Dental variation in African apes with implications for understanding patterns of variation in species of fossil apes

by

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PREFACE

The Blind Men and the Elephant

It was six men of Indostan
To learning much inclined,
Who went to see the Elephant
(Though all of them were blind),
That each by observation
Might satisfy his mind

The First approached the Elephant,
And happening to fall
Against his broad and sturdy side,
At once began to bawl:
"God bless me! but the Elephant
Is very like a WALL!"

The Second, feeling of the tusk,
Cried, "Ho! what have we here
So very round and smooth and sharp?
To me 'tis mighty clear
This wonder of an Elephant
Is very like a SPEAR!"

The Third approached the animal,
And happening to take
The squirming trunk within his hands,
Thus boldly up and spake:
"I see," quoth he, "the Elephant
Is very like a SNAKE!"

The Fourth reached out an eager hand,
And felt about the knee.
"What most this wondrous beast is like
Is mighty plain," quoth he;
" 'Tis clear enough the Elephant
Is very like a TREE!"

The Fifth, who chanced to touch the ear,

Said: "E'en the blindest man
Can tell what this resembles most;
Deny the fact who can
This marvel of an Elephant
Is very like a FAN!"

The Sixth no sooner had begun
About the beast to grope,
Than, seizing on the swinging tail
That fell within his scope,
"I see," quoth he, "the Elephant
Is very like a ROPE!"

And so these men of Indostan
Disputed loud and long,
Each in his own opinion
Exceeding stiff and strong,
Though each was partly in the right,
And all were in the wrong!

John Godfrey Saxe (1816-1887)

ABSTRACT

Studying patterns of diversity and demarcating species in the paleontological context is problematic because fossil remains are fragmentary and samples are typically limited. In contrast, extant species can be potentially diagnosed using several types of data. Yet the assumption is that fossil species are equivalent to modern species. In this thesis I argue that if fossil and modern species are equivalent concepts, then patterns of variation in modern species should provide models that can be used to understand the nature of diversity in fossil forms and help delineate fossil species.

I document patterns of dental variation in *Pan* and *Gorilla* in a nested hierarchy from population to species. The following questions are addressed: (1) what dental characters can be used to differentiate the African apes at subsequently higher taxonomic levels? (2) How do patterns of variation using dental data compare with those based on other types of data? (3) How do adaptive strategies and phylogenetic history influence patterns of variation? These questions help to assess the utility of (1) dental material for recognizing species, and (2) extant species as models for discriminating fossil species.

341 chimpanzees and 299 gorillas were sorted into 16 and 14 populations, respectively, and about 400 dental traits were studied on each individual. Univariate and multivariate statistical techniques were used to analyze the data.

Results indicate that patterns of variation based on dental data match those based on other types of data, confirming the usefulness of dental data for recognizing species. However, patterns of dental variation differ markedly in *Pan* and *Gorilla*, being reflective of their adaptive strategies and unique evolutionary history. This signals the use of caution when applying models based on extant taxa for discriminating fossil species. Taxa that are phylogenetically related serve as better models, but it is advisable to draw common patterns from several taxa when developing models.

Finally, the patterns of variation in incisor morphology in all modern hominoid genera are applied to assessing the utility of lingual incisor morphology for discriminating species of Miocene apes. Based on this study suggestions are made regarding the taxonomy of some Miocene hominoid species.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDICES

CHAPTER ONE

Introduction

Introduction

There is a general consensus among biologists who deal predominantly with fossil material that the task of demarcating species in the paleontological context is qualitatively different from the modern context (Otte & Endler, 1989; Godfrey & Marks, 1991; Kimbel & Martin, 1993; Wheeler & Meier, 2000). In the modern (or neontological) context information pertaining to external morphology, ecology, behavior, genetic structure and patterns of interbreeding are used in recognizing and differentiating species. The nature of fossil data does not permit the use of the same criteria. Fossil data are characteristically fragmentary, mostly comprising teeth, and information about external morphology, ecology, *etc.*, which are paramount in identifying modern species (here also referred to as neontological species), are missing. In addition, the patterns and ranges of variation, which are useful in diagnosing, and drawing the boundaries between extant species cannot be studied because fossils are typically limited in sample size and anatomical representation. A further confounding factor is that unpredictable taphonomic processes often result in the commingling of specimens from a wide range of time periods and ecologies resulting in the likelihood that multiple species are present at a fossil locality. Because they possess these characteristics (or conversely, they lack the ones possessed by neontological species,) paleontological species are

commonly diagnosed using morphological criteria, in particular dental morphological criteria.

In this dissertation I examine the dental morphological correlates of population differentiation and taxonomic diversification in the African apes. Dental characters of presumed taxonomic significance are selected and the degree and patterns of variation are documented within known populations, subspecies and species. The purpose of the study is to establish a correspondence between neontological sytematics and paleontological systematics, and make suggestions regarding the use of extant taxa as models for sorting fossil specimens into species. The following questions are addressed: (1) what, if any, dental characters can be used to differentiate between subgroups of African apes, (2) what is the nature of variation in such characters (3) how do patterns of geographic differentiation revealed using dental data correspond with patterns recognized using other types of data, and (4) can patterns of dental variation be explained from the perspective of the evolutionary history and adaptive strategies of the African apes?

Species concepts

The criteria used in recognizing species differ markedly in the paleontological and neontological world, and accordingly several species concepts have been advanced that define and delineate species based on the data available to systematic biologists. The most well known species concept is the Biological Species Concept (Dobzhansky, 1937; Mayr, 1942). It defines species as "groups of actually or potentially interbreeding natural populations, reproductively isolated

from other such groups" (Mayr, 1942:120). This concept received wide acceptance when first formulated because it helped to provide a theoretical underpinning to the Typological or Morphological Species Concept, which was the dominant species concept for about 250 years prior to that time. The Typological Species Concept refers to the common practice, mentioned in the writings of Plato, Aristotle and Linnaeus, of partitioning the diversity within the natural world into discrete units (variously called *kinds* or *types* of *species*) using purely typological or morphological criteria (Mayr, 2000). This practice ran into difficulties when drawing the boundaries between continuous morphological types. For example, there were no clear criteria to tell apart within-species differences (ontogenetic series, for example) from between-species differences. The idea of reproductive isolation, as put forward by the Biological Species Concept, provides a means of drawing such a boundary. A species, according to the Biological Species Concept, has an inclusive gene pool and there are isolating barriers that confine the gene pool and prevent gene exchange. Recognizing a species merely requires identifying those isolating barriers.

The Biological Species Concept helped to foster the notion that species are real entities with firm boundaries around them (Ghiselin, 1974), and this provided ontological strength to the concept. The practice of recognizing species, however, was no different using this concept than it was using the Morphological Species Concept – the only way to identify the common gene pool and the isolating barriers

was by using indirect morphological and phenotypic criteria, including behavior, ecology and genetic structure.

The Recognition Species Concept was put forward by Paterson (1985) in an attempt to provide an alternate solution to the epistemological weakness of the Biological Species Concept. While the Biological Species Concept emphasized features (isolating mechanisms) that helped keep gene pools apart, the Recognition Concept moved the focus to the features that helped the species to be cohesive. Defined as "the most inclusive population of individual biparental organisms which share a common fertilization system" (Paterson, 1985: 25), the species, according to this concept, was easily recognized by identifying the common fertilization system. Paterson (1985) called this the Specific Mate Recognition System (SMRS) and suggested that studying the physiological and behavioral repertoire by which members of one sex recognize those of the opposite sex as potential mates help to identify the SMRS and thus circumscribe the species. The SMRS, according to this concept, is essential for the successful reproduction and propagation of the species. A fervent supporter of this concept, Vrba (1980) suggested that the SMRS was often tangible and even fossilizable (for example, horn cores of bovids) and therefore the Recognition Concept, unlike the Biological Species Concept, was potentially applicable to the fossil record in recognizing paleontological species.

The Recognition Concept and the Biological Species Concept are similar in that they both define species as reproductive communities sharing a common gene pool. Most biologists think the differences between the two are subtle, and they are

often thought of as slightly different manifestations of the same concept (Szalay, 1993; Mayr, 2000). The criteria of reproductive community and common gene pool being potentially observable only in the extant context, both of these concepts fall under the rubric of "neontological" species concepts. The application of the concepts, however, relies on phenotypic criteria. The major difference between the two concepts, apart from the difference in definition (in the inclusive-exclusivity criteria), is the explicit admission in the Recognition Concept that a species is recognizable only from the phenotypic realm (the SMRS) and not from barriers to gene exchange. The Recognition Concept in this sense has greater operational value than the Biological Species Concept.

Neither of these concepts, however, has much value in the paleontological context. The peculiarities of paleontological data do not permit the observance of the common gene pool or the species isolating mechanisms, and the data most often preserved (teeth) may not belong to the SMRS. Besides, since speciation events are rarely observed in the recent context, neither the Biological Species Concept nor the Recognition Concept defines species with respect to how they originate or go extinct. Recognizing species in the paleontological context affords the rare privilege of observing the temporal dimension and so evolutionary events of speciation and extinction are of particular significance in limiting paleontological species. Two species concepts which are particularly amenable to the paleontological record are the Phylogenetic Species Concept (Nelson & Platnik,

1981; Cracraft, 1983; Nixon & Wheeler, 1990), and the Hennigian Species Concept (Hennig, 1966).

