Relationship Between Dental Topography, Food Type and Jaw

Kinematics in Two Species of Non-Human Primates

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THESIS

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ii

TABLE OF CONTENTS

<u>CHAPTER</u>

<u>PAGE</u>

I. INT	TRODUCTION	1
1.1	Background	1
1.2	Specific Aims	4
1.3	Null Hypotheses	5
II. RE	VIEW OF LITERATURE	6
2.1	Dental Topography	6
2.1.1	The Link Between Diet and Dental Topography	6
2.1.2	Tooth Morphology of Cebus and Macaca	7
2.1.3	Dental Topographic Analysis (DTA)	11
2.2	Non-Human Primate Jaw Kinematics	13
2.2.1	Jaw Kinematics	13
2.2.2	Production of a Swallow Safe Bolus	13
2.2.3	The Chew Cycle and Slow Close (SC) Phase	14
2.2.3.1	1 Importance of the Slow Close ("Power Stroke") Phase	16
2.2.4	Jaw Kinematics of Cebus and Macaca	16
2.2.5	Food Material Properties (FMPs)	18
2.2.6	Effects of FMPs on Jaw Kinematics	19
2.2.7	Natural Diet of Cebus and Macaca Species Within the Wild	21
2.3	Occlusal Fingerprint Analysis (OFA)	23
2.3.1	Purpose and Application of OFA	23
III. N	MATERIALS AND METHODS	25
3.1	Dental Topography	25
3.1.1	Inclusion and Exclusion Criteria	25
3.1.1.1	1 Inclusion Criteria	25
3.1.1.2	2 Exclusion Criteria	26
3.1.2	High-Resolution 3D Digital Tooth Model Acquisition	26

3.1.3	Dental Topography Analysis (DTA) Software	28
3.1.3.1	Occlusal Surface Area and Occlusal Outline Area	28
3.1.3.2	2 Relief Index (RFI)	29
3.1.3.3	3 Dirichlet Normal Energy (DNE)	29
3.1.3.4	Orientation Patch Count-Rotated (OPCR)	30
3.2	Non-Human Primate Jaw Kinematics	32
3.2.1	Inclusion and Exclusion Criteria	37
3.2.1.1	I Inclusion Criteria	37
3.2.1.2	2 Exclusion Criteria	37
3.3	Occlusal Fingerprint Analysis (OFA)	
3.3.1	High-Resolution 3D Digital Tooth Model Acquisition	
3.3.2	Occlusal Fingerprint Analyzer (OFA) Software	
3.4	Data and Statistical Analysis	41
3.5	IRB Exemption and IACUC/ACUP Approval	42
IV. F	RESULTS	43
4.1	Dental Topography	43
4.1.1	Occlusal Surface Area	44
4.1.2	Occlusal Outline Area	44
4.1.3	Relief Index (RFI)	45
4.1.4	Dirichlet Normal Engery (DNE)	45
4.1.5	Orientation Patch Count-Rotated (OPCR)	46
4.2	Non-Human Primate Jaw Kinematics	47
4.2.1	Amount of Time from Ingestion to First Swallow	49
4.2.2	Number of Chews from Ingestion to First Swallow	51
4.3	Occlusal Fingerprint Analysis (OFA)	54
V. DIS	SCUSSION	57
5.1	Dental Topography	57
5.1.1	Occlusal Surface Area and Occlusal Outline Area	58
5.1.2	Relief Index (RFI)	59
5.1.3	Dirichlet Normal Energy (DNE)	60
5.1.4	Orientation Patch Count-Rotated (OPCR)	61

5.2	Non-Human Primate Jaw Kinematics	62
5.2.1	Amount of Time from Ingestion to First Swallow	63
5.2.2	Number of Chews from Ingestion to First Swallow	65
5.3	Occlusal Fingerprint Analysis (OFA)	67
5.4	Limitations of the Study	69
VI. C	CONCLUSIONS	71
6.1	Future Research	72
CITED	LITERATURE	74
APPEN	IDICES	81
Appen	dix A	82
Appen	dix A (Continued)	83
Appendix B		84
VITA		85

LIST OF TABLES

TABLI	<u>E</u>	<u>PAGE</u>
I.	FOOD MATERIAL PROPERTY QUANTITIES CITED IN PREVIOUS LITERATURE	20
II.	DENTAL TOPOGRAPHY VARIABLES DATA AND STATISTICS	47
III.	JAW KINEMATIC DATA AND STATISTICS – ANALYSIS OF DEVIANCE.	48
IV.	AMOUNT OF TIME FROM INGESTION TO FIRST SWALLOW – COMPARISON OF FOOD TYPE CONSUMED	49
V.	MEAN AMOUNT OF TIME FROM INGESTION TO FIRST SWALLOW - FOOD TYPES CONSUMED PER SPECIES	50
VI.	AMOUNT OF TIME FROM INGESTION TO FIRST SWALLOW – COMPARISON OF SPECIES AND FOOD TYPES CONSUMED.	51
VII.	NUMBER OF CHEWS FROM INGESTION TO FIRST SWALLOW – COMPARISON OF FOOD TYPE CONSUMED	52
VIII.	MEAN NUMBER OF CHEWS FROM INGESTION TO FIRST SWALLOW – FOOD TYPES CONSUMED PER SPECIES	53
IX.	NUMBER OF CHEWS FROM INGESTION TO FIRST SWALLOW – COMPARISON OF SPECIES AND FOOD TYPES CONSUMED.	53

LIST OF FIGURES

FIGURE		PAGE
1.	Photographs of Macaca mulatta vs. Cebus apella skulls	8
2.	Digital Cebus vs. Macaca maxillary first molars (M1)	10
3.	Dental topography variables	31
4.	Jaw kinematic model	35
5.	OFA occlusal dynamics	40
6.	Dental topography variables data	43
7.	Jaw kinematic data	48
8.	OFA occlusal contact area data	55
9.	OFA 3D kinematic output	56

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LIST OF ABBREVIATIONS

ACUP	Animal Care and Use Proposal
CEJ	Cementoenamel Junction
СТ	Computed Tomography
DNE	Dirichlet Normal Energy
DTA	Dental Topography Analysis
FMPs	Food Material Properties
GIS	Geographic Information System
IRB	Institutional Review Board
IACUC	Institutional Animal Care and Use Committees
IQR	Interquartile Range
M1	First Molar
M2	Second Molar
OFA	Occlusal Fingerprint Analysis
OPC	Orientation Patch Count
OPCR	Orientation Patch Count-Rotated
RFI	Relief Index

SUMMARY

The post-canine dentitions of living and extinct primates are enormously diverse and used for a wide range of behaviors, including ingestive behaviors to access protected foods, masticatory behaviors to reduce the food bolus, aggressive displays, and fighting. Functional dental morphology seeks to identify relationships between patterns in the occlusal surface of the teeth with the behavior for which the teeth are used. These relationships are clinically important for understanding the evolution of the primate feeding system because they drive hypotheses for reconstructing behaviors in the fossil records, and understanding the selective pressures driving variation in the dental morphology. The purpose of this study was to provide data and observations to help define the relationship of occlusal form and function of the dentition. This will be accomplished through the assessment of dental topography, jaw kinematics, and occlusal contact area. The occlusal contact area is a manifestation of the interaction between dental topography and jaw kinematics.

Primate skulls were digitally from the Du Brul Collection at the University of Illinois at Chicago College of Dentistry and The Field Museum of Natural History (Chicago) for analyzing occlusal morphology. Twelve (12) *Macaca* mulatta and twelve (12) *Cebus apella* each with a complete maxillary and mandibular arch were digitally scanned, standardized planes were created, and the first molars (M1s) were isolated.

ix

To assess dental topography, the isolated M1s were uploaded into the open source *MorphoTester* software to quantify topographic aspects of occlusal morphology to assess complexity. These topographic variables were 1. Occlusal surface area, 2. Occlusal outline area, 3. Relief Index (RFI), 4. Dirichlet Normal Energery (DNE), and 5. Orientation patch count-rotated (OPCR).

To assess jaw kinematics, feeding data from the same species previously collected at the University of Chicago was utilized to calculate *chewing efficiency*. For the purpose of this study, *chewing efficiency* was based on the rate of reaching a swallow safe bolus. This was compared as a metric for the amount of time from ingestion to first swallow or the number of chews from ingestion to first swallow. Food material properties (FMPs) were also considered a variable within the study. The FMPs tested were 1. *Soft* foods (low-toughness/low-stiffness), 2. *Dried Fruits* (high-toughness/low-stiffness), 3. *Nuts* (low-toughness/high-stiffness).

Finally, to assess occlusal contact area, the previously collected and isolated digital *Cebus* and *Macaca* M1s and the jaw kinematic data previously collected at the University of Chicago were uploaded into the open source *Occlusal Fingerprint Analyzer* (OFA) software. The OFA virtual simulator simulated and detected tooth contact during mastication. The occlusal contact area is presented as a percentage of molar cross-sectional area.

Results show that not only do *Cebus* and *Macaca* teeth look different, they have quantifiably different occlusal molar topographies, based on occlusal surface area, occlusal outline area, DNE, and OPCR. Also, *Cebus* molars are

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round and flat, while *Macaca* molars are more sloped and pointed. *Cebus* and *Macaca* jaw kinematic data reveal that both species take more time and more chews from ingestion to first swallow when eating foods similar to *Nuts*. However, *Macaca* chewed nearly twice as long as Cebus when consuming *Nuts*. Finally, OFA is an innovative and viable means to assess occlusal contact area – combining both tooth form and function. Comparatively, *Cebus* has an increased occlusal contact area compared to the *Macaca*. This difference is likely due to the difference in occlusal molar topographies. The greatest difference was noted with the bimodal distribution of the *Macaca*, predicting that the higher molar cusps are guiding their jaw kinematics.

I. INTRODUCTION

1.1 Background

The post-canine dentitions of living and extinct primates are enormously diverse and used for a wide range of behaviors, including ingestive behaviors to access protected foods, masticatory behaviors to reduce the food bolus, aggressive displays, and fighting. Functional dental morphology seeks to identify relationships between patterns in the occlusal surface of the teeth with the behavior for which the teeth are used. These relationships are clinically important for understanding the evolution of the primate feeding system because they drive hypotheses for reconstructing behaviors in the fossil records, and understanding the selective pressures driving variation in the dental morphology.

Morphological characteristics of the occlusal surface of the teeth, have been found to be linked to diet in mammals (primates) (Allen et al., 2015; Anapol and Lee, 1994; Kay, 1975; Ledogar et al., 2013; Rosenberger and Kinzey, 1976; Strait, 1993; Yamashita, 1998). For example, insectivorous and folivorous primates were found to have steeply sloped cusps forming acute shearing surfaces while frugivorous primates, including hard object feeders, were found to have flatter cusps adapted for crushing and grinding (Kay and Hiiemae, 1974; Kinzey, 1978; Rosenberger and Kinzey, 1976; Seligsohn and Szalay, 1978). The most commonly used metric to describe the occlusal morphology in primates is the shearing quotient, a relative measure of the shearing edges of molars (Kay, 1975; Kay and Covert, 1984). However, this metric has shortcomings. The

shearing quotient metrics relies heavily on identifiable occlusal landmarks, and does not take into account the comprehensive topography of the tooth. In addition, the shearing quotient is largely affected by tooth wear. As cusp tips become worn, the crest used for the metric becomes impossible to determine (Ungar and Bunn, 2008). To address this concern, new methodologies have been developed for characterizing and comparing the shape of teeth with variable level of wear. These methodologies are based on the development of 3D digital imaging technology (e.g., CT scans, surface 3D scanners) and the metrics are promising in describing complex occlusal morphologies (e.g., (Dennis et al., 2004; Jernvall and Selänne, 1999; Ungar and Williamson, 2000; Ungar and M'Kirera, 2003). Use of these methods in a comparative context has identified several key *dental variables* that correlate strongly with diet, confirming previously identified patterns (Bunn and Ungar, 2009). Thus, diet and food material properties appear to have a strong influence on variation in the *dental* variables describing tooth morphology (i.e. tooth "topography").

Why certain dental topographies are advantageous for certain food types has yet to be fully resolved. This is partially due to the complicated relationship between dental topography and occlusion. The spatial distribution and topography of the posterior dentition form distinct contact areas, and these contact areas change as the approach angle of the jaw changes. Jaw movements in primates are highly variable, with differences identified between species and in response to food material properties (Iriarte-Diaz et al., 2011). Thus, to understand why certain dental topographies are advantageous for

certain food types, dental topography must be considered in the contact of the three-dimensional movement of the mandible (i.e. jaw kinematics).

Together, dental topography and jaw kinematics act in concert to break down the food bolus. Minimizing the time spent chewing before a swallow is hypothesized to be advantageously selective. The faster an organism can create a *swallow safe bolus* (Prinz and Lucas, 1997), the faster the rate of nutrient assimilation and lowering the overall feeding time to meet daily caloric requirements. Feeding time is an established and critical variable in the health and wellness of all primates. Some gorillas can spend up to 80% of their day feeding (Ross et al., 2009). Thus optimizing the maximum intercuspation of teeth in a food material property dependent manner could lower feeding time, and be a strong selective force for determining dental topography.

