.702	0	-51.752	-15.652
Pa. paniscus	*Pr. thomasi*	18.932	0.197	-9.974	47.837
Pa. paniscus	*Pa. t. schweinfurthii*	-5.625	0.555	-24.456	13.207
Pr. thomasi	*Pa. t. schweinfurthii*	-24.556	0.074	-51.559	2.447

Statistical summary of Pairwise comparisons for N

				95% Confidence Interval	
Post Hoc Test of N					
Tukey's Honestly-Significant-Difference Test					
SPECIES$(i)	SPECIES$(j)	Difference	p-Value	Lower	Upper
H. agilis	*H. lar*	15.415	0.928	-25.855	56.686
H. agilis	*M. fascicularis*	-22.385	0.606	-60.87	16.101
H. agilis	*Po. abelii*	-48.676	0	-82.465	-14.887
H. agilis	*Pa. paniscus*	-21.813	0.509	-56.44	12.813
H. agilis	*Pr. thomasi*	-37.26	0.162	-81.35	6.831
H. agilis	*Pa. t. schweinfurthii*	-15.692	0.761	-47.115	15.731
H. lar	*M. fascicularis*	-37.8	0.098	-79.071	3.471
H. lar	*Po. abelii*	-64.092	0	-101.022	-27.161
H. lar	*Pa. paniscus*	-37.229	0.056	-74.927	0.47
H. lar	*Pr. thomasi*	-52.675	0.015	-99.217	-6.133
H. lar	*Pa. t. schweinfurthii*	-31.108	0.115	-65.887	3.671
M. fascicularis	*Po. abelii*	-26.292	0.247	-60.081	7.497
M. fascicularis	*Pa. paniscus*	0.571	1	-34.055	35.198
M. fascicularis	*Pr. thomasi*	-14.875	0.955	-58.965	29.215
M. fascicularis	*Pa. t. schweinfurthii*	6.692	0.996	-24.731	38.115
Po. abelii	*Pa. paniscus*	26.863	0.098	-2.455	56.182
Po. abelii	*Pr. thomasi*	11.417	0.981	-28.64	51.473
Po. abelii	*Pa. t. schweinfurthii*	32.984	0.003	7.528	58.44
Pa. paniscus	*Pr. thomasi*	-15.446	0.923	-56.212	25.319
Pa. paniscus	*Pa. t. schweinfurthii*	6.121	0.994	-20.436	32.678
Pr. thomasi	*Pa. t. schweinfurthii*	21.567	0.636	-16.515	59.65

Statistical summary of Pairwise comparisons for N (Cont.)

Fisher's Least-Significant-Difference Test

SPECIES(i)	SPECIES(j)	Difference	p-Value	95% Confidence Interval	
				Lower	Upper
H. agilis	H. lar	15.415	0.273	-12.297	43.128
H. agilis	M. fascicularis	-22.385	0.089	-48.227	3.458
H. agilis	Po. abelii	-48.676	0	-71.365	-25.987
H. agilis	Pa. paniscus	-21.813	0.066	-45.064	1.438
H. agilis	Pr. thomasi	-37.26	0.014	-66.866	-7.653
H. agilis	Pa. t. schweinfurthii	-15.692	0.144	-36.793	5.408
H. lar	M. fascicularis	-37.8	0.008	-65.513	-10.087
H. lar	Po. abelii	-64.092	0	-88.89	-39.293
H. lar	Pa. paniscus	-37.229	0.004	-62.543	-11.915
H. lar	Pr. thomasi	-52.675	0.001	-83.927	-21.423
H. lar	Pa. t. schweinfurthii	-31.108	0.009	-54.461	-7.754
M. fascicularis	Po. abelii	-26.292	0.024	-48.981	-3.603
M. fascicularis	Pa. paniscus	0.571	0.961	-22.68	23.823
M. fascicularis	Pr. thomasi	-14.875	0.322	-44.481	14.731
M. fascicularis	Pa. t. schweinfurthii	6.692	0.531	-14.408	27.793
Po. abelii	Pa. paniscus	26.863	0.008	7.176	46.55
Po. abelii	Pr. thomasi	11.417	0.402	-15.481	38.314
Po. abelii	Pa. t. schweinfurthii	32.984	0	15.891	50.077
Pa. paniscus	Pr. thomasi	-15.446	0.266	-42.82	11.927
Pa. paniscus	Pa. t. schweinfurthii	6.121	0.498	-11.712	23.954
Pr. thomasi	Pa. t. schweinfurthii	21.567	0.098	-4.004	47.139