The Hennigian Species Concept is clear in its definition regarding the origin and extinction of species. Hennig (1966) conceived of speciation as the splitting of a stem species into two daughter species, with the stem species then ceasing to exist. As modified by Willman (1985:120), species are defined as "reproductively isolated natural populations or groups of natural populations. They originate via the dissolution of the stem species in a speciation event and cease to exist either through extinction or speciation". The dissolution of the stem species at speciation is essential for the maintenance of monophyly. It is this criterion of monophyly that provides the theoretical strength to the cladistic technique of phylogeny reconstruction, which is Hennig's greatest contribution to evolutionary biology. Applying this concept in the practice of microtaxonomy, however, is problematic because species are conceived as reproductively isolated populations and there is no indication that speciation is coupled with morphological change. At a branching or speciation event the two newly derived sister species do not always possess apomorphic characters relative to one another or to the stem species. Yet, apomorphic characters are of utmost importance in phylogeny reconstruction using cladistic analysis. Recognizing new species after a speciation event is no different using this concept than it is using the Biological Species Concept, and according to Meier & Willman (2000:39), "the two daughter species may be distinguishable only by extrinsic evidence (such as the age of the daughter species)."

The Phylogenetic Species Concept (Nelson & Platnik, 1981) also draws inspiration from the work of Hennig (1966), but unlike the Hennigian Species Concept this concept does not advocate the extinction of a stem species following a speciation event. Speciation, according to this concept, may take place through anagenesis (gradual change from one species to another) or through cladogenesis (a branching event resulting in either one or two daughter species), but species can only be recognized using a character-based approach. A species, according to this concept is "a smallest aggregation of (sexual) populations or (asexual) lineages diagnosable by a unique combination of character states" (Nixon & Wheeler, 1990:218). By putting the emphasis on character reconstruction in recognizing species this concept suggests that morphological change and speciation are inseparable and therefore morphological change implies speciation. This concept is directly applicable to the fossil record in sorting fossil specimens into species. By using only phenotypic criteria in both taxonomy and phylogeny reconstruction this concept is theoretically more consistent compared with the Hennigian Species Concept.

What the Phylogenetic Species Concept gains in epistemological strength it loses in ontology. Species are recognized as phenotypically distinct clusters easily differentiated from other such clusters, but whether such clusters correspond with species in the natural world, with enclosed reproductive communities, or subspecies, with more open reproductive communities, is a moot point. Therefore, species recognized using the Phylogenetic Species Concept are often referred to as

paleospecies or morphospecies, and are not directly comparable to neontological species, which are often referred to as biospecies (papers in Kimbel & Martin, 1993).

There have been tremendous leaps in our understanding of population genetics since the time of the Typological and Morphological Species Concepts, yet this review suggests that translating that knowledge into the practice of recognizing species is unattainable. In essence, although species concepts differ in their ontological strength, indirect phenotypic criteria are predominant in the identification of both neontological and paleontological species.

Unlike paleontological species, however, for which dental data provide the primary material for species diagnosis, the diagnosis of neontological species can be further corroborated using additional morphological, genetic, ecological and behavioral data, justifying the argument that neontological species are better diagnosable than paleontological species – the greater the corroboration, the firmer the diagnosis. There is an implicit assumption that the species recognized using multiple datasets constitute enclosed reproductive communities, but this assumption (or hypothesis) can only be validated, perhaps even strengthened, by subsequent endorsements, it cannot be proven (except, perhaps, in the case of allospecies). This implies that both paleontological and neontological species are morphospecies, but neontological species by virtue of their superior diagnosability are more likely also to be biospecies.

Equivalent Concepts

In spite of this obvious asymmetry in both the systems of information used in identification and ultimately in the testing of hypotheses of neontological and paleontological species, the underlying assumption is always that extinct and extant species should be equivalent concepts (contributions in Wheeler & Meier, 2000; Kimbel & Martin, 1993; Otte & Endler, 1989). In other words, the morphological clusters recognized as fossil species are considered to correspond to populations sharing a common gene pool and a diagnostic morphology, just as they do in the neontological context. This assumption of equivalence is essential if concepts derived from neontological studies of population genetics and evolutionary biology are to be applied to patterns of speciation and phylogeny in the fossil record. It follows from this, then, that the ranges and patterns of variation seen in living species should provide models that can be used to understand the nature of variation that characterized extinct forms, and thus provide criteria and standards for defining (although not necessarily delimiting) fossil species. In fact, given the meager nature of fossil samples, patterns of variation within extant species have been suggested to be the only practical yardstick by which to partition the variation within fossil samples into species (Vitzthum, 1984; Tattersall, 1986; Turner & Chamberlain, 1989; Delson, 1990; Kimbel, 1991; Wood, 1991; Godfrey & Marks, 1991; Kimbel & Martin, 1993; Harrison, 1993; Shea *et al.*, 1993; Miller, 2000; Plavcan & Cope, 2001).

Miocene hominoid systematics

The use of extant ranges of variation as a standard for delimiting fossil species applies, in particular, to the Miocene hominoid fossil record. Large-bodied hominoids from the Miocene period of Africa, Asia and Europe exhibit high levels of diversity even within a single fossil locality. The morphology of molars, which is the best data available, has not proved useful in sorting fossil specimens into species because of the high degree of variation, within and between localities, in this morphology (Kelley & Pilbeam, 1986). Consequently, debates regarding alpha-taxonomy ("taxonomic work concerned with the recognition and diagnosis of species as distinct from others", Szalay & Delson, 1979: 557) abound in this literature (*e.g.*, Kay, 1982a, 1982b; Kay & Simons, 1983; Kelley, 1986; Pickford, 1986a, 1986b; Kelley & Pilbeam, 1986; Harrison, 1991; Ribot *et al*., 1996; Andrews *et al*., 1996).

Following the demonstration that, in mammals, linear dimensions of molars have low ranges of variation (Gingerich, 1974; 1979; Gingerich & Schoeninger, 1979), ranges of variation in molar dimensions of extant primate species have often been used as a standard by which to determine species numbers in Miocene hominoid localities (*e.g.*, Kay & Simons, 1983; Martin, 1983; Martin & Andrews, 1993b; Teaford et al., 1993; Walker et al., 1993; Pilbrow, 1994). Cope & Lacy (1992), Cope (1993), and Plavcan (1993) have demonstrated, however, that dental dimensions have limited value in determining species numbers – extant ranges of variation, they found, can only be used to falsify a single species hypothesis; they

cannot be used to determine the number of species in a mixed-species fossil sample.

Kelley (1986; Kelley & Pilbeam, 1986) made the provocative suggestion that there is no theoretical basis for the assumption that ranges of variation should be the same in extinct and extant life forms. He used this argument to propose the presence of a single, sexually dimorphic species, *Proconsul nyanzae*, from the Miocene locality of Rusinga and Mfangano in East Africa. In the range of canine size dimorphism this species has no modern analogue. Kelley's position has been vociferously debated. Martin & Andrews (1993) and several others (contributions in Kimbel & Martin, 1993) have argued that paleontological systematics, because of lack of verifiability, can only operate under the principles of uniformitarianism. An important tenet of this principle is falsifiability: unless extant ranges of variation are used to set standards, they argue, paleontological systematics has no basis in present-day biology.

Recently, other features of the dentition have been used to differentiate species in Miocene hominoid localities. In particular, it has been demonstrated that the morphology of the lingual side of the upper central incisor is complex and differs between localities (Begun *et al.*, 1990; Begun, 1992). Although fossil samples are not large enough to document the full extent of variability, Begun *et al.* (1990) used characters on the lingual side of the UI1 to differentiate species of *Dryopithecus* in Spain. Since then, this morphology has been used to argue for the presence of multiple species at the site of Pasalar in Turkey (Martin & Andrew,

1993) and to justify generic separation of *Equatorius* from *Kenyapithecus* in Africa (Ward *et al*., 1999). Preliminary studies suggest that this character is variable in appearance in extant species (Kelley *et al.*, 1995; Ribot *et al*, 1996), and therefore its utility in differentiating fossil species is contested (Harrison, 1991; Ribot *et al.*, 1996; Benefit and McCrossin, 2000).

This study

In this thesis the ranges and patterns of variation in dental morphology in extant species of *Pan* and *Gorilla* are used to develop models that are applied to the study of patterns of variation in species of fossil apes. The patterns of variation in the African apes have been studied for many trait systems including external morphology, geographical distribution, behavioral characteristics and genetics (Coolidge, 1929; Schwartz, 1934; Hill, 1969; Groves, 1967; 1970; 2001; Goodall & Groves, 1977; Groves & Stott, 1979; Casimir, 1975; Coolidge & Shea, 1982; Shea & Coolidge, 1988; Morin *et al*., 1994; Ruvolo *et al*., 1994; Gonder *et al*., 1997). These provide a basis for comparison with patterns of dental variation revealed by this study.