From a biologic standpoint, the goal of mastication is to break down and process foods into a *swallow safe bolus* which can then be used by a living organism to sustain form and function. The overall objective of this thesis is to determine if variation in dental occlusal topography is correlated with variation in feeding time and if this relationship depends on the material properties of the food. To address this objective, dental variables describing the dental topography, kinematic variables describing feeding time, and functional variables describing occlusal dynamics were quantified in two species of non-human primates, *Cebus apella* and *Macaca mulatta*. These two species have different dental topographies which were ideal for this analysis. *Cebus* are new world primates with low cusps similar to humans and are considered hard object

feeders (Iriarte-Diaz et al., 2011). *Macaca* are old world primates with high cusps, and are considered more generalized feeders (Iriarte-Diaz et al., 2011). Both species were fed food items grouped into one of three categories: foods with low-toughness/low-stiffness (e.g., soft foods, such as grapes), foods of hightoughness/low-stiffness (e.g., dried fruits), and foods of low-toughness/highstiffness (e.g., nuts). The data collected were used to test three hypotheses regarding dental topography, jaw kinematics and occlusal dynamics.

1.2 Specific Aims

The goal of this study was to determine if variation in occlusal tooth topography is related to variation in feeding time and if this relationship depends on the material properties of food. A comparative analysis will be made between the jaw kinematics and feeding time of two species of non-human primate species, *Cebus apella* (*Cebus*) and *Macaca mulatta* (*Macaca*), each presenting with contrasting occlusal tooth topographies. Occlusal contact area will be constructed and assessed utilizing an innovative three-dimensional digital imaging software, the *Occlusal Fingerprint Analyzer* (DFG FOR 771, ZiFiLo IT Ltd., Ober-Ramstadt, Germany) (Kullmer et al., 2009). Ultimately, the goal would be to define the relationship of occlusal form and function of the dentition.

1.3 Null Hypotheses

- There is no mean difference in quantifiable first molar (M1) dental topography variables [occlusal surface area, occlusal outline area, relief index (RFI), Dirichlet normal energy, and occlusal patch count-rotated (OPCR)] when comparing two non-human primate species, *Cebus apella* and *Macaca mulatta*.
- There is no mean difference in feeding time and number of chews from ingestion to first swallow between two non-human primate species, *Cebus apella* and *Macaca mulatta*, when comparing the consumption of lowtoughness/low-stiffness foods, high-toughness/low-stiffness foods, and low-toughness/high-stiffness foods.
- There is no difference in the amount of occlusal contact area during the period of power stroke into maximum intercuspation between two nonhuman primate species, *Cebus apella* and *Macaca mulatta*, when comparing the consumption of low-toughness/low-stiffness foods, hightoughness/low-stiffness foods, and low-toughness/high-stiffness foods.

II. REVIEW OF LITERATURE

2.1 <u>Dental Topography</u>

2.1.1 The Link Between Diet and Dental Topography

Dental topography is capable of generating ample information in regards to the lifestyle habits of an individual. Physical form closely follows function when comparing dental topography to specific diets of that individual, so much so that the term "dental ecology" was coined by Cuozzo and Sauther (2012) to explain how teeth are affected physically by the foods consumed by individuals and likewise how environmental changes may affect this relationship. Ungar (2010) once said, "Show me your teeth, and I will tell you who you are". From an anatomical standpoint, although they are not bone, teeth are the bridge between the internal skeleton of an individual and that individual's outside environment (Schwartz and Dean, 2000). Even though "dental ecology" is a newly coined term, this concept dates back before Darwin. In 1833, Darwin noted analogous associations in regard to an extinct species of mammals, namely "The teeth indicate, by their simple structure, that these Megatheroid animals lived on vegetable food, and probably on the leaves and small twigs of trees" (Quammen, 2009). Vogel et al. (2008) performed a study comparing the dental morphology of chimpanzees and orangutans to the food material properties of the non-human primates' diet found in their habitat. The study compared previously recorded dental morphology of these species to a live population of non-human primates. The wear patterns and changes to the dental topography were explained by the

observation that "the fallback foods actually consumed by orangutans are indeed harder and thus more mechanically challenging than those of chimpanzees" (Vogel et al., 2008). If this idea were conceptualized nearly two decades ago, why are so many fields (including but not limited to anthropology, primatology, paleontology, and mammalogy) still so fascinated by the study of teeth and the "dental ecology" of various species of animals? Today's technological advancements are moving research on this topic to a whole new level.

2.1.2 Tooth Morphology of Cebus and Macaca

Through physical observation the occlusal morphology of the *Cebus* and *Macaca* species of non-human primates is already known. Upon examination, the immediately glaring difference between the two dentitions would be that the *Macaca mulatta* (Figure 1a) have minute canine teeth compared to the more robust canines of the *Cebus apella* (Figure 1b). Additionally, the *Macaca* only have two sets of post-canine pre-molar teeth (Figure 1c); while the *Cebus* have three sets of pre-molars (Figure 1d).



Figure 1. Photographs of Macaca mulatta vs. Cebus apella skulls

Figure 1: Photographs exhibiting anatomical differences between the Macaca versus Cebus skulls. Macaca (Figure 1a/c) samples courtesy of Dr. E. Lloyd Du Brul Collection (College of Dentistry, University of Illinois at Chicago) and Cebus (Figure 1b/d) samples courtesy of Field Museum of Natural History (Chicago).

For purposes of this study, we are focusing more on the occlusal

morphology of the first molars (M1). While the Cebus have more rounded and

flattened molar occlusal surfaces; the Macaca have higher, more pointed molar

cusps (Figure 2). As discussed in section 2.2.7 (Non-Human Primate Jaw

Kinematics – Natural Diet of Cebus and Macaca Species in the Wild), both the

Cebus and Macaca are labeled "omnivores" according to Gron (2009). It is understood that both species exhibit tendencies of insectivores, folivores and frugivores: however, the "primary" foods exhibited within in their diets vary based on multiple factors. Diets vary greatly based on the habitat in which the animal resides, weather and seasonal changes, intra- and inter-species competition, and cohabitation with humans. Previous studies have been performed on several other species of non-human primates linking their diets to their patterns of occlusal morphology (Kay and Hijemae, 1974; Rosenberger and Kinzey, 1976; Seligsohn and Szalay, 1978). Similarly, we can use the general associations made between diet and patterns of occlusal morphology for both the Cebus and Macaca species. In general, "reciprocally concave, highly crested teeth have been associated with insectivorous and folivorous diets, whereas rounded or flatter cusped teeth have been associated with a more frugivorous diet" (Ungar, 1998). Great consideration must be made to not over simplify the categories of food consumption. Although a particular occlusal morphology may insinuate the consumption of a primary food type, the topography is as equally affected by those foods which are not eaten as frequently (Kinzey, 1978; Ungar, 1998).

Mechanically speaking, the occlusal morphology of molars affects the rate at which food material properties are capable of being broken down and subsequently ingested. The rounded and flattened cusps are more suited for crushing and grinding; whereas the high, pointed cusps are more effective in shearing and tearing (Figure 1). Ungar (1998) and Kay and Sheine (1979) summarized the link between diet and occlusal morphology:

"The molars of leaf- and insect-eaters reflect the fact that plant fiber and insect chitin form resistant, almost two-dimensional sheets and rods that are more efficiently broken by shearing than by crushing. Moreover, chitin and leaf cellulose are both structurally complex and present similar challenges to the digestive tract. In contrast, frugivores consume more crushable three-dimensional fruits and nuts, which often contain proteins and easily digested simple sugars. Because shearing crest length correlates inversely with chewed particle size, and because more finely ground particles are digested more completely, it makes sense that a diet of leaves or insects should select for longer-crested teeth."



Figure 2. Digital Cebus vs. Macaca maxillary first molars (M1)

Figure 2: Digital examples the first molars (M1) of Cebus vs. Macaca, scanned with Lythos[™] Digital Impression System (Ormco Corporation, Orange, CA). These images were viewed and oriented within the open-source MeshLabs advanced 3D mesh processing software. Note the more rounded and flattened cusps of the Cebus maxillary M1 compared to the high, pointed cusps of the Macaca maxillary M1.

As a result, we hypothesize that Cebus apella have an occlusal

morphology indicative of a frugivorous, hard object diet, while Macaca mulatta

have an occlusal morphology indicative of a more generalized frugivorous and

folivorous diet.

2.1.3 Dental Topographic Analysis (DTA)

Dental topographic analysis (DTA) is a relatively new method of analyzing tooth morphology, more specifically looking at the change in function as teeth increase in wear. Paleoprimatologists have used this method to compare form and function while deducing diet from the tooth morphology (Bunn and Ungar, 2009). Prior to such advancements in technology, studies were mostly performed on unworn teeth, since it was easier to compare and measure teeth with little to no wear (Ungar and Williamson, 2000). In order to perform a DTA on a tooth, a platform must be used to assess, measure and quantify the morphology of the tooth surface. Through utilizing a geographic information system (GIS) these data are able to be collected. "GIS is an approach used to compare layers of different types of data connected by locations in geographic space" (Ungar and Williamson, 2000). The technology implemented with GIS is not new; in fact, various government agencies, geologists, biologists, and urban planning specialists have used this technology in their respective fields. GIS has been used by these specialists to map the topography of the earth while rendering, analyzing, and manipulating the data collected as they see relevant. Through innovative thinking, transitioning this technology to analyze dental morphology seems to make sense. Three-dimensional analysis of a tooth surface can be compared to the topography of the earth's surface; tooth cusps are similar to mountains, and pits/fissures are similar to valleys and basins (Ungar and Williamson, 2000). Reed (1997), Zuccotti et al. (1998), Jernvall and

Selänne (1999), and Ungar and Williamson (2000) used GIS technology within their own research of non-human primate dental morphology.

When analyzing dental topography tooth wear must be considered as a factor which changes over time. It is important to remember that teeth may start out flatter to begin with, so when comparing the overall change in slope (i.e. – delta slope or angularity) over time, they may flatten less with wear (Benefit, 1987; Delson, 1975). Previous studies reported no differences between the taxon and the specific stage of wear, meaning that the shape of teeth wear consistently throughout the wear process (M'Kirera and Ungar, 2003; Ungar and M'Kirera, 2003). However, it was concluded that the buccal and lingual cusps of teeth wear away at different rates, the buccal wears away more rapidly than the lingual (Ungar and Williamson, 2000). In the human dentition, genetics plays a role in the hardness of the enamel layer on the tooth. Similarly, a study performed by Ulhaas et al. (2004) on the Cercopithecine primate species, revealed that they presented with a thicker enamel layer compared to the Colobine primate species; this resulted in less change in the shape of teeth over time (Ulhaas et al., 2004). The occlusal topography of primates is said to be based heavily by dietary categories consumed by that taxon (M'Kirera and Ungar, 2003; Ungar and M'Kirera, 2003). It can be anticipated that as time passes, wear may decrease the overall slope of the tooth cusps, permanently changing the dental topography.

2.2 Non-Human Primate Jaw Kinematics

2.2.1 Jaw Kinematics

Occlusal dynamics is affected not only by the topography of the occlusal surface, but also the movement of the mandibular molars relative to the maxillary molars. As such, the kinematics of the jaw play an important role in regulating the period of power stroke into maximum intercuspation during mastication. In this thesis, kinematics are defined as a change in position between the mandible relative to the maxilla during mediolateral shift of the slow close phase of the chew cycle. In general, mammalian mastication breaks down food into smaller particles, yet at the same time increasing the surface area of the food particles for maximum nutrient intake and resulting in an increased energy output (Prinz and Lucas, 1997). In nature, mammalian jaw kinematics is essential for well-being and overall survival.

2.2.2 Production of a Swallow Safe Bolus

The concept of chewing a piece of food to break it down for metabolic absorption, is somewhat simple. However, dissecting the minute details of the initiation and termination process of mastication is a topic of countless scientific studies. Prinz and Lucas (1997) studied the terminal result of jaw kinematics, the "swallow safe bolus," prior to process of nutrient absorption of the mammalian body. The preparation of the "swallow safe bolus" was given the task of dictating when a human can transition from the mastication process to the initiation of the

swallowing mechanism (Prinz and Lucas, 1997). The term "swallow safe" dictates the optimal time a mammal is prepared to begin the process of swallowing. This ideal time is determined by a ratio combination of food particle size and particle lubrication forming the bolus (Prinz and Lucas, 1997). Several elements have a direct effect on bolus formation: the tongue, cheeks/soft tissue musculature, teeth, palate, jaw kinematics, and salivary production. If over manipulation and excessive salivary production occurs, the bolus begins to break apart and the optimum moment to swallow is lost (Prinz and Lucas, 1997). From a standpoint of efficiency, the concept of the "swallow safe bolus" is a regulating mechanism which ensures safe passage of the ingested food into the digestive tract for absorption.