Statistical summary of ANOVA Univariate F-Test and MANOVA for Microwear Feature Analysis

Univariate F-Tests

Source	Type III SS	df	Mean Squares	F-Ratio	p-Value
MAJORX	27,900.33	6	4,650.06	3.831	0.002
Error	146,851.67	121	1,213.65		
MAJORSD	21,527.92	6	3,587.99	2.833	0.013
Error	153,223.58	121	1,266.31		
MINORX	48,549.20	6	8,091.53	7.759	0
Error	126,178.30	121	1,042.80		
MINORSD	48,486.41	6	8,081.07	7.746	0
Error	126,240.60	121	1,043.31		
R	25,285.08	6	4,214.18	3.412	0.004
Error	149,430.93	121	1,234.97		
N	40,628.04	6	6,771.34	6.114	0
Error	134,009.96	121	1,107.52		

Multivariate Test Statistics

Statistic	Value	F-Ratio	df	p-Value
Wilks's Lambda	0.403	3.272	36, 512	0
Pillai Trace	0.77	2.967	36, 726	0
Hotelling-Lawley Trace	1.094	3.473	36, 686	0

Statistical summary of ANOVA Univariate F-Test and MANOVA for Microwear Texture Analysis

Univariate F-Tests

Source	Type III SS	Df	Mean Squares	F-Ratio	p-Value
EPLSAR	6,601.93	6	1,100.32	0.792	0.578
Error	168,149.07	121	1,389.66		
SMFC	58,955.25	6	9,825.88	10.665	0
Error	111,483.25	121	921.349		
HASFC9	21,404.56	6	3,567.43	2.815	0.013
Error	153,346.44	121	1,267.33		
HASFC81	20,471.19	6	3,411.87	2.676	0.018
Error	154,280.31	121	1,275.04		
ASFC	8,786.98	6	1,464.50	1.068	0.386
Error	165,963.52	121	1,371.60		

Multivariate Test Statistics

Statistic	Value	F-Ratio	df	p-Value
Wilks's Lambda	0.488	3.079	30, 470	0
Pillai Trace	0.613	2.818	30, 605	0
Hotelling-Lawley Trace	0.856	3.291	30, 577	0

THETA	S	M	N	p-Value
0.366	5	0	57.5	0

Statistical summary of Pairwise comparisons for *Smfc*

SPECIES$(i)	SPECIES$(j)	Difference	p-Value	95% Confidence Interval	
				Lower	Upper
H. agilis	*H. lar*	13.727	0.935	-23.916	51.37
H. agilis	*M. fascicularis*	-21.769	0.529	-56.871	13.333
H. agilis	*Po. abelii*	-28.006	0.103	-58.825	2.812
H. agilis	*Pa. paniscus*	-40.685	0.003	-72.267	-9.103
H. agilis	*Pr. thomasi*	-18.861	0.811	-59.075	21.354
H. agilis	*Pa. t. schweinfurthii*	-54.744	0	-83.404	-26.083
H. lar	*M. fascicularis*	-35.496	0.08	-73.139	2.146
H. lar	*Po. abelii*	-41.733	0.005	-75.417	-8.05
H. lar	*Pa. paniscus*	-54.412	0	-88.796	-20.028
H. lar	*Pr. thomasi*	-32.587	0.262	-75.038	9.863
H. lar	*Pa. t. schweinfurthii*	-68.471	0	-100.192	-36.749
M. fascicularis	*Po. abelii*	-6.237	0.997	-37.056	24.581
M. fascicularis	*Pa. paniscus*	-18.916	0.571	-50.498	12.667
M. fascicularis	*Pr. thomasi*	2.909	1	-37.306	43.123
M. fascicularis	*Pa. t. schweinfurthii*	-32.974	0.012	-61.635	-4.314
Po. abelii	*Pa. paniscus*	-12.679	0.803	-39.42	14.062
Po. abelii	*Pr. thomasi*	9.146	0.99	-27.389	45.681
Po. abelii	*Pa. t. schweinfurthii*	-26.737	0.012	-49.955	-3.519
Pa. paniscus	*Pr. thomasi*	21.824	0.595	-15.358	59.006
Pa. paniscus	*Pa. t. schweinfurthii*	-14.059	0.608	-38.281	10.164
Pr. thomasi	*Pa. t. schweinfurthii*	-35.883	0.038	-70.617	-1.149