Due to the predominance of teeth in fossil samples, aspects of dental morphology are often the primary criteria used in the diagnosis of fossil species. However, the reliability of dental morphology in fossil species recognition has rarely been evaluated. Recently, the utility of dental morphology in reconstructing fossil phylogenies has been questioned (Collard & Wood, 2000). In this project, dental samples of *Pan* and *Gorilla* are sorted first into populations and then into

subspecies and species, and the range and patterns of variation in occlusal surface characters are documented at each of these levels of organization.

Starting the study at the level of the population helps to assess patterns of variation without the constraints of a formal taxonomy. The taxonomy revealed from dental morphology is then compared with the taxonomy established using other types of data. This helps to assess the utility of dental morphology for recognizing fossil species, and also the validity of the traditional taxonomy.

A "population", in this study, refers to a collection of demes ecologically segregated from other such demes. A "deme" is defined by Endler (1977: 180) as a "spatially discreet breeding unit; an effectively panmictic aggregate of organisms lasting for at least one breeding session, and connected by gene flow with the neighboring demes before and after reproduction". In this study, a geographical locality from which dental specimens were obtained in a museum is considered, as a convenient starting point, to be a "deme". Several demes were combined to form a population. Subpecies and species of *Pan* and *Gorilla* are considered to be the ones commonly accepted by primate systematists (reviewed in Jenkins, 1990; Groves, 2001). When studying patterns of variation at a higher-order taxonomic level, populations were aggregated into subspecies and species, using these traditionally recognized groups. However, since the analysis begins at the level of the population, the traditional taxonomy is evaluated before subscribing to it.

When applying a model one must be aware of the limitations of one's model. Translated into the present situation, when using neontological taxa as

models for recognizing fossil species the appropriateness of modern taxa as models should be evaluated. Patterns of variation in modern taxa are known to differ due to the effects of scaling, differences in adaptive strategies and the random forces of genetic drift. The role of adaptive and non-adaptive forces in promoting variation in the African apes is studied in this project by correlating patterns of dental variation with size and non-size related factors.

Ranges and patterns of variation in modern taxa are also known to differ in a nested hierarchy. The degree and patterns of dental variation in *Pan* and *Gorilla* are studied at different taxonomic levels – the population, the subspecies and the species. A comparison of the type and degree of variation at these levels helps us understand, first, how variation is partitioned, and, second, the types of dental characters that are useful in differentiating modern species and infraspecific groups. This enhances our understanding of the modes of speciation in these two taxa. Based on this comparison, appropriate models can be developed for applying to fossil hominoids.

In addition to providing general models for studying dental variation in fossil species, the ranges and patterns of dental variation within closely related modern taxa can be used to evaluate the utility of particular paleontologically-relevant dental characters. As a test of the model, patterns of dental variation in a single taxonomic character, lingual incisor morphology are examined in this thesis by documenting the nature of variation in this region in all four genera of modern hominoids (*Pan, Pongo, Gorilla* and *Hylobates*). As outlined above, incisor

morphology has been used to differentiate several Miocene ape species, and here I test the taxonomic utility of this character by bringing together a comprehensive analysis of patterns of variation in modern hominoids along with the latest theoretical advances in species concepts and species recognition.

The aims of this thesis are as follows:

(1) To establish firm taxonomic standards for the use of dental characters in paleontological species discrimination. It has been argued that the lack of rigid taxonomic standards in paleontology that are biologically relevant and have universal application is partly the reason why paleontological species discrimination continues to be a problematic issue (Conroy, 1990). This project makes a contribution towards resolving some of these problems by providing a valuable comparative database of the degree and patterns of variation in occlusal surface characters in the African apes from which explicit models can be formulated for evaluating characters used in diagnosing species of fossil hominoids. This will help in understanding the alpha-taxonomy of the fossils. Reconstructing alpha-taxonomy is a critical first step prior to reconstructing the phylogeny and paleobiology of fossils.

(2) To further our understanding of modes of speciation and microevolutionary change in the African apes. The patterning of variation in any modern group is inextricably linked to its adaptive strategies, and its unique evolutionary and biogeographic history. To be useful as a model it is important to understand the patterns of variation within the context of this framework. Documenting the

patterns of dental variation in *Pan* and *Gorilla* at the level of the species and below will help to understand the dental morphological correlates of population differentiation and taxonomic diversification in these apes and improve our understanding of the population dynamics in these groups. This will provide appropriate models that are applicable to examining, not just the range, but the patterning of variation in fossil species.

(3) To use the models based on patterns of dental variation in the African apes to make suggestions regarding the alpha taxonomy of the Miocene apes. Debates in Miocene hominoid systematics center over whether one or more species is present at a fossil locality. Species are differentiated using detailed characters on the occlusal surface of the dentition, but there is lack of agreement over whether the taxonomically relevant characters lie within the range of variation seen in modern species. By documenting the types of occlusal characters that differentiate modern species and subspecific groups and the range of variation in such characters, this study provides a theoretical basis for accepting or rejecting the current hypothesis concerning the taxonomy of the Miocene apes.

Background

Dental Morphology

Mammalian fossil assemblages are mostly composed of teeth because teeth have a unique preservational quality – they are made of dense organic and inorganic material that does not decompose easily. Molars, perhaps because their

contoured shape is conducive to preservation, have a disproportionately high representation in the fossil samples. Because of their large occlusal area with more complex morphology compared to incisors, canines and premolars, molar morphology is commonly used in differentiating fossil species. Molar morphology forms the primary focus of this study given its significance for fossil species recognition. Detailed characters on the occlusal surface of molars that are of taxonomic value in identifying and differentiating the African apes are selected and the range and patterns of variation in these characters documented. Image analysis techniques are used for measuring the characters. In addition to quantifiable dental characters, other dental characters that also have taxonomic utility but cannot be easily measured are studied using qualitative criteria.

Dental studies form an integral part of anthropological studies. For several decades the role of dental morphology in paleontological studies has been critically evaluated (*e.g.*, Gregory, 1922; Remane, 1960; Butler, 1956; 1963; Butler & Joysey, 1978; Dahlberg, 1968; Brothwell, 1963; Hiiemae & Kay, 1973; Kay & Hiiemae, 1974; Robinson, 1956; Molnar & Gantt, 1977; Grine, 1981; Hartman, 1988; Martin, 1990; Plavcan, 1990; Jernvall & Jung, 2001). Using ranges of variation within extant primate species the importance of dental characters as taxonomic discriminators has been appraised (*e.g.* Ashton, 1953; Dahlberg, 1945; 1949, 1950; Schuman & Brace, 1954; 1955; Frisch, 1963; 1965; Mahler, 1973; Simons & Pilbeam, 1965; Gingerich & Schoeninger, 1979; Martin, 1983; Jørgensen, 1955; Garn *et al.*, 1963; 1967; Howells, 1973; Biggerstaff, 1969;

Korenhof, 1960; 1978; Corruccini, 1975; Swindler, 1976; Pickford, 1986a; 1986b; Tattersall, 1993; Cameron, 1995; Kelley, 1995; Waddle et al., 1995). The conclusions of such studies have then been applied in taxonomic revisions of paleontological species (e.g. Pilbeam, 1969; Simons & Pilbeam, 1965; Kay & Simons, 1983; Pickford, 1986a; 1986b). These early estimates of ranges of variation, however, were based on visual assessments of the taxonomic characters, and no objective measures of variability were provided.

There have been few instances where image analysis techniques have been used to measure features on the occlusal surface of molars (Erdbrink, 1965; Wood & Abbott, 1983a; Uchida, 1996). This technique, by which measurements are taken on a scaled image of a molar, provides accurate measurements of features that are continuous in their nature of variation but were previously described qualitatively because of difficulty in quantification. The molar crowns of the extant apes being bunodont (that is, they have low occlusal relief) are particularly amenable for this technique. In this project qualitative dental traits that are commonly used in differentiating fossil species are measured in a quantitative manner using the image analysis methodology. Dental traits that are discrete in their manner of appearance, or that are difficult to measure on an image are measured in a qualitative manner using descriptive codes.

The extant apes

Chimpanzees and gorillas are the two extant taxa most closely related to modern humans. Humans are more closely related to chimpanzees, but gorillas are

the closest sister taxon to this clade (Ruvolo, 1997). Because of this phylogenetic affinity patterns of variation in African apes are commonly used as models in differentiating species of fossil hominids. Also, because of this phylogenetic affinity, the African apes are the most well studied group of non-human primates. However, there are very few studies (except, for example, Johanson, 1974; Kinzey, 1984) that document the nature and patterns of variation in dental morphology in these apes. Such a study, while directly applicable to assessing the taxonomy of fossil hominids and hominoids, also provides a comparative data set against which to compare patterns of variation in previous studies.

Pan is commonly divided into two species, *P. paniscus* and *P. troglodytes*, separated by the River Congo in Zaire. *Pan paniscus* is a monotypic species. It has a restricted range of distribution along the southern bank of the Congo River. *Pan troglodytes* has a wide distribution from Senegal in west Africa to Tanzania in east Africa. It is traditionally divided into three subspecies – *P. t. troglodytes, P. t. schweinfurthii* and *P. t. verus*. *Pan troglodytes verus* is found in the western range of its distribution from Senegal to Nigeria. *Pan troglodytes troglodytes* and *P. t. schweinfurthii* are found in central Africa. The River Ubangi in the Congo Republic separates the two. Recent research supports the presence of another subspecies, *P. t. vellerosus* (Gonder *et al.*, 1997) along the north of the Sanaga River in Cameroon.