2.2.3 <u>The Chew Cycle and Slow Close (SC) Phase</u>

The chew cycle has been the topic of immense research in the past. One of the founding-fathers of such research was K.M. Hiiemae. Hiiemae (1978) defined the complex, cyclic jaw movements I into series of "gape cycles" which occur within the oral apparatus while interacting with the tongue muscles. The entire process of mastication involve movements of the mandible and the tongue which are regulated by afferents sensorimotor controls (Lund, 1991). The gape cycles can be characterized by the food changing position within the oral apparatus. The "ingestion cycle", begins the process of chewing as food enters the oral cavity from the external environment; the manipulation stage, depicts the time in which the tongue and buccal mucosa come in contact with the food

particles; "stage 1 transport cycle", is the movement of food past the point of ingestion to the posterior of the oral cavity to begin mastication; "stage 2 transport cycle" is the movement of a swallow safe food bolus from the posterior oral cavity into the oropharynx region, initiating the process of swallowing (Hiiemae and Kay, 1973). In mammals, a single open-close sequence of feeding has been broken down into cycle phases. This cycle was first defined in "Hiiemae's four gape-cycle phases"(Hiiemae, 1978):

- 1) Fast close (FC)
- 2) Slow close (SC)
- 3) Slow open (SO)
- 4) Fast open (FO)

The slow close (SC) or "power stroke" phase begins once food comes in contact with the teeth in conjunction with the slower closing movements of the mandible. The point at which the least amount of space is between the maxillary and mandibular teeth, is termed "minimum gape." This is the point at which the mandible starts slow opening (SO). Next is the transition into a fast open (FO) which is the point (if a swallow safe bolus has formed) where the tongue initiates the process of the swallow. "Maximum gape" is the transition from the fast open (FO) to the fast close (FC), also the point at which the cycle begins again (Hiiemae, 1978).

2.2.3.1 Importance of the Slow Close ("Power Stroke") Phase

For the purpose of this research, the phase of interest is the "slow close" (SC) or "power stroke" phase. The SC is the point at which the teeth come in contact with the food (Hiiemae, 1978). The greatest amount of variation occurs within this phase, particularly due to the great variation in period of power stroke into maximum intercuspation and occlusal topography when comparing individuals and between species. This study is attempting to compare the differences in occlusal topography between two species of primates, *Cebus* vs. *Macaca*. Previously collected jaw kinematic data from the University of Chicago provided a means to assess various food material properties (FMPs) against the non-human primates' occlusal topography are dynamic factors between the two species of non-human primates, and together they exert an effect on the SC phase of the chewing cycle.

2.2.4 Jaw Kinematics of Cebus and Macaca

It is known that the SC phase of the chew cycle results in the mastication of the food bolus for both species of *Cebus* and *Macaca*. However, variable jaw kinematics exists between the two species. Anatomically, *Cebus* and *Macaca* have nearly the same general skeletal and muscular structure, yet differ from one another in jaw length: *Macaca* 84.87mm and *Cebus* 57.53mm (Ross et al., 2009). When assessing occlusal dental topography, *Cebus* present with flatter cusps when compared to the more steeply cusped *Macaca*. The purpose of this

study is to provide insight as to how all of these variables affect the jaw kinematics in these two non-human primates.

Several sources state that foods which are characterized as *tough* must be broken down in the slow close (SC) phase of chewing utilizing increased horizontal jaw kinematics (Agrawal et al., 2000; Agrawal et al., 1997; Lucas, 2004; Lucas et al., 2002). However, Reed and Ross (2010) did not witness these same lateral displacements in a *Cebus* sample; rather the opposite occurred, and low-toughness foods elicited increased horizontal and smaller vertical kinematics (Reed and Ross, 2010). These increased horizontal movements were noted in the first several chews of the chew cycle. As the chew number increases and the food bolus is mechanically broken down, resulting in a decrease in the horizontal jaw kinematics. Iriarte-Diaz et al. (2011) stated, "Reed and Ross (2010) hypothesized that longer durations of cycle are needed when chewing on low-toughness foods because such foods fragment faster, requiring more complex tongue movements to manipulate the larger number of fragments."

Jaw kinematics vary between species. However, previous studies (Foster et al., 2006; Vinyard et al., 2008) support "inter-cycle, intra-sequence variation in jaw kinematics likely reflects variation in external physical attributes of the bolus, including adhesive and cohesive properties, size and shape, which vary through the chewing sequence" (Iriarte-Diaz et al., 2011). It was proposed by Thexton et al. (1980) that harder foods are placed more posteriorly within the mouth to provide a more favorable mechanical advantage at the temporomandibular joint, and this resulted in more vertical jaw movements. However, Iriarte-Diaz et al.

(2011) determined that irrespective of the food being consumed, the Macaca species demonstrated increased vertical jaw movements along with increased duration of the SC phase (Iriarte-Diaz et al., 2011). It is hypothesized that the more steeply cusped occlusal topography of the Macaca teeth could be a physical factor guiding the vertical jaw kinematics of the species. The flatter occlusal surface of the *Cebus* may make allowances for a more variable gape cycle compared to the cusp guided kinematics of the Macaca. Data collected from Iriarte-Diaz et al. (2011) suggest that when feeding on low-toughness foods, the more sporadic jaw kinematics of the *Cebus*, which may be driven by a flatter occlusal topography, can decrease the number of chew cycles by virtually half when compared to the *Macaca* data. When consuming low-toughness foods, the interquartile range (IQR) for number of chew cycles was 30-57 (Macaca) versus 16-33 (Cebus) (Iriarte-Diaz et al., 2011). Through the analysis of Cebus and Macaca dental topography, this study may present quantifiable variables affecting the kinematics of mammalian food processing.

2.2.5 Food Material Properties (FMPs)

Published food material properties (FMPs) attempt to categorize and quantify foods into groups based on their *stiffness* and *toughness*. *Stiffness*, or Young's modulus of elasticity (E), defines the relationship of stress (force) and strain (point of deformation) for a material (Agrawal et al., 2000; Lucas, 2004). *Toughness*, or resistance to fracture (R), is the ability of a material to absorb energy and resist fracture (Agrawal et al., 2000; Lucas, 2004). Based on

comparative studies previously performed comparing FMP values, *stiffness* is inversely proportional to *toughness*, and vice versa (Agrawal et al., 2000; Agrawal et al., 1997; Ross et al., 2009). Although *E* and *R* are always calculated in FMP studies, \sqrt{ER} and $\sqrt{R/E}$ are said to provide more accurate quantities for *hardness* and *toughness* approximation, respectively (Ashby, 1989).

In the study performed by Reed and Ross (2010), the primates were fed two categories of foods: 1) high-toughness/low-stiffness and 2) lowtoughness/high-stiffness. Specifically, the *Cebus apella* were fed hightoughness/low-stiffness foods, including apricot, date, gummy bear, pineapple, and raisin; and low-toughness/high-stiffness foods, including almond, brazil nut, cashew, hazelnut, peanut, pecan, popcorn kernel, and walnut. The *Macaca mulatta* were fed high-toughness/low-stiffness foods, including carrot, date, raisin, and sweet potato; and low-toughness/high-stiffness foods, including almond, hazelnut and popcorn kernel. The non-human primates were trained to feed themselves under retrained and controlled conditions (Reed and Ross, 2010). For the purposes of this study, the same methods of assessing and quantifying FMPs were utilized.

2.2.6 Effects of FMPs on Jaw Kinematics

The length of the chew cycle is dictated by the amount of time it takes for a food bolus to be broken-down. As reported by Reed and Ross (2010), food material properties (FMPs) directly affect this fragmentation process. According

to Iriarte-Diaz et al. (2011), the only statistically significant effect FMPs had on the jaw kinematics was on the lateral displacement of the mandible during the chew cycle. For both *Cebus* and *Macaca*, the total lateral displacement of the mandible was higher when feeding on low-toughness foods than for hightoughness foods. These differences were due to an increase of the lateral displacement during the SC phase of the chew cycle (Iriarte-Diaz et al., 2011).

TABLE I

FOOD MATERIAL PROPERTY QUANTITIES CITED IN PREVIOUS LITERATURE. CITATIONS ARE BELOW THE FOOD IN PARENTHESES.

Types of Food	Stiffness (E)	Toughness (R)	√ <i>ER</i>	√ <i>R/E</i>
LOW-Toughness				
HIGH-Stiffness				
Brazil nut	33.84	160.8	73.76	2.17
(Agrawal et al., 2000)				
Hazel nut	12.2	166.2	45.02	3.69
(Agrawal et al., 1997)				
Almond	8.7	105.7	37.4	4.29
(Ross et al., 2009)				
HIGH-Toughness				
LOW-Stiffness				
Dried apricot	5.95	830.04	70.27	11.81
(Ross et al., 2009)				
Date	3.15	964.63	55.12	17.49
(Ross et al., 2009)				
Dried pineapple	2.37	1058.65	50.08	21.13
(Ross et al., 2009)				

 TABLE ADAPTED FROM (Reed and Ross, 2010)

Note: *E* unit of measure: Pascal (Pa or N/m² or m⁻¹·kg·s⁻²)

• *R* unit of measure: J·m⁻³·10⁴

• \sqrt{ER} = "Hardness" estimation; $\sqrt{R/E}$ = "Toughness" estimation

2.2.7 Natural Diet of Cebus and Macaca Species Within the Wild

There are multiple publications citing the natural diet of both primate species, *Cebus apella* (Galetti and Pedroni, 1994; Izawa, 1979) and *Macaca mulatta* (Goldstein and Richard, 1989). Although certain non-human primates are indigenous to particular areas, diet is influenced heavily by their habitat location as well as seasonal availability of the foods which are being consumed. A study regarding the seasonal diets of the *Cebus* was performed in the semi-deciduous forest in southeastern Brazil. The study was conducted for 44 consecutive months, resulting in 367 feeding occurrences (Galetti and Pedroni, 1994). The *Cebus* was cited to eat a total of 71 different plant species, and the combined records of their frugivorous primate diet was broken down as follows: 53.9% consumption of fruit pulp; 16% consumption of seeds; 11.1% consumption of flowers; 6.3% consumption of leaves and new shoots; 1.5% consumption of roots; 13.9% consumption of plantations surrounding the forest (Galetti and Pedroni, 1994).

Living in Brazil, the *Cebus* also has to battle the seasonal changes involved with living in that habitat. In the semi-deciduous forests of Brazil, the two main seasons are the wet and dry season. During the dry season, the abundance of life which normally fills the forest turns rather scarce. There is a decrease in the fleshy fruits which the *Cebus* typically consume (Galetti and Pedroni, 1994). As a result, the *Cebus* predominantly consume seeds and flowers at this time (Galetti and Pedroni, 1994). It was also noted in this study that the *Cebus* seem to intentionally avoid the limited fruits which are available

during the dry season. It was concluded, that the *Cebus* chose to avoid these fruits due to high competition between themselves and other frugivorous vertebrates (including: Howler monkeys, parrots, squirrels, etc.) (Galetti and Pedroni, 1994).

A similar behavioral study was conducted on *Macaca mulatta* in northwestern Pakistan. Over a three-year period (1978-1981), the combined records of the folivorous diet of the *Macaca* was revealed to consist primarily of 11 different plant species (however 24 other plant species were observed to be occasionally eaten) (Goldstein and Richard, 1989).

For both species of primates, there were fluctuations of foods available during the different seasons. Both *Cebus* and *Macaca* species, in the summer months and wet season, shift to a more fruit-based diet. *Cebus* remained fairly consistent in maintaining a frugivorous type diet; while the *Macaca* predominantly consumed a folivorous type diet. As habitats change, these species of primates are left to adapt to the ever-changing world around them. Both species of wild non-human primates maintain their dietary preferences. However, as their frequency of interactions with humans increase, industrialized dietary changes have also been seen to affect these species (Gron, 2009).

2.3 Occlusal Fingerprint Analysis (OFA)

2.3.1 Purpose and Application of OFA

Paleontologists, anthropologists, mammologists, and even forensic dentists all have a common interest between their varied lines of work. Each have an interest of studying living (as well as deceased) things to assess where they have come and how they evolved. If found, a tooth is a piece of the mammalian body which is capable of answering ample questions of past diet and overall fitness of that individual. Forensic dentists are even capable of identifying individuals based solely off of a previous dental record and dental remains which may be found.

The advancements made in technology have allowed for information to be gathered and shared at a faster rate than ever before. High resolution threedimensional modeling allows for samples to be studied in a way which does not harm the original specimen (Kullmer et al., 2009). History is able to be preserved while countless questions are able to be answered. More specifically, it is a commonly known fact that as time passes tooth enamel wears down, or undergoes tooth abrasion. This abrasion has been used by scientists to determine the jaw kinematics and the specific diets of that individual. The objective of the *Occlusal Fingerprint Analyzer* (OFA) (DFG FOR 771, ZiFiLo IT Ltd., Ober-Ramstadt, Germany) as stated by the developers in 2010: "The objective of the OFA [is to assess] the 'Function and increased efficiency in the dentition of mammals – phylogenetic and ontogenetic influences on the chewing apparatus." Making the study of "the influence of tooth morphology on jaw

movement throughout mammal phylogeny and ontogeny" possible (Kullmer et al., 2009). "The OFA provides an individual three-dimensional dental occlusal compass that indicates the major pathways of interaction between antagonists, revealing information about development, spatial position, and enlargement of wear facets" (Kullmer et al., 2009). The software developers went on to explain that "the software's open source license permits users to improve the programs, specializing it for various specific needs and purposes;" including being used by dental clinicians for the purpose of "reconstructing tooth surfaces" (Kullmer et al., 2009). From the perspective of occlusal articulation, orthodontics, prosthodontics, and restorative dentistry the applications for OFA (DFG FOR 771, ZiFiLo IT Ltd., Ober-Ramstadt, Germany) research within the dental profession are infinite.