Post Hoc Test of SMFC
Tukey's Honestly-Significant-Difference Test

Statistical summary of Pairwise comparisons for *Smfc* (Cont.)

Fisher's Least-Significant-Difference Test

SPECIES$(i)	SPECIES$(j)	Difference	p-Value	95% Confidence Interval	
				Lower	Upper
H. agilis	*H. lar*	13.727	0.284	-11.55	39.003
H. agilis	*M. fascicularis*	-21.769	0.07	-45.34	1.801
H. agilis	*Po. abelii*	-28.006	0.008	-48.701	-7.312
H. agilis	*Pa. paniscus*	-40.685	0	-61.892	-19.478
H. agilis	*Pr. thomasi*	-18.861	0.169	-45.864	8.143
H. agilis	*Pa. t. schweinfurthii*	-54.744	0	-73.989	-35.498
H. lar	*M. fascicularis*	-35.496	0.006	-60.773	-10.22
H. lar	*Po. abelii*	-41.733	0	-64.352	-19.115
H. lar	*Pa. paniscus*	-54.412	0	-77.5	-31.323
H. lar	*Pr. thomasi*	-32.587	0.025	-61.092	-4.083
H. lar	*Pa. t. schweinfurthii*	-68.471	0	-89.771	-47.17
M. fascicularis	*Po. abelii*	-6.237	0.552	-26.931	14.457
M. fascicularis	*Pa. paniscus*	-18.916	0.08	-40.123	2.291
M. fascicularis	*Pr. thomasi*	2.909	0.831	-24.095	29.912
M. fascicularis	*Pa. t. schweinfurthii*	-32.974	0.001	-52.22	-13.729
Po. abelii	*Pa. paniscus*	-12.679	0.165	-30.635	5.278
Po. abelii	*Pr. thomasi*	9.146	0.462	-15.387	33.679
Po. abelii	*Pa. t. schweinfurthii*	-26.737	0.001	-42.328	-11.147
Pa. paniscus	*Pr. thomasi*	21.824	0.086	-3.143	46.792
Pa. paniscus	*Pa. t. schweinfurthii*	-14.059	0.09	-30.324	2.207
Pr. thomasi	*Pa. t. schweinfurthii*	-35.883	0.003	-59.207	-12.559

Statistical summary of Pairwise comparisons for *HAsfc9*

Post Hoc Test of HASFC9

Tukey's Honestly-Significant-Difference Test

SPECIES$(i)	SPECIES$(j)	Difference	p-Value	95% Confidence Interval	
				Lower	Upper
H. agilis	*H. lar*	-2.188	1	-46.337	41.96
H. agilis	*M. fascicularis*	8.423	0.997	-32.745	49.591
H. agilis	*Po. abelii*	22.337	0.533	-13.808	58.481
H. agilis	*Pa. paniscus*	25.247	0.408	-11.793	62.288
H. agilis	*Pr. thomasi*	-19.913	0.877	-67.078	27.251
H. agilis	*Pa. t. schweinfurthii*	0.628	1	-32.986	34.242
H. lar	*M. fascicularis*	10.612	0.992	-33.537	54.76
H. lar	*Po. abelii*	24.525	0.527	-14.98	64.03
H. lar	*Pa. paniscus*	27.436	0.411	-12.891	67.762
H. lar	*Pr. thomasi*	-17.725	0.942	-67.511	32.061
H. lar	*Pa. t. schweinfurthii*	2.817	1	-34.387	40.02
M. fascicularis	*Po. abelii*	13.913	0.917	-22.231	50.058
M. fascicularis	*Pa. paniscus*	16.824	0.834	-20.216	53.865
M. fascicularis	*Pr. thomasi*	-28.337	0.568	-75.501	18.828
M. fascicularis	*Pa. t. schweinfurthii*	-7.795	0.994	-41.409	25.819
Po. abelii	*Pa. paniscus*	2.911	1	-28.452	34.273
Po. abelii	*Pr. thomasi*	-42.25	0.056	-85.099	0.599
Po. abelii	*Pa. t. schweinfurthii*	-21.708	0.22	-48.939	5.522
Pa. paniscus	*Pr. thomasi*	-45.161	0.037	-88.768	-1.553
Pa. paniscus	*Pa. t. schweinfurthii*	-24.619	0.14	-53.028	3.79
Pr. thomasi	*Pa. t. schweinfurthii*	20.542	0.753	-20.196	61.279