Gorilla is found in two disjunct areas – in west Africa from Nigeria to the mouth of the Congo River, and in east Africa in Rwanda and Burundi. No gorillas

are found along the north or the south of the Congo River. Gorillas in west Africa are, on the whole, more widespread than in east Africa. The east African populations are found at variable altitudes and several of them are isolated. This patchy pattern of distribution is reflected in the current state of flux in gorilla taxonomy. Until the 1970s the east and west African gorillas were recognized as two subspecies: *G. g. gorilla* in west Africa and *G. g. beringei* in east Africa. Since then, several isolated east African populations have become known and these have also been designated as distinct subspecies. *Gorilla gorilla beringei* is restricted to populations found at the highest altitudes; populations from the lowest altitudes are known as *G. g. graueri*, and several others are known in between (see Chapter Four).

Chimpanzees and gorillas are both large-bodied primates that dominate their ecosystem (they have no known predators), yet they occur in sympatry in equatorial Africa. Kelley (1993) has argued that large body size places a limit on the number of species that can occur in sympatry, particularly in tropical forest habitats. He argues that reduced diversity in numbers of species in great apes, therefore, is not a recent phenomenon but was part of their evolutionary history. Kelley's model suggests that if large bodied mammals are found in sympatry in tropical forests they are unlikely to be closely related. This explains why sympatric *Pan* and *Gorilla* differ markedly in morphology and ecology, and are taxonomically differentiated at the level of genus.

Kelley's hypothesis fits with the allopatric nature of distribution of chimpanzees and bonobos, the two species of *Pan*. It suggests, however, that particularly in areas of sympatry the niches utilized by chimpanzees and gorillas should be non-overlapping. Recent research has shown, contrary to this hypothesis, that in areas of sympatry lowland gorillas from west Africa converge on the niche of chimpanzees in diet and substrate use by incorporating a frugivorous component to their diet and being more arboreal than mountain gorillas from east Africa (Remis, 1997).

A study of patterns of dental variation in the African apes provides an opportunity to test Kelley's hypothesis. For the purposes of this study, the hypothesis predicts that sympatric chimpanzees and gorillas will have easily differentiated dental morphology, and the patterns of dental variation will be substantially different. This will be tested by examining if, and how, patterns of sympatry and allopatry impact on patterns of dental variation in the African apes. Their patterns of dental variation will then provide models for mixed species samples of fossil hominoids.

Lingual incisor morphology

This study provides a database of the degree and patterns of variation in dental characters in species and infraspecific groups of African apes. From this, appropriate models can be selected for evaluating dental characters used in discriminating species of fossil hominoids. After documenting the nature and

patterns of variation in the extant apes the relevance of lingual incisor morphology for taxonomic differentiation will be examined. The nature and patterns of variation in this morphology is first documented in all four genera of modern hominoids at different taxonomic levels. The role size, sex and dietary difference in causing this variation is explored. Based on this study the utility of this morphology for differentiating Miocene apes species is evaluated. This dental character serves as an example to consider the role of variation in promoting diversification and speciation.

Outline of the thesis

The study of dental variation in *Pan* and *Gorilla* each form a separate chapter (Chapter 3 and 4), and they both have a similar layout. First, previous studies documenting the nature and patterns of variation in these genera are reviewed. The conclusions of these studies are used to formulate hypotheses for testing using dental data. Dental samples are then sorted into populations and the patterns of geographic variation are examined. The population structure revealed using dental data is then compared with previous taxonomic studies so as to assess the reliability of dental data in discriminating fossil species. The role of functional and non-functional factors in promoting variation is also evaluated. Populations are then combined into the recognized subspecies and species, and the ranges of variation compared in a nested hierarchy. These are used to explore patterns of gene flow and modes of speciation.

In chapter five the patterns of dental variation in *Pan* and *Gorilla* are compared. An attempt is made to explain the patterns of variation within the context of the biogeographical history, patterns of gene flow and the evolutionary history of these apes. Based on the differences, the implications of these models for discriminating fossil species are discussed. In chapter six, the patterns of variation in all four hominoid genera are used in examining the taxonomic utility of incisor morphology for discriminating species of Miocene apes, as explained above. This comparative study is used to comment on the proposed taxonomy of some Miocene ape species. In chapter seven, the main findings of the study are summarized and these are used to evaluate the utility of various species concepts in differentiating species.

Thus, the thesis is divided into three sections: description, comparison and application. The first section describes the nature of dental variation in the African apes, in the second section patterns of variation are compared and their utility as models investigated, and in the final section the patterns of variation in all four modern hominoid genera are applied towards studying the relevance of incisor morphology for fossil species discrimination.

CHAPTER TWO

Materials and Methods

Introduction

This chapter provides the procedural details of the steps involved in collecting dental data and analyzing it. The first section describes the study sample – the criteria used in selecting the material, where the samples were studied, and the numbers of specimens examined. In the next section, the practical and theoretical considerations used in dividing the extant hominoids into demes and populations are first explained, and then the population divisions for each of the genera are outlined. The procedures used in collecting the quantitative and qualitative data are described in the next section, along with details of the dental characters selected for study and the measurements taken. In the final section the statistical techniques employed in the thesis are described, including the methods used for exploratory data analysis for identifying outliers and missing data points, the statistics used to correct these missing data, the data transformations used, and the statistics used in analyzing the corrected data.

Materials

A total of 1133 modern hominoid maxillary and mandibular specimens was studied from five museums in the USA and seven museums in Europe (Table 2.1). Sample sizes vary quite considerably between subspecies and the sample sizes for some of the subspecies of *Hylobates* are small. This is because of a bias in museum

Table 2.1 Extant hominoid study sample. Taxonomic attributions follow Jenkins (1990). For list of abbreviations see Table 2.3.

Subspecies	Museum	Number of specimens
Pan troglodytes troglodytes	AS/Z, FMNH, MNHN, PCM., RG, USNM, ZSM	152
Pan troglodytes verus	AS/Z, AMNH, BMNH, MNHN, MCZ, PM, RG, USNM	64
Pan troglodytes schweinfurthii	RG, USNM, ZMB	79
Pan paniscus	RG, MCZ	46
Gorilla gorilla gorilla	AMNH, AS/Z, BMNH, FMNH, MNHN, MCZ, PCM, RG, USNM, ZMB, ZSM	208
Gorilla gorilla graueri	BMNH, FMNH, ZMB	61
Gorilla gorilla beringei	BMNH, MNHN, MCZ, RG	30
Pongo pygmaeus pygmaeus	AS/Z, MCZ, USNM, ZMB, ZSM	143
Pongo pygmaeus abelli	AS/Z, ZSM, ZMB	21
Hylobates lar lar	BMNH, USNM	6
Hylobates lar vestitus	BMNH, USNM, ZMB	9
Hylobates agilis unko	BMNH, USNM, ZMB	20
Hylobates lar entelloides	AS/Z, BMNH, FMNH, MCZ, USNM, ZMB	112
Hylobates agilis agilis	FMNH, USNM, ZMB	4
Hylobates agilis albibarbis	USNM, ZMB, ZSM	9
Hylobates moloch	BMNH, MCZ, USNM, ZSM	5
Hylobates muelleri abbotti	AMNH, BMNH, FMNH, MNHN, ZMB, ZSM	38
Hylobates muelleri funereus	AMNH, AS/ Z, BMNH, FMNH, MCZ, MNHN, USNM, ZSM	32
Hylobates pileatus	AS/Z, BMNH, USNM	12
Hylobates klossii	BMNH, FMNH, MCZ, USNM, ZMB	15

Table 2.1 Extant hominoid study sample (continued)

Subspecies	Museum	Number of specimens
Hylobates hoolock hoolock	BMNH	7
Hylobates hoolock leuconedys	BMNH, USNM	3
Hylobates leucogenys leucogenys	BMNH, FMNH	7
Hylobates leucogenys gabriellae	BMNH, FMNH, MNHN	11
Hylobates concolor concolor	BMNH, FMNH, MCZ, USNM	21
Hylobates syndactylus syndactylus	AS/Z, BMNH, USNM, ZMB, ZSM	18
TOTAL		**1133**

Table 2.2 Fossil hominoids studied. See Table 2.3 for list of abbreviations.

Species	Museum	Number of specimens
Dryopithecus	IPS; MNHN; MHNBx; NHMW; GIW; UW; RUD; SMNS; GPIT; SMF/RH	134
Proconsul	BMNH; KNM	295
TOTAL		429

collections discussed in greater detail in the next section. Sample size correction criteria (Sokal & Rohlf, 1981) and posthoc discriminant analyses were used when analyzing these data. 134 cranial and dental specimens of *Dryopithecus* and 295 specimens of *Proconsul* were also studied from ten museums in Europe and Africa (Table 2.2).

Only wild-caught individuals were included in the extant sample and both recent and fossil samples comprised only adult individuals. As far as possible, a balance was maintained in the representation of the sexes. Specimens of unknown provenience were excluded from the analysis, as were specimens with heavily worn teeth.