III. MATERIALS AND METHODS

3.1 <u>Dental Topography</u>

Twelve (N=12) *Cebus apella* maxillae and mandibles were collected from the non-human primate archives of the Field Museum of Natural History (Chicago) and twelve (N=12) *Macaca mulatta* maxillae and mandibles were collected from the Dr. E. Lloyd Du Brul Collection (College of Dentistry, University of Illinois at Chicago).

3.1.1 Inclusion and Exclusion Criteria

3.1.1.1 Inclusion Criteria

- Prior to data collection, *Cebus* and *Macaca* specimen were evaluated to confirm species type.
- The Cebus and Macaca maxillary and mandibular jaws were evaluated for completeness of their dentition. The specimen must have had a full complement of teeth at least through the second molars (must have presented with incisors, canines, pre-molars, and the first and second molars).
 - Specimens were accepted if they presented with minimally broken/chipped anterior incisors.
- A factor which must be considered: *Cebus* present with three sets of post-canine pre-molar teeth; while the *Macaca* only present with two sets of pre-molars.
- Maxillae and mandibles must be capable of being hand articulated with a firm posterior maximum intercuspation.
- For purposes of record keeping, male and female specimen were noted, however no final statistics were calculated separating males and females.

3.1.1.2 Exclusion Criteria

- Any specimen with broken mandibles, maxillae, and/or condyles were excluded from this study.
- Any specimen missing teeth anterior to the third molars (must have had a full complement of incisors, canines, pre-molars, and the first and second molars) were excluded.
- Any specimen with moderately broken/chipped posterior teeth (premolars and molars) were excluded.

3.1.2 High-Resolution 3D Digital Tooth Model Acquisition

Data acquisition was performed utilizing the Lythos[™] Digital Impression System (Ormco Corporation, Orange, CA). High resolution scans were taken of the maxillary (N=12) and mandibular (N=12) dentitions for the twelve specimen (Total digital scans = 24 per species) in each species. The scan included the complete occlusal, buccal, and lingual surfaces of each tooth within the nonhuman primates' oral apparatus. Due to the interproximal tooth contacts, the mesial and distal surfaces were incomplete; this incomplete data set was digitally reconstructed post-data collection. The maxilla and mandible were then placed in maximum intercuspation. The condylar position and wear facets on the teeth were considered when placing the maxilla and mandible into their proper maximum intercuspation. A posterior to anterior buccal digital scan of the maximum intercuspation (from the specimens' most posteriorly occluding molar through the canine) was taken to confirm the interaction between the maxillary and mandibular dentition. The final scans were assessed for errors and any erroneous digital scatter was removed from the final digital impression.

Further analyses were focused on the occlusal characteristics of the first maxillary and mandibular molars (M1) which were digitally isolated and processed using Geomagic[®] Control[™] (3D Systems, San Jose, CA). Although the M1 and second molar (M2) are similar in shape, the M1 is the tooth of interest rather than the M2 due to differences in their eruption pattern as well as their location in the jaw (Bunn and Ungar, 2009). For each individual model, once M1 was isolated, the model was cropped to include only the tooth crown based on the location of the cementoenamel junction (CEJ). A plane was fitted through the CEJ and the model was rotated so that this plane was parallel to the X-Y (horizontal) plane and the crown was pointing upwards. After the individual teeth were reoriented, the mesial and distal surfaces of the isolated model were digitally reconstructed in Geomagic® Studio[™] (3D Systems, San Jose, CA), using a predicted mesh generation with a tangent method that creates a new mesh which matches the curvature of the surrounding mesh. Finally, the meshes were simplified to 10,000 polygons to allow comparisons between teeth of

different size. Again, the images were assessed for errors and any erroneous digital scatter was removed. The final isolated models were saved as a 3D mesh PLY format that was used for dental topographical analyses (DTA).

3.1.3 Dental Topography Analysis (DTA) Software

To evaluate the overall differences in occlusal morphology, five dental topography variables were measured using the open source MorphoTester scientific computing software (Winchester, 2016). These dental variables were: 1) occlusal surface area, 2) occlusal outline area, 3) relief index (RFI), 4) Dirichlet normal energy (DNE), and 5) orientation patch count-rotated (OPCR).

3.1.3.1 Occlusal Surface Area and Occlusal Outline Area

The occlusal surface area corresponds to the three-dimensional area of the occlusal surface of the teeth. In contrast, the occlusal outline area corresponds to the two-dimensional area of the occlusal surface projected into the occlusal plane calculated in the previous section. Thus, the occlusal surface area will always be larger than the occlusal outline area, because the first accounts for the vertical slopes and inclinations of the occlusal surface. By themselves, these variables are not useful for distinguishing either feeding behaviors or phylogenetic groups because they are strongly correlated with body size. These variables were measured in mm².

3.1.3.2 Relief Index (RFI)

RFI is defined simply as the ratio between the occlusal surface and the occlusal outline areas (Boyer, 2008; Ungar and M'Kirera, 2003; Winchester, 2016). RFI is a measure of the relative occlusal surface area. Because the occlusal surface area is always larger than the occlusal outline area, the RFI will always be larger than 1. The larger the RFI, the larger the relative occlusal surface area. Since the RFI is the ratio between areas, the variable will be without a unit of measure. Tooth wear must be considered when assessing RFI, being that the three-dimensional occlusal surface area is reduced over the lifetime of mastication (Evans, 2013). It has been shown that RFI can differentiate based on dietary habits of some primates (Boyer et al., 2010; Bunn et al., 2011).

3.1.3.3 Dirichlet Normal Energy (DNE)

DNE can briefly be described as a quantification of the curvature (or deviation of the surface from a plane) of the occlusal surface (Bunn et al., 2011; Evans, 2013; Winchester, 2016). Thus, the more complex or curved the surface, the higher the DNE. DNE has the advantage of being independent of position, orientation and scale, and it is without units of measure. Additionally, it can provide overall measures of local curvature over crests and flat surfaces. This measure is highly correlated with RFI (Evans, 2013).

The MorphoTester software assigns a color gradient based on the level of local curvature (Figure 3c/d/i/j). This color gradient allows for visualization of the areas with the most curvature (e.g., cusp tips and occlusal valleys) to the areas with the least curvature (e.g., more flat, sloping regions and areas which express patterns of wear) when viewed in a two-dimensional form. The areas with the most curvature were assigned *red*, followed by *orange*, *yellow*, *green*, and *blue* was assigned to the areas with the least curvature on the tooth's crown (Figure 3c/d/i/j).

3.1.3.4 Orientation Patch Count-Rotated (OPCR)

Orientation patch count (OPC) can be defined as the number of regions ("patches") on a surface where neighboring polygons in a patch are facing in the same direction (Evans et al., 2007). OPC can be understood as a metric that quantifies the complexity of the surface, i.e., viewed as the variation in the slopes and angulations of the surface (Evans, 2013; Winchester, 2016). This variable can potentially be affected by the orientation of the model on the occlusal plane, so a modified variable was created by rotating the model multiple times, calculating the OPC for each rotation and then averaging those values (Winchester, 2016). This is called the orientation patch count-rotated (OPCR) (Winchester, 2016). OPCR organized these patches quantitatively and assigns them a color that is coordinated into a map for analysis (Figure 3e/f/k/l). Similar to RFI, tooth wear must be considered when assessing OPCR, being that the

three-dimensional occlusal surface area is reduced over the lifetime of mastication (Evans, 2013).





<u>Figure 3:</u> Morphotester software output comparing a random digital sample of *Cebus* vs. *Macaca*, and *Upper* (maxillary) vs. *Lower* (mandibular) first molars. The meaning of color gradients for each (Figure 3a/b/g/h, Figure 3c/d/i/j, and Figure 3e/f/k/l) vary. For Figure 3a/b/g/h, the most occlusal point was assigned *red*, followed by *orange*, *yellow*, *green*, and *blue* was assigned to the most cervical position on the tooth's crown. In Figure 3c/d/i/j, the areas with the most curvature was assigned *red*, followed by *orange*, *yellow*, *green*, and *blue* was assigned to the areas with the least curvature on the tooth's crown. And in Figure 3e/f/k/l, OPCR: the following colors were used to highlight common surface angulations and directions: *red*, *pink*, *orange*, *brown*, *yellow*, *dark* green, *light* green, *light* blue, and *dark* blue.

The MorphoTester software assigns a color code to the various patches of

OPCR on the model being analyzed (Figure 3e/f/k/l). The colors were assigned

based on common slope patterns and directions. Due to the increased complexity of the occlusal surface of a tooth, the following colors were used to highlight common surface angulations and directions: *red, pink, orange, brown, yellow, dark green, light green, light blue,* and *dark blue* (Figure 3e/f/k/l).

3.2 Non-Human Primate Jaw Kinematics

The following thesis chapter is the continuation of a larger ongoing project evaluating how variation in the primate feeding systems drives variation in the motor control of mastication (Iriarte-Diaz et al., 2011). All kinematic data were collected at the University of Chicago and were previously approved by the Institutional Animal Care and Use Committees/Animal Care and Use Proposal (IACUC/ACUP; Original ACUP#: 72154 and Renewal ACUP#: 71489) and performed in accordance with Federal regulations.

Chewing kinematics were recorded from five adult males *Cebus apella* and five adult female *Macaca mulatta* while the subjects were feeding in a laboratory setting. For *Cebus*, 229 feeding sequences were analyzed (60 from individual C1, 71 from individual C2, 10 from individual C3, 59 from individual C4, and 29 from individual C5). For *Macaca*, 304 feeding sequences were analyzed (102 from individual M1, 29 from individual M2, 113 from individual M3, 20 from individual M4, and 40 from individual M5).

Jaw kinematics were collected with a three-dimensional motion-capture system (Vicon Motion Capture System, Denver, CO). The recording

methodology has been described in detail elsewhere (Iriarte-Diaz et al., 2011; Reed and Ross, 2010). Briefly, reflective markers were coupled to the mandible and cranium using bone screws (Iriarte-Diaz et al., 2011). The motion-capture system is able to track the three-dimensional position of these reflective markers with high spatial and temporal resolution. All kinematic data were collected at a sampling rate of 100 to 250 frames per second (Iriarte-Diaz et al., 2011). Because the markers are coupled to the cranium and mandible, their movement also reflects the movement of both these segments. The position of the reflective markers to the cranium and mandible were measured using a 3D digitizer ([Inmersion, Microscribe G2], Vicon Motion Capture System, Denver, CO). Using the relative position of these markers and the kinematic data, the movement of the markers was reoriented so that the kinematic output was the 3D position of the mandibular incisor relative to a fixed cranium, where the antero-posterior, medio-lateral and infero-superior displacement of the mandible was defined by the X-, Y-, and Z-axes, respectively.

Post-processed data from the Iriarte-Diaz et al. (2011) study were analyzed in MATLAB® data analysis software (MathWorks®, Natick, Massachusetts). Raw kinematic data was then summarized in a linear projection which allowed one to see the entire chew cycle from initial ingestion to swallow. The chew cycle phases were assessed based on the study performed by Hiiemae (1978) which created the four phases of the chew cycle: 1) slow open (SO), 2) fast open (FO), 3) fast close (FC), and 4) slow close (SC). The phase of interest was positioned at the transition from SC to SO/FO, at the time when a

swallow safe bolus began to enter the swallow sequence. "SO and FO are the phases of the chewing cycle when the tongue is brought into contact with the food item, sensory information is collected about the external properties of the bolus, and fragments are collected by the tongue and transported posteriorly toward the pharynx" (Iriarte-Diaz et al., 2011). Utilizing MATLAB® data analysis software (MathWorks®, Natick, Massachusetts) the raw kinematic data provided by (Iriarte-Diaz et al., 2011) were analyzed for each individual feeding experiment per individual within both species. Two points were manually defined from the linear plots of the chew sequence: 1) the point at which ingestion occurred and 2) the point at which the first swallow occurred. Determining points which denoted the initiation of the swallow sequence was dependent upon the shape of the linear model at its apex. A steep or pointed rhythmic chew sequence meant the subject was not pulling its tongue back for the swallow, so likely the bolus had not yet reached its "swallow safe" form. While a broad or prolonged opening to the chew sequence indicated that the kinematics were slowing, allowing for the tongue to move the swallow safe bolus to the back of the mouth; the swallowing sequence had been initiated. The numeric values at the point of ingestion and the first swallow were collected and organized into an Excel 2016 (Microsoft® Corporation, Redmond, Washington) spreadsheet for statistical analysis. Due to inconsistency between individual experiments, the sampling rate of each experimental feeding varied between 100 to 250Hz. To compensate for this discrepancy via Excel 2016 (Microsoft® Corporation, Redmond, Washington),

the point of ingestion was subtracted from the point of the first swallow and that number was divided by the known recording speed (in Hz) from each experiment.