Statistical summary of Pairwise comparisons for *HAsfc₉* (Cont.)

SPECIES\$(i)	SPECIES\$(j)	Difference	p-Value	95% Confidence Interval	
				Lower	Upper
H. agilis	*H. lar*	-2.188	0.884	-31.833	27.456
H. agilis	*M. fascicularis*	8.423	0.547	-19.221	36.067
H. agilis	*Po. abelii*	22.337	0.071	-1.934	46.607
H. agilis	*Pa. paniscus*	25.247	0.047	0.375	50.12
H. agilis	*Pr. thomasi*	-19.913	0.216	-51.584	11.757
H. agilis	*Pa. t. schweinfurthii*	0.628	0.956	-21.943	23.199
H. lar	*M. fascicularis*	10.612	0.48	-19.033	40.256
H. lar	*Po. abelii*	24.525	0.07	-2.002	51.052
H. lar	*Pa. paniscus*	27.436	0.047	0.357	54.514
H. lar	*Pr. thomasi*	-17.725	0.296	-51.156	15.706
H. lar	*Pa. t. schweinfurthii*	2.817	0.824	-22.165	27.798
M. fascicularis	*Po. abelii*	13.913	0.259	-10.357	38.184
M. fascicularis	*Pa. paniscus*	16.824	0.183	-8.048	41.696
M. fascicularis	*Pr. thomasi*	-28.337	0.079	-60.007	3.334
M. fascicularis	*Pa. t. schweinfurthii*	-7.795	0.495	-30.366	14.776
Po. abelii	*Pa. paniscus*	2.911	0.785	-18.149	23.97
Po. abelii	*Pr. thomasi*	-42.25	0.004	-71.023	-13.477
Po. abelii	*Pa. t. schweinfurthii*	-21.708	0.02	-39.993	-3.424
Pa. paniscus	*Pr. thomasi*	-45.161	0.003	-74.443	-15.879
Pa. paniscus	*Pa. t. schweinfurthii*	-24.619	0.012	-43.695	-5.543
Pr. thomasi	*Pa. t. schweinfurthii*	20.542	0.14	-6.813	47.896