Population divisions

Museums provide invaluable skeletal material for population studies, especially for studies using dental material as undertaken here. A major shortcoming in using museum material, however, is that the geographical distribution of animals in the wild is not adequately reflected in the museum collections. Probably because of a collector's bias, many museums have specimens from the same localities, resulting in an abundance of material from certain locales, whereas other areas are poorly represented. For example, a combined sample of more than 400 *Pan troglodytes verus* individuals from Liberia is available for study at the Peabody Museum at Harvard University and the Senckenberg Museum in Frankfurt, but other populations of this subspecies are not well represented in museums. In this study I was able to study large samples of chimpanzees from

Table 2.3 List of Abbreviations

AMNH	American Museum of Natural History, NY
AS/Z	Anthropologisches Institüt und Museum der Universität Zürich-Irchel, Zürich
BMNHBritish	Museum of Natural History, London
FMNH	Field Museum of Natural History, Chicago
MCZ	Museum of Comparative Zoology, Cambridge
MNHN	Muséum National d'Histoire Naturelle, Paris
PCM	Powell-Cotton Museum, Kent
PM	Peabody Museum, Cambridge
USNM	United States National Museum, Washington, D.C.
RG	Musée Royal de l'Afrique Centrale , Tervuren
ZMB	Zoologisches Museum, Berlin
ZSM	Anthropologische und Zoologische Staassammlung, Münich.
MHNBx	Muséum d'Histoire Naturelle, Bordeaux
NHMW	Naturhistorisches Museum, Vienna
GIW	Geologisches Bundesanstalt, Vienna
UW	University of Vienna, Vienna
RUD	Geological Institute of Hungary, Budapest
SMNS	Staatlisches Museum für Naturkunde, Stuttgart
GPIT	Karl-Eberhardt Universität, Tübingen
SMF/RH	Senckenberg Museum, Frankfurt
KNM	Kenya National Museum, Nairobi
IPS	Institut Paleontologic Dr. Miguel Crusafont, Sabadell.
IUCN	International Union for Conservation of Nature and Natural Resources
MD	Mesiodistal
LaLi	Labiolingual
BL	Buccolingual
MB	Mesiobuccal
DL	Distolingual
CEJ	Cementoenamel junction
UI1	Upper central incisor
UI2	Upper lateral incisor
LI1	Lower central incisor
LI2	Lower lateral incisor
UC	Upper canine
LC	Lower canine
UP3	Upper first premolar
UP4	Upper second premolar
LP3	Lower first premolar
LP4	Lower second premolar

Table 2.3 List of Abbreviations (continued)

UM1	Upper first molar
UM2	Upper second molar
UM3	Upper third molar
LM1	Lower first molar
LM2	Lower second molar
LM3	Lower third molar
CV	Coefficient of Variation
R%	Range as a percentage of mean
mtDNA	Mitochondrial DNA
DNA	Deoxyribonucleic acid
DF	Discriminant function

Liberia, and chimpanzees and gorillas from Cameroon and Gabon. This is reflected in the large sample size for the subspecies these populations represent (*P. t. verus*, *P. t. troglodytes* and *G. g. gorilla* as depicted in Table 2.1). However, as also seen in Table 2.1, sample sizes for *P. paniscus* and *G. g. beringei* were small.

On account of this imbalance in museum collections, previous studies examining regional differentiation established demes based on available museum material and then coalesced these demes to form populations (*e.g.*, Groves, 1967; 1970b; Shea *et al.*, 1993). Thus, while some populations were made up of a single locality, in other cases several localities were combined to form a population. Statistical techniques of clustering were used to combine demes into populations, and ecological information such as vegetation zones, rivers, and altitude was taken into account when determining the boundaries between populations (e.g., Braga, 1995). Many of the ecological zones used to draw the boundaries between populations were arbitrarily assumed to be of importance in maintaining genetic discontinuity. Biogeographic information now emerging suggests that some of these ecological boundaries may not be as effective in impending gene flow as was previously assumed (Oates, 1996; Grubb, 1990; Gonder *et al.*, 1997). One such example is the Niger River in West Africa. This river has traditionally been used to mark the boundary between *P. t. verus* and *P. t. troglodytes*, and several other primate taxa. Recent research suggests that the importance of the Niger River is overstated; the western boundary of *P. t. troglodytes* may lie further to the east (Grubb, 1990; Gonder *et al.*, 1997). The River Sanaga in Cameroon, on the other

hand, is now acknowledged to be a major ecological boundary (Oates, 1996; Grubb, 1990; Gonder *et al.*, 1997). Ongoing field studies have helped map the distribution of primates and other animals in the wild more accurately and the most effective ecological boundaries are now being identified.

Hominoid material in this study was sorted into demes and populations in the following manner. Locality data were obtained from museum records and verified against the US Official Standard Names Gazetteers (published by the United States Geological Survey). Specimens whose locality could not be verified were dropped from the study. Dental specimens with known provenience were then sorted into populations using as a guideline the locality lists outlined in previous museum based studies: Groves (1967; 1970b) for gorillas; Shea *et al.* (1993) for chimpanzees; Röhrer-Ertl (1984) for orangutans and Marshall and Sugardjito (1986) for gibbons. These initial groups of localities (or demes) were then redistributed into populations using primate distribution patterns and information about centers of species abundance taken from works such as Oates (1996), Grubb (1990), and Wolfheim (1983). Statistical techniques of hierarchical clustering were also used along with geographical data to combine demes into populations by identifying closely related populations.

Grubb's (1990) research was most influential in assembling African ape populations and needs to be explained in greater detail. Grubb collected information about the distribution of African primates and other species from museum records and combined this with observations about primate distribution

patterns from field studies. He used these to identify areas where several species or subspecies of primates congregate. He designated these areas as primate biozones or centers of species endemism. He then identified the ecological boundaries surrounding these centers, suggesting that these were most likely to have been effective for allopatric speciation. These boundaries are used in this study to demarcate populations. Grubb's analysis is preliminary, however, and not all biozones are identified. In particular more work needs to be done to recognize the east African primate biozones (Grubb, 1990).

Chimpanzees

The 341 chimpanzee specimens were first sorted into 36 localities as outlined in Shea *et al.* (1993). These were then clustered into 16 populations using the criteria outlined above. The populations and the localities included are as follows:

Pan troglodytes verus

(1) Between rivers Gambia and Sassandra: Guinea, Sierra Leone, Liberia

(2) Between rivers Sassandra and the Volta: Ivory Coast, Ghana, Togo

(3) Between rivers Ogun and Niger: Lagos, Benin (City)

Pan troglodytes troglodytes

(4) Bamenda highlands: Cameroon/Nigeria border (Cross River district), Mt. Cameroon and Bamenda highlands

(5) Lower river Sanaga: Edea/Ongue Kribi/Bipindi (Cameroon Coast)

(6) Inland of Coast: Efulen/Ebolowa, Yaounde/Akonolinga, Lomia/Dja River,

Batouri and upper Sanaga, Southeast Cameroon (middle Sanaga)

(7) Rio Muni: Rio Muni and borders, Gabon estuary, Lamberene/ Mimongo, Makokou/Belinga (northeast Gabon), Mambili/Ouesso (northeast Congo)

(8) Southern Gabon: Brazzaville, Sette Camma/ Fernan Vaz (southern Gabon coast), Mayombe

Pan troglodytes schweinfurthii

(9) Between rivers Ubangi and Zaire: Lisala region

(10) Uele River

(11) Kisangani district

(12) Lake Albert to north of Lake Tanganyika: Ituri/Lake Albert, Rutshuru/Toro/Ankole, Entebe, Rwanda, Burundi

(13) Lake Kivu and Lake Tanganyika: Kivu/Maniema, Fizi/Boko, Moba, Kibwesa

Pan paniscus

(14) Between rivers Zaire and Kasai: Mbandaka/Bolobo

(15) Between rivers Lomani and Zaire: Befale, Lopori, Wamba, Lomela, Lubefu

(16) Between rivers Wamba and Kasai: Kasai

Table 2.4 shows how the 16 populations compare with Shea *et al*.'s localities and Grubb's (1990) biozones. Several of the localities identified by Shea *et al.* did not fall within the centers identified by Grubb, and therefore modifications were made to include these localities. For instance, Population 8 and 13 identified in this study do not fall within any of Grubb's centers. Moreover, although the Rio Muni marks a boundary between Grubb's centers, localities on

both sides of the Rio Muni were combined into one population here because sample sizes for the individual localities were small and clustering analyses, using the neighbor-joining method, suggested that they are closely allied. On the other hand, some localities with small sample sizes were left as distinct populations in order to test recent hypotheses regarding their affinity. Population 3 on the right bank of the River Niger is one such example. Figure 2.1 is a map of Central Africa showing the 16 geographical groupings.

These population divisions are also similar in many respects to the ones identified by Braga (1995). Braga recognized the rivers Dja in Cameroon and the rivers Aruwimi and Elia in Zaire as possible boundaries. Although further research in biogeographic patterns may confirm their status as boundaries, in this study, because of limited sample sizes these rivers were not considered to be of consequence for separating populations.