Figure 4: Sample non-human primate chewing sequence from ingestion (blue) to final swallow (orange). The first bite (green) is followed by a sequence of swallows (red) before completing the chewing sequence with the final swallow (orange). The enlarged image represents Hijemae's four phases of the gape cycle – fast close (FC), slow close (SC), slow open (SO), and fast open (FO). FC is represented between the *blue point* to the *pink point*; SC is between the *pink point* and the red point; SO is represented by the red linear projection on the graph; FO is between the *black point* to the completion of the cycle (Hiiemae, 1978). The SC phase occurs as the food substance comes into contact with the occlusal surfaces of the teeth. The black point represents the transition point between SO and FO, this is the point at which a swallow safe bolus (if the food is ready to be swallowed) begins to be transported to the back of the mouth by the tongue. During the process of swallowing, the SO phase becomes somewhat delayed and elongated, breaking the otherwise rhythmic chew cycles of the sequence. At the SC to SO transition, or the highest apex point (represented by the red points is termed the minimum gape or "point of minimum opening." While the FO to FC transition, or the lowest point of the cycle (represented by *blue points*) is termed the *maximum* gape, or "point of maximum opening."

Figure 4. Jaw kinematic model

For each sequence, the number of chews was counted from ingestion (Figure 4 – *blue* indicates "ingestion") to initiation of the first swallow (Figure 4 – *red* indicates all "swallows" within the example chew sequence; the first swallow is the first *red* mark from the left). The number of chews was also organized into the Excel 2016 (Microsoft® Corporation, Redmond, Washington) spreadsheet for each feeding experiment. For purposes of consistency and reliability, the two points and number of chews were recorded by three separate raters. Agreement between all three raters suggested that the data were reliable. Any disagreements between raters was settled based on the third rater's record. If a point was disagreed upon by all three raters and no consensus was made, the feeding experiment was excluded from the statistical analysis. If necessary, swallows were confirmed with video records accompanying the specific chew sequence.

For the purpose of this study, the *Food Types* that were provided to the experimental subjects were categorized into three groups, depending on their food material properties (FMPs). The first group (*Soft* foods) included foods items of low-stiffness and low-toughness, including foods such as grapes, bananas and strawberries. The second group (*Dried Fruits*) included FMPs of high-toughness and low-stiffness, including foods such as **dates**, **dried apricots**, **dried pineapples**, and raisins (TABLE I – Foods with previously published FMPs in bold). The third group (*Nuts*) included FMPs of low-toughness and high-stiffness, including foods such as **dates**, **dried pineapples**, and raisins (TABLE I – Foods with previously published FMPs in bold). The third group (*Nuts*) included FMPs of low-toughness and high-stiffness, including foods such as **almonds**, **brazil nuts**, cashews, **hazel nuts**,

pecans, popcorn kernels, and walnuts (TABLE I – Foods with previously published FMPs in bold).

3.2.1 Inclusion and Exclusion Criteria

3.2.1.1 Inclusion Criteria

- Clearly defined chewing sequences were assessed for their time from *Ingestion* to *First Swallow* and the number of chews from *Ingestion* to *First Swallow* were analyzed.
- Food Types from Soft foods, Dried Fruits and Nuts with clear food material property (FMP) information were assessed.

3.2.1.2 Exclusion Criteria

- Any jaw kinematic data which were missing the *Ingestion* (or start) of the chewing sequence were excluded from the study.
- Any jaw kinematic data which were incomplete or discontinuous (broken chewing sequences) was excluded.
- If a point was disagreed upon by all three raters and no consensus was made, the feeding experiment was excluded from the statistical analysis.
- The time from *Ingestion* to *Final Swallow* and number of chews from *Ingestion* to *Final Swallow* were excluded from final data/statistical analysis due to the inability to achieve rater consensus.

 Food Types in the miscellaneous food category were excluded from this study due to their lack of food material property (FMP) information (this group included apples, carrots, un-ripened pears, and sweet potatoes).

3.3 Occlusal Fingerprint Analysis (OFA)

The occlusal contact area during feeding in our studied species was estimated utilizing the *Occlusal Fingerprint Analyzer* (OFA) software (DFG FOR 771, ZiFiLo IT Ltd., Ober-Ramstadt, Germany), a virtual simulator that simulates and detects tooth contact during mastication.

3.3.1 High-Resolution 3D Digital Tooth Model Acquisition

The three-dimensional models created for the *MATERIALS AND METHODS* – *Dental Topography* (*section 3.1* – *MATERIALS AND METHODS*) were also used for the *MATERIALS AND METHODS* – *Occlusal Fingerprint Analysis* section (*section 3.3*) of this thesis. Unlike the dental topographical analyses, the maxillary and mandibular teeth from only one individual subject per species were used. Also, similar to the *MATERIALS AND METHODS* – *Dental Topography* section (*section 3.1*), the maxillary first molar (M1) was isolated and processed. However, because occlusal relationship is a point a interest, and maxillary M1 is related to the mandibular M1 and M2, as a result mandibular first (M1) and second (M2) molars were isolated. The materials and methods of postprocessing of those selected molars was identical to section 3.1.2 (MATERIALS AND METHODS – Dental Topography – High-Resolution 3D Digital Tooth Model Acquisition).

3.3.2 Occlusal Fingerprint Analyzer (OFA) Software

The Occlusal Fingerprint Analyzer (OFA) software (DFG FOR 771, ZiFiLo IT Ltd., Ober-Ramstadt, Germany) is a virtual tool that simulates occlusal contacts and detects collisions between interacting teeth during dynamic reliefguided masticatory movements (Benazzi et al., 2011; Schultz and Martin, 2014). With this software, occlusal pathway of antagonistic teeth can be reconstructed, providing a sequence of contact surfaces as well as the orientation and areas of those surfaces. The software uses collision, deflection, and break-free algorithms to determine the occlusal-guided path of interacting teeth. For this thesis, two approaches were used to compare and contrast the occlusal dynamics between the studied Species. First, the contact dynamics of both Species during simple vertical period of power stroke into maximum intercuspation were evaluated. In this case, the mandibular teeth were brought into maximum intercuspation in a purely vertical manner. As the teeth came into contact, the total contact area was recorded until it reached a plateau indicating maximum intercuspation (Figure 5). Also with this setting, the effect of variation in the position of occluding teeth was assessed by changing the antero-posterior and medio-lateral position of the mandibular molars with respect to the maxillary molar.



Figure 5. OFA occlusal dynamics

Figure 5: Maxillary M1 is seen in white, while the mandibular M1 is seen as a clear mesh lattice allowing for visualization of the occlusal surface of the maxillary M1. From the reader's point-of-view, the images are being viewed from the posterior. The total occlusal contact area is outlined in red. The OFA software assigns a color gradient based on the points of collision; colors are embedded based on the oldest and newest collision points. The color gradient ranges from green to red: green is the newest point of collision, yellow is the second oldest point of collision, orange is the third oldest point of collision, and red is the fourth (most) oldest point of collision. The turquoise dots represent the jaw kinematic movements of the chew cycle [based on the Hiiemae gape cycle (1978)]. The turquoise dots are a representation of the end to a FC phase (reference Figure 4 – Jaw kinematic model), the start of a SC phase, and the start of a SO phase. Follow the arrows through the power stroke of the chew cycle: FC → SC → SO.

In the second method, the occluding teeth were brought into maximum

intercuspation using real 3D jaw kinematic data obtained experimentally from

Cebus apella and Macaca mulatta subject, gathered and processed at the

University of Chicago (Iriarte-Diaz et al., 2011). Since it has been shown that the 3D kinematics vary depending on the type of food being processed (Iriarte-Diaz et al., 2011; Reed and Ross, 2010), the occlusal dynamics were tested using kinematics specific to *Soft* foods, *Dried Fruits*, and *Nuts*.

3.4 Data and Statistical Analysis

To assess differences in dental topography (occlusal surface area, occlusal outline area, RFI, DNE, and OPCR) of M1 between *Species*, a three-way ANOVA was used with *Species* (*Cebus* vs. *Macaca*), molar *Position* (maxillary vs. mandibular), and *Side* (left vs. right) as factors, as well as the interaction between *Species* and tooth *Position*.

For comparing jaw kinematics, significant differences were assessed with a mixed-model ANOVA, with *Species* (*Cebus* vs. *Macaca*) and *Food Type* (*Soft* foods vs. *Dried Fruits* vs. *Nuts*) as fixed effects, as well as their interaction (*Species*Position*). The factor of *Individuals* was considered nested with *Species* as a random effect. If significant differences in *Food Type* were found, a post-hoc Tukey test was used to test significant differences between the *Food Types* consumed (*Soft* foods, *Dried Fruits*, and *Nuts*).

All statistical tests were performed utilizing *R* version 3.0.2 (The R Foundation, Vienna, Austria) (Team, 2014). Mixed-model analysis was performed with the *Ime4* package (Bates et al., 2014) and post-hoc Tukey tests

were performed with the *Ismeans* package (Lenth and Hervé, 2014). Data are presented as mean ± standard error (s.e.).

3.5 IRB Exemption and IACUC/ACUP Approval

All non-human primate data were collected at the University of Chicago and were approved by the Institutional Animal Care and Use Committees/Animal Care and Use Proposal (IACUC/ACUP; Original ACUP#: 72154 and Renewal ACUP#: 71489) (Appendix A).

This study was exempted by the University of Illinois at Chicago Institutional Review Board, Office of the Protection of Research Subjects, on October 28, 2014, due to the study not conducting experiments with live human subjects. Dr. Mary Bowman, Director of the University of Illinois at Chicago Office of Animal Care and Institutional Biosafety, exempted the submission to the University of Illinois at Chicago Animal Care Committee (ACC), on October 28, 2014, because the non-human primate data assessed within this study were previously collected at the University of Chicago under an approved IACUC/ACUP protocol (Appendix B).

IV. RESULTS

4.1 Dental Topography

The five dental topography variables [dental topography variables: 1) occlusal surface area, 2) occlusal outline area, 3) relief index (RFI), 4) Dirichlet normal energy (DNE), and 5) orientation patch count-rotated (OPCR)] were compared over four dental variables to assess statistical significance. These dental variables included 1) *Species* (*Cebus* vs. *Macaca*), 2) *Side* (right side of the mouth vs. left side of the mouth), 3) molar *Position* (maxillary molars vs. mandibular molars), and 4) interaction effect between *Species* and molar *Position* (species*position: Cebus vs. *Macaca* and maxillary vs. mandibular molars).



Figure 6. Dental topography variables data

<u>Figure 6:</u> Dental topography variables (occlusal surface area, occlusal outline area, relief index (RFI), Dirichlet normal energy (DNE), and orientation patch count-rotated (OPCR)) comparing *Species* (*Cebus apella* vs. *Macaca mulatta*) and molar *Position* ("upper"/maxillary first molars) vs. "lower"/mandibular first molars).

4.1.1 Occlusal Surface Area

The only significant variable affecting the dental topography variable, occlusal surface area, is between the Species (Cebus vs. Macaca) (TABLE II and Figure 6). The data supported that the Macaca species possess an increased occlusal surface area when compared to the Cebus species (p<0.0001). The absence of a significant comparison between Side (right vs. left sides of the mouth), tooth Position (maxillary vs. mandibular molars), and interaction between Species*Position means that the occlusal surface area of the M1 molars are fairly comparable when comparing individuals within the same species. However, when comparing the occlusal surface area between the *species* (Cebus vs. Macaca), the Macaca species have a larger occlusal surface area.

4.1.2 Occlusal Outline Area

The significant variables affecting the dental topography variable, *occlusal outline area*, are between *Species* (*Cebus* vs. *Macaca*), molar *Position* (maxillary molars vs. mandibular molars), and the interaction between *Species*Position* (TABLE II and Figure 6). The data supported that the *Macaca* species possess an increased occlusal outline area when compared to the *Cebus* species (p<0.0001); the maxillary molars possess an increased occlusal outline area when compared to the mandibular molars (p<0.0001). As a result, the interaction between *Species* and molar *Position* present significant differences from one another (p=0.0266, or p<0.05). The absence of a significant comparison

between *Side* (right vs. left sides of the mouth) means that the occlusal outline area of the M1 molars are fairly comparable when comparing individuals within the same species. However, when comparing the occlusal outline area between *Species* (*Cebus* vs. *Macaca*) and molar *Position* (maxillary vs. mandibular molars), the *Macaca* species and maxillary molars have larger occlusal surface areas.

4.1.3 Relief Index (RFI)

The only significant variable affecting the dental topography variable, *relief index* (*RFI*), is between the molar *Position* (maxillary vs. mandibular molars) (TABLE II and Figure 6). The data supported that the mandibular first molars possess an increased RFI when compared to the maxillary first molars (p=0.0006, or p<0.001). The absence of a significant comparison between *Side* (right vs. left sides of the mouth), *Species* (*Cebus* vs. *Macaca*), and interaction between *Species*Position* means that the RFI of the M1 molars are fairly comparable when comparing individuals between different species. However, when comparing the RFI between the molar *Position* (maxillary vs. mandibular molars), the mandibular first molars have larger RFI values.