Statistical summary of Pairwise comparisons for *HAasfc$_{81}$*

Tukey's Honestly-Significant-Difference Test

SPECIES$(i)	SPECIES$(j)	Difference	p-Value	95% Confidence Interval	
				Lower	Upper
H. agilis	*H. lar*	-2.677	1	-46.959	41.605
H. agilis	*M. fascicularis*	1.269	1	-40.024	42.563
H. agilis	*Po. abelii*	22.548	0.525	-13.706	58.803
H. agilis	*Pa. paniscus*	28.161	0.277	-8.992	65.314
H. agilis	*Pr. thomasi*	-8.577	0.998	-55.885	38.731
H. agilis	*Pa. t. schweinfurthii*	0.628	1	-33.088	34.344
H. lar	*M. fascicularis*	3.946	1	-40.336	48.228
H. lar	*Po. abelii*	25.225	0.496	-14.4	64.85
H. lar	*Pa. paniscus*	30.838	0.27	-9.611	71.287
H. lar	*Pr. thomasi*	-5.9	1	-55.838	44.038
H. lar	*Pa. t. schweinfurthii*	3.305	1	-34.012	40.622
M. fascicularis	*Po. abelii*	21.279	0.595	-14.976	57.533
M. fascicularis	*Pa. paniscus*	26.892	0.332	-10.261	64.045
M. fascicularis	*Pr. thomasi*	-9.846	0.996	-57.154	37.461
M. fascicularis	*Pa. t. schweinfurthii*	-0.641	1	-34.357	33.075
Po. abelii	*Pa. paniscus*	5.613	0.998	-25.845	37.071
Po. abelii	*Pr. thomasi*	-31.125	0.332	-74.105	11.855
Po. abelii	*Pa. t. schweinfurthii*	-21.92	0.213	-49.233	5.393
Pa. paniscus	*Pr. thomasi*	-36.738	0.168	-80.478	7.002
Pa. paniscus	*Pa. t. schweinfurthii*	-27.533	0.066	-56.028	0.962
Pr. thomasi	*Pa. t. schweinfurthii*	9.205	0.994	-31.656	50.066

Statistical summary of Pairwise comparisons for *HAsfc₈₁* (Cont.)

Fisher's Least-Significant-Difference Test

SPECIES$(i)	SPECIES$(j)	Difference	p-Value	95% Confidence Interval	
				Lower	Upper
H. agilis	*H. lar*	-2.677	0.859	-32.412	27.058
H. agilis	*M. fascicularis*	1.269	0.928	-26.459	28.997
H. agilis	*Po. abelii*	22.548	0.069	-1.796	46.893
H. agilis	*Pa. paniscus*	28.161	0.027	3.213	53.109
H. agilis	*Pr. thomasi*	-8.577	0.594	-40.343	23.19
H. agilis	*Pa. t. schweinfurthii*	0.628	0.956	-22.012	23.268
H. lar	*M. fascicularis*	3.946	0.793	-25.789	33.681
H. lar	*Po. abelii*	25.225	0.063	-1.383	51.833
H. lar	*Pa. paniscus*	30.838	0.026	3.677	57.999
H. lar	*Pr. thomasi*	-5.9	0.728	-39.433	27.633
H. lar	*Pa. t. schweinfurthii*	3.305	0.794	-21.753	28.363
M. fascicularis	*Po. abelii*	21.279	0.086	-3.066	45.623
M. fascicularis	*Pa. paniscus*	26.892	0.035	1.944	51.84
M. fascicularis	*Pr. thomasi*	-9.846	0.541	-41.613	21.92
M. fascicularis	*Pa. t. schweinfurthii*	-0.641	0.955	-23.281	21.999
Po. abelii	*Pa. paniscus*	5.613	0.6	-15.51	26.737
Po. abelii	*Pr. thomasi*	-31.125	0.035	-59.985	-2.265
Po. abelii	*Pa. t. schweinfurthii*	-21.92	0.02	-40.26	-3.579
Pa. paniscus	*Pr. thomasi*	-36.738	0.015	-66.109	-7.367
Pa. paniscus	*Pa. t. schweinfurthii*	-27.533	0.005	-46.667	-8.399
Pr. thomasi	*Pa. t. schweinfurthii*	9.205	0.508	-18.233	36.643

Descriptive statistics

Results for SPECIES$ = *Po. abelii*

	Major x	Major sd	Minor x	Minor sd	R	N	Eplsar	Smfc	Hasfc 9	Hasfc 81	Asfc
N	24	24	24	24	24	24	24	24	24	24	24
Min	122.85	76.67	3.62	1.11	0.23	13	0.001	0.564	0.067	0.176	1.467
Max	290.48	203.59	4.76	2.96	0.75	118	0.008	1.769	0.638	2.412	9.846
Mean	211.45	146.946	4.103	1.541	0.426	61	0.004	0.896	0.254	0.516	4.175
S.D.	38.978	31.822	0.347	0.36	0.138	28.067	0.002	0.264	0.131	0.444	1.965