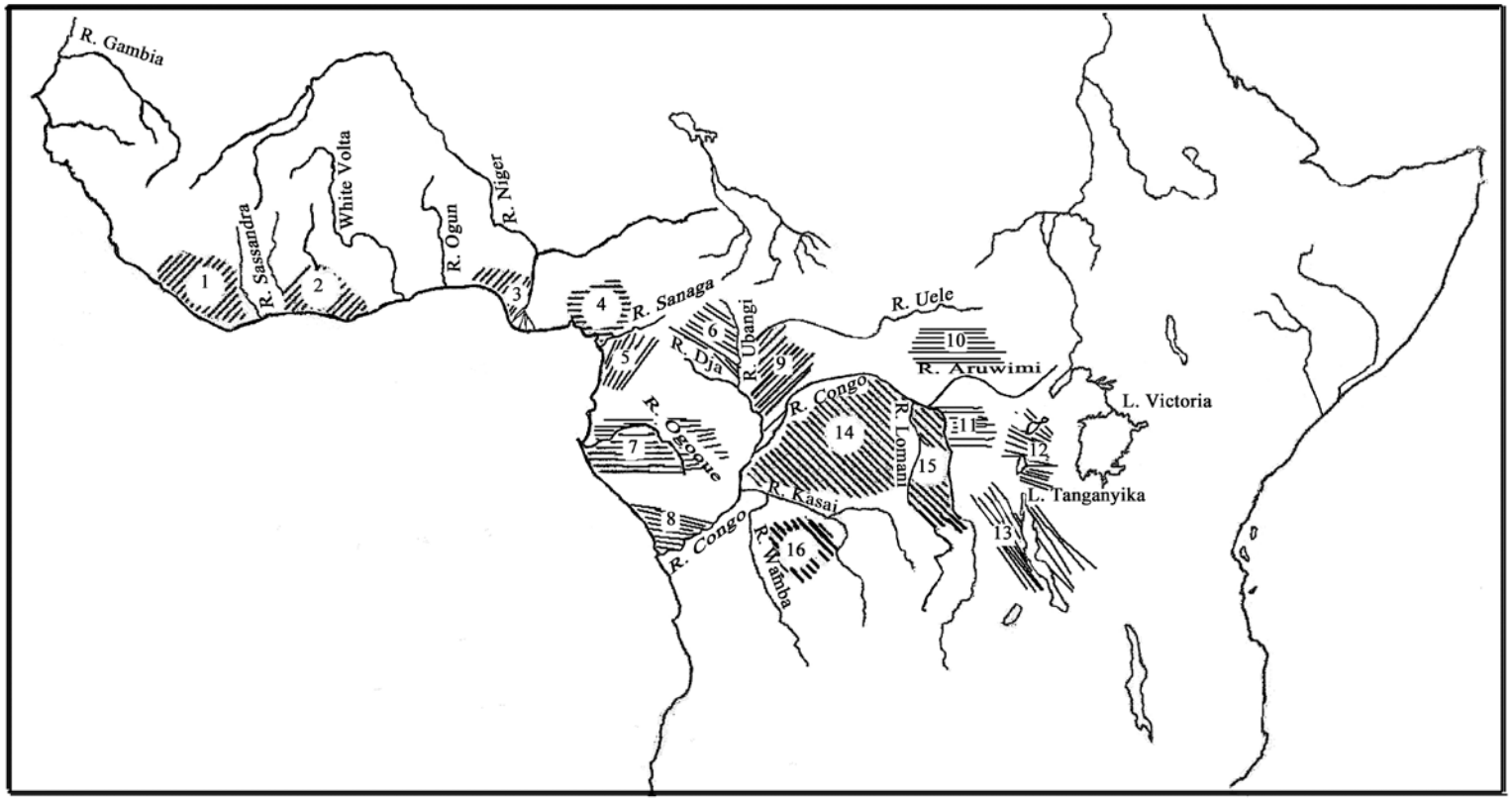


Figure 2.1 Map of Central Africa showing population groupings for chimpanzees used in this study. Adapted from Grubb (1990).

Table 2. 4. The 16 chimpanzee populations identified in this study and corresponding groups from Shea *et al.* (1993) and Grubb (1990)

Deme	Subspecies	Shea *et al.* (1993)	Grubb (1990)
1	*P. t. verus*	1	1a
2		2	1b
3		3	Part of 1c
4	*P. t. troglodytes*	4,5	2a
5		6,7,8	Part of 2b
6		9,10,11,12	Part of 2b
7		13,14,15,16,17	Part of 2b and 2c
8		18,19,20	
9	*P. t. schweinfurthii*	21	3[1]
10		22	3[1]
11		23,	3
12		24, 25, 26,27, 28	3
13		29, 30, 31, 32	
14	*P. paniscus*	33	4a
15		34,35	Part of 4c
16		36	4b

Gorillas

The gorilla sample comprised 299 individuals. These were first allocated to 19 localities as described by Groves (1970b) and then regrouped into 14 populations. The 14 populations and correspondence with Groves' 19 populations are shown in Table 2.5. Figure 2.2 shows the distribution of the 14 populations in equatorial Africa. The localities from the Cross River area and the ones from east Africa were maintained as distinct localities without recombining them with others because their affinities are under review. The 14 populations that Groves (1970b) identified from West Africa were regrouped to form 6 populations. West African localities with large enough samples (for example Groves' locality 2, 3 and 10)

were also left as distinct units in order to study the patterns of variation within the West African gorillas. The resulting 14 populations are described below with the localities included in each:

(1) Cross River region at the Nigeria-Cameroon border

(2) Coastal Cameroon south of Sanaga River: Campo, Lolodorf, Kribi

(3) Gabon and Ogooue River region: Sangatanga, Cap Lopez, Libreville

(4) Southern Gabon and Cabinda: includes Sette Gamma, Mayombe, Mambili, Fernan Vaz, Opa, Bade, Zalangoye

(5) Sangha River region: includes Ouesso, Nola, Youkadouma, Ziendi, Kadei, M'Bimou

(6) Batouri, between the upper reaches of the Sangha and Sanaga River

(7) Inland Cameroon: Lomie, Abong Mbang, Metet, Ebolowa, Acam, Djaposten, Obala, Meyoss, Lobomouth, Akonolinga, Northeast Rio Muni

(8) Utu: all lowland localities in eastern Democratic Republic of Congo

(9) Mwenga-Fizi: Wabembe, Baraka, Itombwe

(10) Tshiaberimu: Lubero, Luofo, Alimbongo, Butembo

(11) Virunga volcanoes

(12) Kayonza Forest: Kumbi

(13) Mt. Kahuzi: Tshibinda, Mt. Nakalongi

(14) Uele River: Djabbir

Table 2.5 Correspondence between gorilla populations from this study and localities identified by Groves (1970b)

Population	Groves (1970) localities
1	1
2	2
3	3
4	4,5,6
5	7,8,9
6	10
7	11,12,13,14,15
8	16
9	17
10	18
11	19
12	A
13	B
14	Uele River