4.1.4 Dirichlet Normal Engery (DNE)

The significant variables affecting the dental topography variable, *Dirichlet normal energy (DNE)*, is between *Species (Cebus* vs. *Macaca)* and molar

Position (maxillary molars vs. mandibular molars) (TABLE II and Figure 6). The data supported that the *Macaca* species possess an increased DNE when compared to the *Cebus* species (p<0.0001); the maxillary molars possess an increased DNE when compared to the mandibular molars (p=0.0190, or p<0.05). The absence of a significant comparison between *Side* (right vs. left sides of the mouth) and interaction between *Species*Position* means that the DNE of the M1 molars are fairly comparable when comparing individuals within the same species. However, when comparing the DNE between *Species* (*Cebus* vs. *Macaca*) and molar *Position* (maxillary vs. mandibular molars), the *Macaca* species and maxillary molars have larger DNE values.

4.1.5 Orientation Patch Count-Rotated (OPCR)

The only significant variable affecting the dental topography variable, orientation patch count-rotated (OPCR), is between the Species (Cebus vs. Macaca) (TABLE II and Figure 6). The data supported that the Macaca species possess an increased OPCR when compared to the Cebus species (p<0.0001). The absence of a significant comparison between Side (right vs. left sides of the mouth), molar Position (maxillary vs. mandibular molars), and interaction between Species*Position means that the OPCR of the M1 molars are fairly comparable when comparing individuals within the same species. However, when comparing the OPCR between the Species (Cebus vs. Macaca), the Macaca species have larger OPCR values.

TABLE II

Variables	Factors	F Ratio	P value	
Occlusal	Species	411.1	<0.0001***	
Surface Area	Side	1.2	0.2737	
	Position	2.5	0.1161	
	Species*Position	1.1	0.3018	
Occlusal	Species	772.7	<0.0001***	
Outline Area	Side	0.6	0.4332	
	Position	27.8	<0.0001***	
	Species*Position	5.1	0.0266*	
Relief Index	Species	0.06	0.8073	
(RFI)	Side	0.5	0.4642	
	Position	12.7	0.0006**	
	Species*Position	0.0001	0.9907	
Dirichlet normal	Species	479.9	<0.0001***	
engery (DNE)	Side	0.004	0.9523	
	Position	5.7	0.0190*	
	Species*Position	1.5	0.2293	
Orientation	Species	56.5	<0.0001***	
Patch Count-	Side	1.0	0.3135	
Rotated (OPCR)	Position	0.2	0.6631	
	Species*Position	3.1	0.0795	

DENTAL TOPOGRAPHY VARIABLES DATA AND STATISTICS, 2016

• Note: Asterisks indicate statistical significance:

○ * = <0.05</p>

• Degrees of Freedom, d.f. = 1, 91 for the factorial ANOVA statistical analysis.

4.2 Non-Human Primate Jaw Kinematics

Overall significant differences were compared within three data variables

(data variables: 1) Food Type, 2) Species, and the interaction between 3) Food

*Type*Species*) in context to the amount of time from ingestion to the first swallow

and the number of chews from ingestion to the first swallow (TABLE III).

TABLE III

JAW KINEMATIC DATA AND STATISTICS - ANALYSIS OF DEVIANCE, 2016

Variables	Factors	d.f.	Chi-squared (χ²)	P value
Amount of time	Food Type	2	184.5	<0.0001***
from ingestion to	Species	1	15.0	0.0001**
first swallow	Food Type*Species	2	82.8	<0.0001***
Number of chews	Food Type	2	227.2	<0.0001***
from ingestion to	Species	1	9.6	0.0019*
first swallow	Food Type*Species	2	88.9	<0.0001***

• Note: Asterisks indicate statistical significance:

- * = <0.05</p>
- o ** = 0.0001
- *** = <0.0001</p>



Figure 7. Jaw kinematic data

Figure 7: (Featured on the left) Assessing the number of chews from ingestion to first swallow when comparing two Species (Cebus vs. Macaca) and three Food Types [Soft foods, low-toughness/low-stiffness (yellow); high-toughness/low-stiffness Dried Fruits, (orange); Nuts, lowtoughness/high-stiffness (dark orange)]. (Featured on the right) Assessing the time from ingestion to first swallow when comparing two Species (Cebus vs. *Macaca*) and three *Food Types* [Soft foods, low-toughness/low-stiffness (yellow); Dried Fruits, high-toughness/low-stiffness (orange); Nuts, lowtoughness/high-stiffness (dark orange)]. Significant differences are indicated by differences in lettering over the plots.

4.2.1 Amount of Time from Ingestion to First Swallow

When comparing the time required from ingestion to first swallow, significant differences were observed between Species, among *Food* Types, as well as for the interaction between *Species* and *Food Type* (p<0.0001 for all; TABLE III). Overall, *Cebus* used less time to the first swallow compared to *Macaca* (4.85±0.36 sec vs. 6.96±0.35 sec, respectively). The time to first swallow also varied based on the *Food Type* consumed. On average, *Cebus* and *Macaca* together took longer to swallow when eating *Nuts* (8.23±0.32 sec) than when eating *Dried Fruits* (5.36±0.32 sec) and when eating *Soft* foods (4.12±0.31 sec). Post-hoc Tukey analysis showed that the time from ingestion to first swallow when comparing between all three *Food Types* were significantly different (p<0.001 for all comparisons; TABLE IV).

TABLE IV

AMOUNT OF TIME FROM INGESTION TO FIRST SWALLOW – COMPARISON OF FOOD TYPE CONSUMED, 2016

Food Type Consumed	Food Type Consumed	t-ratio	d.f.	P value
Dried Fruits	Nuts	-8.395	497.3	<0.0001***
Dried Fruits	Soft	3.710	437.2	0.0007**
Nuts	Soft	12.604	512.5	<0.0001***

• Note: Asterisks indicate statistical significance:

o ** = <0.001

o *** = <0.0001

• Results are averaged over the levels of species

The interaction effect between *Species* and *Food Type* was significant, so post-hoc comparisons were performed to evaluate the effect of different *Food Types* on both *Species* (Figure 7; TABLE V). This analysis showed that the effect of *Food Type* on the time to swallow is significant for *Macaca* but not for *Cebus*. No significant differences were found for *Cebus* when comparing the consumption of *Soft* foods, *Dried Fruits* and *Nuts* (p>0.07 for all three comparisons; TABLE VI). In contrast, *Macaca* significantly increase its time from ingestion to first swallow when consuming *Soft* foods (4.1±0.4 sec) to *Dried Fruits* (5.8±0.4 sec) to *Nuts* (11.0±0.5 sec) (p<0.01 for all three comparisons; TABLE V; Figure 7). As an average when comparing *Species*, both *Cebus* and *Macaca* (TABLE V) took more time from ingestion to swallow for food type *Nuts* (low-toughness/high-stiffness); although *Macaca* took over twice as long as *Cebus* to consume this *Food Type*.

TABLE V

MEAN AMOUNT OF TIME FROM INGESTION TO FIRST SWALLOW - FOOD TYPES CONSUMED PER SPECIES, 2016

Species	Food Type Consumed	Mean Time from Ingestion to First Swallow (seconds)
Cebus	Soft	4.13±0.48
Macaca	Soft	4.12±0.39
Cebus	Dried Fruits	4.96±0.46
Macaca	Dried Fruits	5.76±0.43
Cebus	Nuts	5.46±0.43
Macaca	Nuts	11.01±0.48

TABLE VI

AMOUNT OF TIME FROM INGESTION TO FIRST SWALLOW – COMPARISON OF SPECIES AND FOOD TYPES CONSUMED, 2016

Species / Food Type	Species / Food	t-ratio	d.f	P value
Consumed	Type Consumed			
Cebus / Dried Fruits	Macaca / Dried Fruits	-1.3	17.5	0.7980
Cebus / Dried Fruits	Cebus / Nuts	-1.1	525.8	0.8858
Cebus / Dried Fruits	Macaca / Nuts	-9.1	20.2	<0.0001***
Cebus / Dried Fruits	Cebus / Soft	1.6	508.6	0.5735
Cebus / Dried Fruits	Macaca / Soft	1.4	14.5	0.7379
Macaca / Dried Fruits	Cebus / Nuts	0.5	16.1	0.9961
Macaca / Dried Fruits	Macaca / Nuts	-10.4	420.42	<0.0001***
Macaca / Dried Fruits	Cebus / Soft	2.5	17.6	0.1805
Macaca / Dried Fruits	Macaca / Soft	3.8	315.4	0.0025*
Cebus / Nuts	Macaca / Nuts	-8.5	18.7	<0.0001***
Cebus / Nuts	Cebus / Soft	2.7	494.9	0.0716
Cebus / Nuts	Macaca / Soft	2.3	13.2	0.2658
<i>Macaca /</i> Nuts	Cebus / Soft	10.0	20.2	<0.0001***
<i>Macaca /</i> Nuts	Macaca / Soft	16.0	525.2	<0.0001***
Cebus / Soft	Macaca / Soft	0.01	14.8	1.0000

• Note: Asterisks indicate statistical significance:

○ * = <0.05</p>

o *** = <0.0001

4.2.2 Number of Chews from Ingestion to First Swallow

For the number of chews from ingestion to first swallow, significant differences were found between *Species*, among *Food Types*, and between the interaction between *Species* and *Food Types* (TABLE III). Similar to the time to first swallow, when data from all *Food Types* are pooled together, *Macaca* shows more chews before the first swallow than *Cebus* (17.5 \pm 0.9 chews vs. 13.1 \pm 13.1 chews, respectively). However, when comparing the effect of *Food Type* (combining both *Species* together), feeding on *Nuts* takes more chews to first swallow (22.1 \pm 0.8 chews) than feeding on either *Soft* foods (11.1 \pm 0.8 chews) or

Dried Fruits (12.6±0.8 chews), but there is no significant differences between *Soft* foods and *Dried Fruits* (TABLE VII).

Again, the interaction effect between *Species* and *Food Type* was significant, so post hoc comparisons were performed to evaluate the effect of *Food Type* for each *Species* (Figure 7; TABLE IX). For both *Species*, feeding on *Nuts* takes more chews from ingestion to first swallow than either *Soft* foods and *Dried Fruits* (Figure 7; TABLE IX). However, in *Macaca* the difference was larger than in *Cebus* (Figure 7). No differences in the number of chews to first swallow were found between *Soft* foods and *Dried Fruits*, in either *Species* (Figure 7; TABLE IX). As an average between *Species*, both *Cebus* and *Macaca* (TABLE VIII) took more time from ingestion to swallow *Nuts*: again *Macaca* took nearly twice as many chews as *Cebus* to consume *Nuts*.

TABLE VII

NUMBER OF CHEWS FROM INGESTION TO FIRST SWALLOW – COMPARISON OF FOOD TYPE CONSUMED, 2016

Food Type Consumed	Food Type Consumed	t-ratio	d.f.	P value
Dried Fruits	Nuts	-11.146	501.4	<0.0001***
Dried Fruits	Soft	1.890	446.6	0.1427
Nuts	Soft	13.642	515.2	<0.0001***

• Note: Asterisks indicate statistical significance:

o *** = <0.0001

• Results are averaged over the levels of species.

TABLE VIII

MEAN NUMBER OF CHEWS FROM INGESTION TO FIRST SWALLOW – FOOD TYPES CONSUMED PER SPECIES, 2016

Species	Food Type Consumed	Mean Number of Chews from Ingestion to First Swallow
Cebus	Soft	11.6±1.2
Macaca	Soft	10.5±1.0
Cebus	Dried Fruits	12.1±1.2
Macaca	Dried Fruits	13.2±1.1
Cebus	Nuts	15.5±1.1
Macaca	Nuts	28.7±1.2

TABLE IX

NUMBER OF CHEWS FROM INGESTION TO FIRST SWALLOW – COMPARISON OF SPECIES AND FOOD TYPES CONSUMED, 2016

Species / Food Type Consumed	Species / Food Type Consumed	t-ratio	d.f.	P value
Cebus / Dried Fruits	Cebus / Nuts	3.0	525.5	0.0375*
Cebus / Dried Fruits	Cebus / Soft	0.4	512.3	0.9991
Cebus / Dried Fruits	Macaca / Dried Fruits	0.7	16.8	0.9785
Cebus / Dried Fruits	Macaca / Nuts	-9.9	19.3	<0.0001***
Cebus / Dried Fruits	Macaca / Soft	1.0	17.1	0.9145
Cebus / Nuts	Cebus / Soft	3.2	500.2	0.0184*
Cebus / Nuts	Macaca / Dried Fruits	1.4	15.5	0.7031
Cebus / Nuts	Macaca / Nuts	-8.0	17.9	<0.0001***
Cebus / Nuts	Macaca / Soft	3.3	12.8	0.0522
Cebus / Soft	Macaca / Dried Fruits	-1.0	17.1	0.9242
Cebus / Soft	Macaca / Nuts	-9.9	19.5	<0.0001***
Cebus / Soft	Macaca / Soft	0.7	14.4	0.9830
Macaca / Dried Fruits	Macaca / Nuts	-12.4	431.2	<0.0001***
Macaca / Dried Fruits	Macaca / Soft	2.5	328.7	0.1361
Macaca / Nuts	Macaca / Soft	17.0	525.7	<0.0001***

• Note: Asterisks indicate statistical significance:

4.3 Occlusal Fingerprint Analysis (OFA)

The differences in overall contact area between *Cebus* and *Macaca* first molars (M1) were evaluated when coming into contact based on the observed kinematics for each species when feeding on different *Food Types* (Figure 9 - *Macaca*). The occlusal contact area for *Macaca* shows a bimodal profile, with an early peak in the power stroke and then another peak later in the power stroke for all *Food Types* (Figure 8 - *Macaca*). The occlusal profiles when using the kinematics from *Soft* foods and *Dried Fruits* are temporally very similar, but the contact area of the first peak is smaller for the *Soft* foods. The occlusal profile for *Nuts* also shows a bimodal profile but it is more extended and the occlusal contact area during the second peak is only 10% of the molar cross-sectional area, in contrast to the >20% observed for *Soft* foods and *Dried Fruits*.