Results for SPECIES$ = *H. agilis*

	Majorx	Major sd	Minor x	Minor sd	R	N	Eplsar	Smfc	Hasfc 9	Hasfc 81	Asfc
N	13	13	13	13	13	13	13	13	13	13	13
Min	87.37	18.19	1.77	0.78	0.24	5	0.001	0.546	0.075	0.248	0.969
Max	277.66	281.39	4.24	1.56	0.89	65	0.006	0.999	0.927	1.404	17.04
Mean	196.561	127.326	3.518	1.301	0.535	24.385	0.004	0.711	0.417	0.657	4.882
S.D.	60.554	70.839	0.599	0.204	0.205	16.616	0.002	0.125	0.282	0.384	4.908

Results for SPECIES$ = *H. lar*

	Majorx	Major sd	Minor x	Minor sd	R	N	Eplsar	Smfc	Hasfc 9	Hasfc 81	Asfc
N	10	10	10	10	10	10	10	10	10	10	10
Min	147.87	73.31	2.69	1.14	0.13	5	0.001	0.006	0.133	0.269	0.78
Max	239.39	188.31	4.04	1.69	0.97	35	0.006	0.751	2.307	2.558	25.96
Mean	197.496	127.598	3.444	1.335	0.659	15.7	0.004	0.555	0.566	0.782	6.69
S.D.	29.004	39.133	0.425	0.179	0.235	10.285	0.002	0.233	0.652	0.678	8.451

Results for SPECIES$ = *M. fascicularis*

	Majorx	Major sd	Minor x	Minor sd	R	N	Eplsar	Smfc	Hasfc 9	Hasfc 81	Asfc
N	13	13	13	13	13	13	13	13	13	13	13
Min	128.41	48.72	3.16	1.15	0.29	6	0.001	0.424	0.104	0.283	1.599
Max	356.55	256.03	4.48	2.21	0.75	114	0.005	1.769	1.15	4.444	18.55
Mean	181.852	113.095	3.624	1.374	0.517	39	0.003	0.898	0.392	0.866	5.742
S.D.	58.838	54.779	0.323	0.29	0.151	26.966	0.001	0.368	0.329	1.106	4.645

Results for SPECIES\$ = *Pr. thomasi*

	Major x	Major sd	Minor x	Minor sd	R	N	Eplsar	Smfc	Hasfc 9	Hasfc 81	Asfc
N	8	8	8	8	8	8	8	8	8	8	8
Min	95.61	56.26	2.05	0.79	0.29	15	0.002	0.564	0.31	0.384	1.542
Max	211.57	158.68	3.86	1.39	0.59	151	0.007	1.217	0.884	0.933	6.094
Mean	149.268	97.547	3.131	1.145	0.464	64	0.004	0.835	0.449	0.614	2.842
S.D.	31.794	33.36	0.52	0.207	0.126	54.24	0.002	0.223	0.188	0.174	1.449

Results for SPECIES\$ = *Pa. t. schweinfurthii*

	Major x	Major sd	Minor x	Minor sd	R	N	Eplsar	Smfc	Hasfc 9	Hasfc 81	Asfc
N	39	39	39	39	39	39	39	39	39	39	39
Min	117.36	53.712	2.35	0.253	0.226	3	0	0.319	0.1	0.192	0.488
Max	276.23	186.57	4.78	2.267	0.988	116	0.007	4.317	0.792	1.637	7.173
Mean	184.293	118.933	3.702	1.212	0.595	36.487	0.003	1.078	0.36	0.588	3.466
S.D.	36.49	36.509	0.577	0.364	0.194	28.608	0.001	0.666	0.177	0.261	1.57

Results for SPECIES\$ = *Pa. paniscus*

	Major x	Major sd	Minor x	Minor sd	R	N	Eplsar	Smfc	Hasfc 9	Hasfc 81	Asfc
N	21	21	21	21	21	21	21	21	21	21	21
Min	127.11	62.931	2.19	0.8	0.286	11	0.001	0.431	0.054	0.178	1.574
Max	232.87	167.858	4.32	1.359	0.775	93	0.006	2.432	0.627	0.802	8.799
Mean	173.456	116.674	3.361	1.116	0.553	37.429	0.003	0.918	0.25	0.422	3.655
S.D.	30.527	27.815	0.519	0.15	0.133	21.579	0.001	0.447	0.148	0.174	1.718