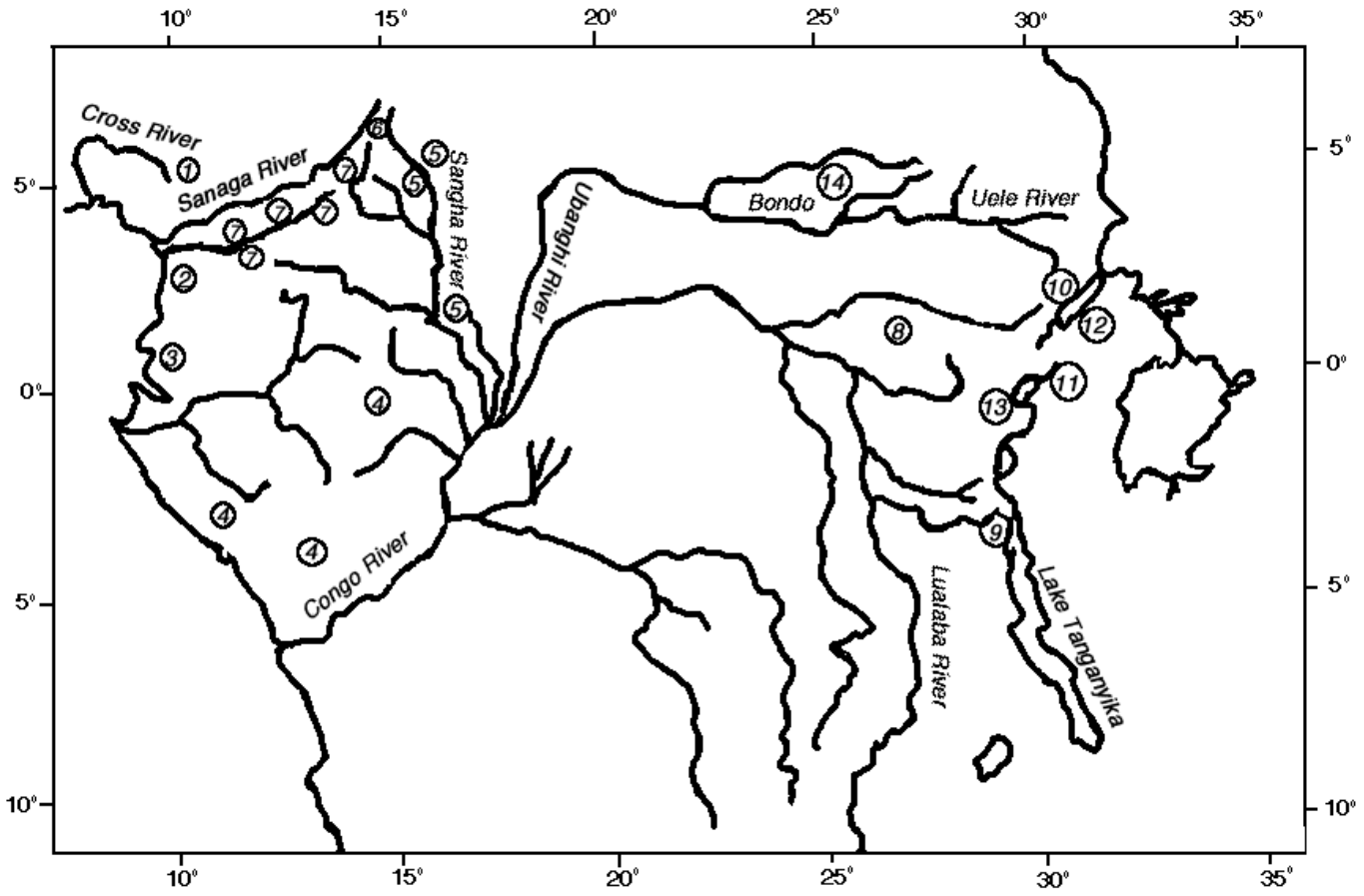


Figure 2.2 Map of equatorial Africa showing distribution of gorilla populations employed in this study.

Data collection and description of technique

Dental characters were selected for study by culling the literature to identify traits commonly used in fossil species discrimination, and by studying extant hominoid dental material to identify traits that characterize each group. The objective here was to include characters of presumed taxonomic relevance so as to study the significance of dental morphology for fossil species discrimination. The following studies were particularly helpful for selecting traits: Schuman & Brace (1954), Frisch (1963; 1965), Schultz (1963), Mahler (1973), Garn, Lewis & Kerewsky (1963), Swindler (1976), Szalay & Delson (1979), Uchida (1996), Wood & Abbott (1983a; 1983b); Hartman (1988); Dahlberg (1950); Jørgensen (1955); Corruccini (1975); Biggerstaff (1969); Korenhof (1960; 1978) Kinzey (1984), Andrews (1978), Simons & Pilbeam (1965), Pilbeam (1969), Harrison (1982), Le Gros Clark & Leakey (1951), Pickford (1986a, 1986b), Kelley (1986), Walker *et al.*, (1993), Begun (1989a, 1992), Begun & Kordos (1993), and Cameron (1997). Close to 400 dental traits were either coded by a scoring technique or measured using calipers and images.

Data collection in the museum started by recording information on the provenience of the specimen, its sex and body weight (when available), and the stage of wear of the tooth. I coded incisors and canines using the following stages of wear: (1) Thin line of dentine exposed along incisive/ occlusal edge (2) Thick strip of dentine exposed, and (3) Dentine exposure ascending onto lingual side. For molars I noted these three stages of wear: (1) No dentine: wear facets

present on molars, but no dentine exposed (2) Dentine perforations: dentine exposed on tips of lingual cusps of upper molars and buccal cusps of lower molars, but not on all cusps (3) Dentine pits: Larger areas of dentine exposed on lingual cusps of upper and buccal cusps of lower molars, but not obliterating cusps.

Data collection took place in three stages: I took dental measurements using sliding calipers, I recorded information on discrete characters, and I photographed the specimen in occlusal view.

Dental measurements

Using Mitutoyo Digimatic calipers calibrated to the nearest 0.01 mm, I recorded the length, breadth and height of the five ante molar teeth (incisors, canines and premolars) in an Excel (Microsoft Excel 5.0) spreadsheet. For the molars, I only recorded the height of the cusps; all other measurements were taken on a digitized image. On a specimen that included a complete set of teeth in the maxilla and mandible I was able to take a maximum of 57 measurements. Because of missing or damaged teeth the actual number of measurements taken was often less. The right half of the dentition was customarily studied except in the case of loss or damage of teeth when the left side was substituted. Table 2.6 provides details of the measurements taken and the landmarks used in taking measurements.

Qualitative data

Incisors, canines and premolars have cusps that exhibit a high amount of relief in the occlusal plane and therefore they cannot be measured using the image

analysis techniques employed in this study. These were studied by coding analysis. The characters were coded either as binary or multistate discrete variables. This method of coding is a less than optimal strategy for measuring dental traits because many traits were found to have a high degree of variation. Defining character states for such characters involved assigning arbitrary boundaries to a continuous trait. Problems were also encountered analyzing these data as discussed in the Data Analysis section below.

About 120 discrete characters were recorded on a MacClade 3.07 (Maddison & Maddison, 1992) spreadsheet (Table 2.6). Definitions of the traits were adapted from works such as Begun (1992); Ribot *et al.,* (1996); Wood & Abbott (1983a; 1983b); Hartman (1988); Dahlberg (1950); Jørgensen (1955); Corruccini (1975); Biggerstaff (1969); Korenhof (1960; 1978); Szalay & Delson (1979) and Kinzey (1984). Table 2.7 describes the qualitative characters studied and the character states defined for each one. Figure 2.3 shows the discrete characters using schematic figures.

Photographs

The primary method of data collection was by taking photographs of the occlusal surface of molars and measuring dental traits using an image analysis technique. Hominoid molars are relatively bunodont and therefore allow accurate measurement of dental traits on a two-dimensional image of the occlusal surface. The technique for preparing the specimen for image analysis and measuring crown

Table 2.6 Measurements taken using sliding calipers. See also Table 2.3.

Tooth type	Character measured	Description
Incisors	Length	MD dimension at apex
	Breadth	LaLi dimension at median-most point
	Height	From CEJ to apex on labial side
Canines	Length	Longest dimension (Mesial to distal, or MB to DL)
	Breadth	Perpendicular to length
	Height	Labial height from CEJ to apex
Premolars	Length of long axis	Longest dimension (MD or MB to DL)
	Breadth	Perpendicular to length
	Cusp height	Labial height from CEJ to tip of paracone or protoconid
		Lingual height of protocone or metaconid
Molars	Cusp height	From CEJ to tip of cusp

Table 2.7 List of qualitative characters studied

Tooth type	Character	Description	Character states
Incisors	Wear pattern	Degree of wear along incisive margin	0: Thin incisive strip; 1: Thick incisive strip; 2: Onto lingual side
	Cingulum	Ridge of enamel along cervical margin on lingual side	0: Discontinuous; 1: Continuous; 2: Bulge tapering towards apex
	Median lingual pillar	Vertical ridge of enamel on lingual side centrally placed rising towards apex	0: Absent; 1: Weak; 2: Strong
	Mesial lingual pillar	Vertical ridge of enamel on lingual side rising towards apex at mesial margin of tooth	0: Absent; 1: Weak; 2: Strong
	Mesial notch	Notch on lingual face by mesial side	0: Absent; 1: Shallow; 2: Deep
	Distal notch	Notch on lingual face by distal side	0: Absent; 1: Shallow; 2: Deep
Canines	Wear pattern	Degree of wear along tip and distal margin	0: Sharp tip; 1: Slightly worn; 2: Moderately worn

Table 2.7 List of qualitative characters studied (continued)

Tooth type	Character	Description	Character states
Canines	Lingual cingulum	Ridge of enamel at base along lingual face	0: Unclear; 1: Well-defined
	Mesial groove	Groove along mesial face	0: Absent; 1: Present
	Mesial tubercle	Supenumerary cusp at base of mesial groove	0: Absent; 1: Present
	Lingual groove	Groove along lingual face	0: Absent; 1: Present
	Lingual tubercle	Supernumerary cusp at base of lingual groove	0: Absent; 1: Present
	Distal groove	Groove along distal margin	0: Absent; 1: Present
	Distal tubercle	Supernumerary cusp at base of distal groove	0: Absent; 1: Present
Premolars	Wear pattern	Degree of wear on tip of cusp	0: Unworn; 1: Slightly worn; 2: Moderately worn
	Enamel extension	Extension of enamel onto root on mesial side	0: Absent; 1: Present
	Mesiobuccal tubercle	Supernumerary cusp at mesial most tip of preparacrista	0: Absent; 1: Present
	Mesiolingual tubercle	Supernumerary cusp at mesialmost tip of preprotocrista	0: Absent; 1: Present
	Distobuccal tubercle	Supernumerary cusp at distal most tip of preparacrista	0: Absent; 1: Present
	Distolingual tubercle	Supernumerary cusp at mesial most tip of preprotocrista	0: Absent; 1: Present
	Transverse ridge	Crest connecting mesial cusps	0: Absent; 1: Straight; 2: Mesially concave; 3: Distally concave; 4: V-shaped; 5: Cut by groove
	Mesial cingulum	Low ridge of enamel along mesial edge of tooth	0: Absent; 1: Present
	Distal cingulum	Low ridge of enamel along distal edge of tooth	0: Absent; 1: Present