The occlusal contact area in *Cebus*, however, shows a very different profile than *Macaca* (Figure 8 – *Cebus*). The change in occlusal contact area shows only one peak, with a smooth increase in contact area and then a sharp decrease. For all *Food Types*, the increase in occlusal contact is very similar until they reach about 20% of occlusal area, and then food-specific differences can be observed. For *Soft* foods, the occlusal contact area drops rapidly. For *Nuts*, there is a sharp increase in contact area and then a rapid drop. And for *Dried Fruits*, the contact area remains constant for a long time before dropping rapidly at the end.



Figure 8. OFA occlusal contact area data

<u>Figure 8:</u> Occlusal contact area during a single power stroke of Macaca (upper panel) and Cebus (lower panel) first molars, based on the kinematics when feeding on different Food Types (Soft foods, Dried Fruits, and Nuts). Output generated from from the OFA software (DFG FOR 771, ZiFiLo IT Ltd., Ober-Ramstadt, Germany). Please reference Figure 9 – OFA 3D kinematic output to compare points of the chew cycle based on Food Type and Species, the apex of the linear projections in Figure 8 correlate with the maximum occlusal areas (green and yellow) in Figure 9. Note the difference between Macaca vs. Cebus contact areas.



Figure 9. OFA 3D kinematic output

Figure 9: Output from the OFA software (DFG FOR 771, ZiFiLo IT Ltd., Ober-Ramstadt, Germany) illustrating how occlusal contact areas change as a function of tooth morphology and jaw kinematic differences in the movements of the mandibular first molar (M1). Please reference Figure 6 – OFA occlusal dynamics for visual orientation of the OFA output. Macaca reaches maximum occlusal contact area when chewing on Soft foods (low-toughness/low-stiffness foods) while Cebus reach maximum occlusal contact area when chewing on Nuts (low-toughness/high-stiffness foods). Please reference Figure 8 – OFA occlusal contact area data to compare points of the chew cycle based on Food Type and Species, the maximum occlusal contact areas (green and yellow) in Figure 9 correlate with the apex of the linear projections in Figure 8.

V. DISCUSSION

5.1 Dental Topography

Based on the literature review and dental knowledge acquired in a clinical setting, occlusal shapes and angulations are constantly in a state of change, remodeling, and settling. In all mammals, teeth are subjected to abrasive external entities multiple times a day when feeding. In nature and less industrialized countries, the food being consumed is not often cleared of debris (including dirt and sand) prior to consumption, which increases the abrasive effect on the tooth enamel (Begg, 1965). The foods themselves present with specific food material properties (FMPs) which vary on spectrums from low- to high-stiffness and toughness, and exert a different effect on the tooth. Furthermore, on an individual basis, bruxism and clenching can be exerted consciously, or subconsciously, affecting the wear patterns of teeth. Specific locations of a tooth are also said to vary in hardness; according to Ungar and Williamson (2000), the buccal tooth cusps wear at a faster rate than the lingual. Finally, one must consider that genetics also play a role in enamel thickness and/or hardness, resulting in varying wear patterns. Ulhaas et al. (2004), reported that two different species of non-human primates presented with different enamel thicknesses. In general, all of the factors mentioned will vary between each individual and age can only have an increased effect on wear.

This study proposes a variety of methods to help categorize and measure relationships comparing the FMPs and the constantly changing state of occlusal topography. The dental topography variables within this study have never been

utilized to compare *Cebus apella* and *Macaca mulatta*. Although Iriarte-Diaz et al. (2011) did not quantify occlusal morphology of *Cebus* and *Macaca* molars, phenotypic observations of the teeth were made stating that the *Cebus* species has a flatter occlusal topography compared to the more highly crowned *Macaca* molars. As discussed below, through the dental topography data collected in this study, we succeeded in quantitatively confirming the phenotypic observations made by Iriarte-Diaz et al. (2011).

5.1.1 Occlusal Surface Area and Occlusal Outline Area

The data revealed that the *Macaca* species possess an increased occlusal surface area when compared to the *Cebus* species. This should not come as a surprise (as discussed in *section 2.1.2 – REVIEW OF LITERATURE – Tooth Morphology of the Cebus and Macaca*), because the *Cebus* present with more rounded and flattened molar occlusal surfaces; while the *Macaca* present with higher, more pointed molar cusps. The higher and more pointed molar cusps of the *Macaca* would increase the total overall surface area when compared to the flatter molar cusps of the *Cebus*. Time and the external environment will exert a continued effect on the overall occlusal surface area. Age and increased wear patterns will result in decreased occlusal surface area measurements.

As in humans, great variation lies within the size of teeth compared between individuals within the same species, let alone when comparing two different species. However, in the mammalian species, genetics determine the

size of teeth (assuming there is no interruption or an obtrusive factor which disrupts the development), and once this is determined teeth no longer grow in size past their genetic predisposition. This study confirmed differences between *Species* when comparing the occlusal outline areas. This is expected considering that the *Macaca* is, on average, larger than *Cebus* (7.7kg vs. 3.6kg for males, respectively; and 5.34kg vs. 2.62kg for females, respectively) (Fleagle, 2013; Fooden, 2000; Singh and Sinha, 2004). *Macaca mulatta* possess increased occlusal outline areas when compared to *Cebus apella*. This effect of species dimorphism in the molar size will be explained and compensated for in *section* 5.3 [*DISCUSSION – Occlusal Fingerprint Analysis (OFA)*].

5.1.2 <u>Relief Index (RFI)</u>

The relief index (RFI) is another shape metric to compare the dynamic three-dimensional structure of a tooth crown to a standardized two-dimensional form (Boyer, 2008). Particularly, occlusal surface complexity of teeth. Previous studies showed significant correlations linking increased wear patterns with a decrease in RFI (Dennis et al., 2004; M'Kirera and Ungar, 2003). M'Kirera and Ungar (2003) utilized the RFI to compare the occlusal complexities of taxons which were categorically different based on their diets – frugivores, omnivores, folivores, and insectivores. Rather drastic differences were noted between each taxon's occlusal complexity, and statistically significant differences were noted between each group (M'Kirera and Ungar, 2003).

This study revealed molar *Position* (maxilla vs. mandible), as being the only statistically significant variable when comparing the RFIs within the sample. The mandibular molars presented with the statistically significant RFI compared to the maxillary molars. No statistically significant data existed between the two Species (Cebus vs. Macaca). Lack of significance between the two Species can indicate one of two things, a lack of sensitivity to the RFI analysis system or lack of variability between the Cebus and Macaca occlusal complexities within the sample. RFI has been a successful means to compare the metrics of occlusal topography, however the orientation patch count-rotated (OPCR) (discussed in sections 4.1.5 RESULTS – OPCR and 5.1.4 DISCUSSION – OPCR) was said to be even more sensitive when comparing occlusal complexities (Plyusnin et al., 2008). Lack of occlusal variance between the two Species (Cebus vs. Macaca) may be a legitimate retort due to dietary overlap between the two species. Although Cebus are considered primarily frugivorous while the Macaca are frugivorous and folivorous, seasonal food sources and competition between other species have caused more overlap between the two species in dietary consumption.

5.1.3 Dirichlet Normal Energy (DNE)

Dirichlet normal energy (DNE) measures the total curvature of a tooth surface based on a standardized orientation of the teeth in a three-dimensional plane (Bunn et al., 2011). Within the experimental sample, the *Macaca* dentition provided statistically significant data suggesting a greater DNE over the *Cebus*

species. This finding correlates well with a study performed by Evans (2013) which stated that, "higher DNE may be the result of taller tooth features." The results of this study also presented statistically significant results suggesting an increased DNE of maxillary molars compared to the mandibular molars.

In the wild, the *Macaca* species were reported to consume a more folivorous diet (Goldstein and Richard, 1989). This finding is supported by the more highly cusped occlusal topography of their teeth, insinuating that the *Macaca* is more capable of processing foliage through sheering mechanics (Kay and Sheine, 1979; Ungar, 1998). Furthermore, the decreased DNE in the *Cebus* implies a consistent contrasting effect when compared to the increased DNE of the *Macaca*. The flatter, more round curvature of a *Cebus* tooth implies an increased ability of that species to crush and grind their food (Kay and Sheine, 1979; Ungar, 1998). This finding coincides with the more frugivorous (or hard object) diet of the *Cebus* species found in the wild (Galetti and Pedroni, 1994).

5.1.4 Orientation Patch Count-Rotated (OPCR)

The orientation patch count-rotated (OPCR) is the final method implemented to measure tooth surface complexities. Multiple previous studies have utilized OPCR as a reliable means to make occlusal topography comparisons (Evans, 2013; Hunter and Jernvall, 1998; Reed, 1997; Zuccotti et al., 1998). OPCR utilizes Geographic Information Systems (GIS) algorithms to assess various slopes and angulations upon a tooth's surface. The OPCR
organizes common slopes into color-coded "patches" to illustrate similarities (Evans, 2013).

This study revealed Species (Cebus vs. Macaca), as being the only statistically significant variable when comparing the OPCRs within the sample. Previous studies have indicated that occlusal patch count (OPC) vary between species based on their dietary consumption (Boyer, 2008; M'Kirera and Ungar, 2003). Boyer et al. (2010) stated that "OPC strongly correlate with a fibrous and structural carbohydrate-dominated diet." The OPCR results from this study therefore support the hypothesis that the Macaca species is more capable of mechanically breaking down a more folivorous diet than the Cebus. Although the opposite might be expected, the OPC remains constant or often increases as the enamel of a crown begins to show signs of wear (Evans et al., 2007; King et al., 2005). It is believed that this occurs because as teeth wear there is often an increase in "small scale crenulations" in the tooth surface which would increase the OPC (Boyer et al., 2010). When comparing Cebus vs. Macaca, the increased Macaca OPCR quantitatively confirms statistically significant occlusal complexity over the *Cebus* species.

5.2 Non-Human Primate Jaw Kinematics

The acquisition of nutrients into the body for basic metabolic needs starts with the process of mastication. The chew cycle can be divided into different phases and here we focus on the slow close (SC) phase as defined by Hiiemae

(1978). This phase starts when the teeth come in contact with the food bolus and produces a force compressing a piece of food between the maxillary and mandibular teeth. The end of the SC phase is the point of minimum gape. The regulatory mechanism which initiates the swallow sequence is triggered by the production of a swallow safe bolus (Prinz and Lucas, 1997). The rate and efficiency of producing a swallow safe bolus is dependent on anatomical factors as well as material properties of the food being consumed. As discussed in section 5.1 (DISCUSSION - Dental Topography) the occlusal morphology of the teeth can often convey the preferred diet consumed by an individual or species. This link between occlusal morphology and diet is further complicated by the addition of food material properties (FMPs) – toughness and stiffness (Iriarte-Diaz et al., 2011). For this reason, jaw kinematics can be viewed as a metric of chewing efficiency while comparing two species of non-human primates and the food material properties (FMPs) of the diet being consumed. For the purposes of this study, jaw kinematics (or chewing efficiency) was measured based on 1) the amount of time from ingestion to first swallow and 2) the number of chews from ingestion to first swallow. Statistical significance was achieved for both the amount of time and chew number when assessing Food Type, Species, and the interaction between Food Type and Species (Food Type*Species).

5.2.1 Amount of Time from Ingestion to First Swallow

When assessing the amount of time from ingestion to first swallow, it was noted that *Macaca* chew, on average, significantly longer than *Cebus*. Also,

within each *Species*, differences between *Food Types* were observed, in particular, both *Species* chew *Nuts* longer than other *Food Types*. These data support the previous observation made by Iriarte-Diaz et al. (2011) that *Macaca* tends to chew longer than *Cebus*.

Although Iriarte-Diaz et al. (2011) did not quantify occlusal morphology of the *Cebus* and *Macaca*, they proposed that differences in occlusal morphology between these *Species* might be related to their feeding kinematics and their ability to process food. The chew cycle of *Cebus* was observed to be more variable, both spatially and temporally, than the *Macaca*. It was suggested that this variability was driven by the flatter occlusal topography of *Cebus* and that could reduce the number of chews required to swallow, when compared to *Macaca*. By decreasing the number of chews within a cycle, this likewise had a diminishing effect on the amount of time from ingestion to swallow.

To review, the FMPs of the *Food Types* tested within the study were categorized into three groups: *Soft* foods (low-toughness/low-stiffness), *Dried Fruits* (high-toughness/low-stiffness), *Nuts* (low-toughness/high-stiffness). Reed and Ross (2010) suggest that foods which possess low-toughness/high-stiffness FMPs increase total chew time because harder foods mechanically break down more easily and require more intricate movements of the tongue which lengthens each individual chew cycle. This increased amount of time spent in each chew cycle hypothetically increases the total amount of time from ingestion to first swallow. In addition, Iriarte-Diaz et al. (2011) reported increased lateral jaw movements when consuming low-toughness/high-stiffness foods (*Nuts*)

compared to eating high-toughness/low-stiffness foods (*Dried Fruits*). Again, this increase in total jaw displacements directly correlates with the mean amount of time from ingestion to first swallow.

5.2.2 Number of Chews from Ingestion to First Swallow

When assessing number of chews from ingestion to first swallow, statistically significant differences were noted within the both *Cebus* and *Macaca* species when making the comparisons between the following *Food Types*: *Dried Fruits* vs. *Nuts* and *Soft* foods vs. *Nuts*. However, no statistically significant differences were noted when making the comparison between Soft foods vs. *Dried Fruits* within either *Species*. Again, out of the statistically significant data collected, the *Macaca* always had more chews from ingestion to first swallow when compared to the *Cebus*.

The data collected for number of chews to from ingestion to first swallow, as expected, closely correlate with the data collected for the amount of time from ingestion to first swallow. The results from this study were consistent with previous observations for the same *Species*. Iriarte-Diaz et al. (2011) observed that the interquartile range (IQR) for the number of chews to swallow in *Cebus* was between 16 and 33 chews, while *Macaca* was between 30 and 57 chews. The mean values observed in the current study are lower than the lower limit of the IQR for both *Species*. This is because the Iriarte-Diaz et al. (2011) study used the number of chews to the *final* swallow, rather than to the *first* swallow as

in this current study. However, comparisons can still be made regarding the relative differences between *Species* instead of absolute values. For example, this study shows that *Macaca* uses on average 85% more chews than *Cebus* until the first swallow (28.7 vs. 15.5 chews, respectively). This is similar to the relative differences between *Species* reported by Iriarte-Diaz et al. (2011). The lower and upper limits of the reported IQR shows that *Macaca* uses 87% and 72% more chews, respectively.

These comparable increases in number of chews from ingestion to swallow ratios (*Cebus* vs. *Macaca*) provide further evidence that the data reliably coincide with Iriarte-Diaz et al. (2011). Variation is seen between the two because mean is not equivalent to median. Variation between the two studies resulted from our study examining data from ingestion to *first* swallow while the study by Iriarte-Diaz et al. (2011) examined data from ingestion to *final* swallow.

As mentioned in section 5.2.1 (DISCUSSION – Non-Human Primate Jaw Kinematics – Amount of Time from Ingestion to First Swallow) Iriarte-Diaz et al. (2011) suggested that when feeding on low-toughness foods, the more sporadic jaw kinematics of the *Cebus*, which may be driven by a flatter occlusal topography, can decrease the number of chews cycles by virtually half when compared to the *Macaca* data. The data support the finding that *Cebus* are capable of reaching the state of a swallow safe bolus more efficiently when compared to the *Macaca*.

5.3 Occlusal Fingerprint Analysis (OFA)

Combining the dental topography of *Cebus* and *Macaca* with the FMP based jaw kinematic profiles (Iriarte-Diaz et al., 2011) into the OFA software (DFG FOR 771, ZiFiLo IT Ltd., Ober-Ramstadt, Germany), allows visual representations of how all of these theories are intricately related to one another. Please reference *Figure 8 – OFA occlusal contact area data* to compare points of the chew cycle based on *Food Type* and *Species*, the maximum occlusal contact areas (*green* and *yellow*) in *Figure 8 – OFA 3D kinematic output* correlate with the apex of the linear projections in *Figure 8*. Finally, the OFA output is the occlusal contact area within the *power stroke*. According to Hiiemae (1978), the *power stroke* can be defined as the active phase of the chew cycle which mechanically breaks down the food. The *power stroke* begins with the slow close (SC) phase and continues through the slow open (SO) phase.

The greatest species difference noted within the OFA output presented as the bimodal linear projection of occlusal contact area noted within the *Macaca* species. The bimodal contact area not only reveals information about the jaw kinematics, it also provides information to explain dental topography and the FMPs of the *Food Types* consumed (*Figure 8 – OFA occlusal contact area data – Macaca*). With a bimodal projection of the occlusal contacts, comparisons can be made based on the dental topography seen within the *Macaca* molars. The more highly cusped M1s of the *Macaca* are thought to produce a more guided jaw kinematic sequence due to possible cuspal interferences. Due to the more pointed and highly cusped *Macaca* M1 dental topography, the occlusal contact

area changes based on the FMPs of the *Food Types* consumed. The *Dried Fruits* (high-toughness/low-stiffness) present with the highest initial occlusal contact area which increases only slightly as the food is chewed. The increased toughness (resistance to fracture) of the *Dried Fruits* allows for an immediate increase in occlusal contact area when compared to *Soft* foods and *Nuts*. The *Nuts* (low-toughness/high-stiffness) do not immediately reach their maximum occlusal contact area. This could be related to the fact that the pointed cusps of the *Macaca* are not as efficient in chewing *Nuts* (low-toughness/high-stiffness foods). Initially, having more pointed crowns while eating harder foods will cause more point-contact until the food is fractured. For the *Macaca*, the *Soft* foods (low-toughness/low-stiffness) have the smallest initial occlusal contact area, however these foods are mechanically broken-down quickly and this contact area almost triples in size later in the *power stroke*.

The OFA total occlusal contact area of the *Cebus* is drastically different from that of the *Macaca* (*Figure 8 – OFA occlusal contact area data – Cebus*). The *Cebus molars* with the more rounded cusps and flatter occlusal topography combined with the jaw kinematics while consuming *Food Types* with varying FMPs, results in a single peak OFA profile. As time progresses, this single peak is reached after a smooth, gradual increase in contact area, and ending in a sharp decrease. The peak occlusal contact area when consuming *Soft* foods and *Dried Fruits* were somewhat similar between the two *Species*. The *Cebus* peak occlusal contact area is nearly double that of the *Macaca* when consuming *Nuts* (low-toughness/high-stiffness). If contact area correlates directly with

chewing efficiency, with a *Cebus* contact area nearly double the size of the Macaca, the Cebus should reach the point of first swallow more quickly than the Macaca. This statement would coincide with the data collected within the jaw kinematic section of this study (Section 4.2 – RESULTS – Non-Human Primate Jaw Kinematics), stating that the Cebus consumes Nuts in less time and fewer chews than the *Macaca*. The *Food Type* consumed (Soft foods vs. Dried Fruits) vs. *Nuts*) is the rate-limiting factor. Both Soft foods and *Nuts* are capable of being crushed and ground-down more efficiently by the flatter occlusal topography of the Cebus. This finding coincides with Iriarte-Diaz et al. (2011), when it was said that the rounded cusps and flatter occlusal topography of *Cebus* results in a more sporadic (yet efficient, when assessing number of chews) jaw kinematic sequence when consuming *Food Types* of low-toughness. *Dried* Fruits (high-toughness/low stiffness) maintain their maximum occlusal contact area for the longest time. This plateau to the OFA data suggests that the occlusal topography of Cebus is less suited to efficiently crush and break-down Dried Fruits (high-toughness/low-stiffness foods) compared to the other Food Types tested.

5.4 <u>Limitations of the Study</u>

The data collected by Iriarte-Diaz et al. (2011) and Reed and Ross (2010) suggested that *Cebus* are primarily hard object, frugivorous feeders while *Macaca* are mixed, frugivorous/folivorous feeders. For purposes of this study, *Macaca* jaw kinematic data consuming a more folivorous diet were not provided.

When performing the experimental feeding at the University of Chicago, in an attempt to acquire ample jaw kinematic data, the non-human primate specimen was given a choice of foods to consume. Often times the specimen developed favorite foods within their diets and may have ignored other available foods.

Upon examination of the jaw kinematic data, occasionally a feeding sequence was noted which continued much longer. During the experimental feedings at University of Chicago, occasionally the keeper (or trainer) allowed the specimen to consume multiple pieces of food within one feeding sequence. This caused an inability to isolate the feeding events from one another. This caused the primary focus of this study to be on the *first swallow* rather than the *final swallow*.

Through the examination of the jaw kinematic data, "broken" or discontinuous chewing cycles were occasionally noted within the linear data projections. If this were to occur, that chewing sequence was excluded from the data and statistics of this study. These exemptions had a minor effect on the chewing sequence sample size.

VI. CONCLUSIONS

There are clear phenotypic differences between *Cebus* and *Macaca* molars. The open source MorphoTester software is a reliable way of achieving quantifiable dental topography variables; metrics used to categorize the occlusal complexities of a tooth. Statistically significant differences exist when comparing the quantifiable dental topography variables [occlusal surface area, occlusal outline area, Dirichlet normal energy, and occlusal patch count-rotated (OPCR)] when comparing *Cebus apella* and *Macaca mulatta*. However, no significant difference existed when comparing relief indexes (RFI) between the two *Species*.

The goal of jaw kinematics is to assure the production of a *swallow safe bolus* which dictates the initiation of the swallowing sequence and, eventually, nutrient assimilation into the body. Efficiency of jaw kinematics data can be measured in a variety of different ways. For the purpose of this study, the amount of time and the number of chews from ingestion to first swallow were categorized as an assessment for jaw kinematic efficiency. Statistically significant differences exist when comparing between *Species* (*Cebus* vs. *Macaca*), between *Food Types* (*Soft* foods vs. *Dried Fruits* vs. *Nuts*), and the interaction between *Species* and *Food Type.* The *Food Types* are categorized based on their previously published food material properties (FMPs): *Soft* foods (low-toughness/low-stiffness) vs. *Dried Fruits* (high-toughness/low-stiffness) vs. *Nuts* (low-toughness/high-stiffness). In context of efficiency, there is statistical significance indicating that both *Cebus apella* and *Macaca mulatta* take longer with an increased amount of time and number of chews from ingestion to first

swallow when consuming foods with low-toughness/high-stiffness FMPs (*Food Type – Nuts*). However, between *Species*, there is increased statistical significance indicating that *Macaca* are less efficient than *Cebus* when consuming foods with low-toughness/high-stiffness FMPs (*Food Type – Nuts*).

The Occlusal Fingerprint Analyzer (OFA) software (DFG FOR 771, ZiFiLo IT Ltd., Ober-Ramstadt, Germany) is an innovative method of assessing occlusal contact areas through combining high-resolution digital dental scans and dynamic jaw kinematic data. Through utilization of the most modern technology today, OFA provides a means to assess and quantify if tooth form follows function. The role of this software within the dental profession has yet to be fully explored. However, potential of OFA from the aspects of occlusal articulation, orthodontics, and restorative dentistry/prosthodontics appears limitless.

6.1 <u>Future Research</u>

In the past, tooth morphology and feeding physiology have been heavily researched topics. Today's technology is allowing old research topics to be revisited and improved upon. This is especially true for those within the dental profession, both in the university setting and in the private practice sector. Intraoral digital scanners are evolving and becoming less expensive by the day. This is allowing for an immense increase in the high-resolution digital dental models. Through open source software, such as MorphoTester, the dental variables of the digital models can be quantified and used for comparative research studies.

Finally, within the last decade, Occlusal Fingerprint Analyzer (OFA) software (DFG FOR 771, ZiFiLo IT Ltd., Ober-Ramstadt, Germany) has opened doors to innovative research regarding occlusal contact areas and jaw kinematics. This software has been utilized within the realm of anthropology, paleontology, mammalology, and oral science research, but has yet to be used within the dental profession. With occlusal articulation being a major emphasis within the professions of restorative dentistry, prosthodontics, and orthodontics, this software could prove to be very useful in the assessment of final restorations and/or tooth alignment.

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APPENDICES

Appendix A



Appendix A (Continued)



Appendix B



October 28, 2014

Office of Animal Care and Institutional Biosafety Committees (MC 672) Office of the Vice Chancellor for Research 206 Administrative Office Building 1737 West Polk Street Chicago, Illinois 60612-7227

To: University of Illinois Graduate College

From: Dr. Mary Bowman, Director, Office of Animal Care and Institutional Biosafety

Re: Thesis work involving the data collected from vertebrate animals conducted by John Polivka

This letter is to inform you that the thesis work comparing the relationship of jaw kinematics and occlusal dynamics to feeding efficiency in two species of nonhuman primates to be conducted by John Polivka will use 3D kinematic data of mandibular landmarks, morphological data of CT scans, and video to supplement the kinematic data that was previously collected from animals that were covered under an approved IACUC protocol at the University of Chicago. As this project does not involves only data and the data was collected previously and not at UIC, this project does not require a submission to the UIC Animal Care Committee (ACC). Should you have any questions regarding this matter, please contact the Office of Animal Care and Institutional Biosafety at the number listed below.

Phone (312) 996-1972 * Fax (312) 996-9088 * www.research.uic.edu

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