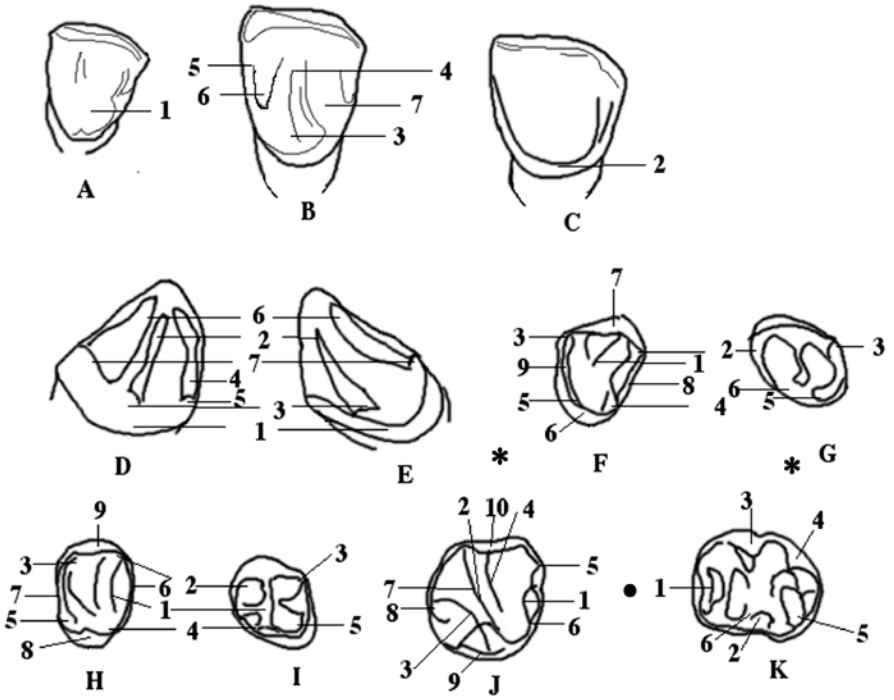
Table 2.7 List of qualitative characters studied (continued)

Tooth type	Character	Description	Character states
Premolars	Lingual cingulum	Low ridge of enamel along lingual side of tooth	0: Absent; 1: Present
	Buccal cingulum	Low ridge of enamel along buccal side of tooth	0: Absent; 1: Present
Molars	Wear pattern	Dentine perforations on lingual tips of upper and buccal tips of lower molar cusps	0: No dentine 1: Small dentine perforations 2: Larger dentine perforations
	Anterior transverse crest	Crest from paracone to protocone	0: Absent; 1: Meets preprotocrista; 2: Meets protocone; 3: V-shaped
	Crista obliqua	Crest from paracone to hypocone	0: Continuous; 1: Discontinuous
	Sulcus obliquus	Groove starting between protocone and hypocone and proceeding distally between metacone and hypocone	0: Absent; 1: Lingual and distal; 2: Only lingual; 3: Only distal
	Buccal developmental groove	Groove between paracone and metacone	0: Absent; 1: Present
	Paraconule	Supernumerary cusp at end of preparacrista	0: Absent; 1: Present
	Protoconule	Supernumerary cusp at end of preprotocrista	0: Absent; 1: Present
	Metaconule	Supernumerary cusp at midpoint of crista obliqua	0: Absent; 1: Present
	Distoconule	Supernumerary cusp between metacone and hypocone	0: Absent; 1: Present
	Pericone (Carabelli's cusp)	Supernumerary cusp on lingual cingulum between protocone and hypocone	0: Absent; 1: Present
	Mesostyle	Supernumerary cusp on buccal side between paracone and metacone	0: Absent; 1: Present

Table 2.7 List of qualitative characters studied (continued)

Tooth type	Character	Description	Character states
	Trigonid crest	Crest connecting two mesial cuspids	0: Continuous; 1: Interrupted; 2: Twinned continuous; 3: Twinned interrupted
	Lingual developmental groove	Groove between metaconid and entoconid	0: Absent; 1: Present
	Mesiobuccal developmental groove	Groove between protoconid and hypoconid	0: Absent; 1: Thin; 2: Wide notch
	Distobuccal developmental groove	Groove between hypoconid and hypoconulid	0: Absent; 1: Thin; 2: Wide notch
	Tuberculum intermedium	Supernumerary cusp between metaconid and entoconid	0: Absent; 1: Present
	Tuberculum sextum	Supernumerary cusp on lingual side of hypoconulid	0: Absent; 1: Present

Figure 2.3 Discrete characters



A, B, C: UIs 1. No cingulum 2. Continuous cingulum 3. Bulging cingulum tapering towards apex 4. Median lingual pillar 5. Mesial lingual pillar 6. Mesial notch 7. Distal notch

D: UC, E: LC 1. Lingual cingulum 2. Lingual groove 3. Lingual tubercle 4. Mesial groove 5. Mesial tubercle 6. Distal groove 7. Distal tubercle

F: UP3, G: LP3 1. Transverse ridge 2. Mesiobuccal tubercle 3. Distobuccal tubercle 4. Mesiolingual tubercle 5. Distolingual tubercle 6. Lingual cingulum 7. Buccal cingulum 8. Mesial cingulum 9. Distal cingulum

H: UP4, I: LP4 1. Transverse ridge 2. Mesiobuccal tubercle 3. Distobuccal tubercle 4. Mesiolingual tubercle 5. Distolingual tubercle 6. Mesial cingulum 7. Distal cingulum 8. Lingual cingulum 9. Buccal cingulum

J: UM • Mesial, * Buccal. 1. Anterior transverse crest 2. Crista obliqua 3. Sulcus obliquus 4. Buccal development groove 5. Paraconule 6. Protoconule 7. Metaconule 8. Distoconule
9. Pericone 10. Mesostyle

K: LM • Mesial, * Buccal. 1. Trigonid crest 2. Lingual development groove 3. Mesiobuccal development groove 4. Distobuccal development groove 5. Tuberculum sextum 6. Tuberculum intermedium

base and cusp areas is described by Wood & Abbott (1983a, 1983b) and Uchida (1992). A slight modification of their technique was used in this study so as to measure traits not included in their studies, such as length of cingulum, size and position of foveae and lengths of crests.

The following technique was used for taking photographs: a Sigma 50mm F2.8 macro lens was attached to a Minolta X-700 camera and the camera was secured on the tripod in such a way that its optical axis was perpendicular to the occlusal plane of the molar. Care was taken to ensure that the crown being photographed was at the center of focus of the lens, and that the scale was placed on the same horizontal plane as the occlusal surface. The placement of the scale on the same horizontal plane as the occlusal surface was important for taking accurate measurements. This was achieved simply by ensuring that both the scale and crown were clearly in focus – the macro lens, which is sensitive to slight changes in depth facilitates this. The presence of large projecting canines in the hominoid dental arcade makes it difficult for the macro lens (with shallow depth of field) to be moved close enough to the subject to reproduce an image of 1:1 magnification (as used by Wood & Abbott, 1983). A reproduction ratio of 1.3:1 was most commonly achieved. There was no loss of accuracy in measurement however, because the image analysis software used to execute measurements, enables one to set a scale calibrated against the pixels used (*e.g.*, 300 dpi) in displaying the image. Each molar crown formed a separate image resulting in six images for each complete specimen.

The enlarged positive print was scanned into a Macintosh computer and dental characters listed in Table 2.7 were measured using NIH Image. NIH Image is a public domain program for image processing and analysis developed at the United States National Institute of Health and available at http://rsb.info.nih.gov/nih-image/. Measurement of dental characters started with setting the scale. The line selection tool was used to trace over the scale present in each image. This known distance in millimeters was then calibrated against the pixels measured resulting in a scale of "x" pixels = 1 mm.

A pilot study was conducted to estimate the measurement error in using image analysis for measuring dental traits. Using 23 gorilla specimens it was found that the average rate of error in measuring linear dimensions (length) of molars using the above technique compared with measurements taken using sliding calipers was 1.33% (SD 0.53%, Range 0.12-2.76%).

Four selection tools were used in NIH Image: the polygon, the straight line, the freehand line, and the angle tool. These were used to take three kinds of measurements: areas, lengths and angles. The area of the crown base and mesial and distal foveae were measured using the polygon tool; the mesiodistal and buccolingual lengths, and lengths between cusps were measured with the straight line; the lengths of crests were measured using the freehand line, and the positions of the cusps, foveae, cristid obliqua and hypoconulid were measured using the angle tool (see Figure 2.4). About 25 measurements were taken on each tooth.

Table 2.8 Measurements taken on photograph of occlusal surface of molar

Measurement taken	How measured
Length of crown	Longitudinal axis from the mesialmost point of contact with previous tooth to distalmost point
Breadth	Length from buccal edge to lingual edge at mesial and distal cusps
Distance between mesial and distal cusps	Length between tips of mesial cusps (paracone/protoconid to protocone/metaconid) and distal cusps (metacone/hypoconid and hypocone/entoconid)
Length of crests/ cristids	Lengths of crests/ cristids
Area	Occlusal surface including cingulum
Area of mesial fovea	Line circumscribing mesial fovea
Area of distal fovea	Line circumscribing distal fovea
Cingulum	Length of cingulum along buccal or lingual side
Orientation of mesial fovea on upper molar	Angle formed by line connecting midpoint of foveal basin, tip of protocone and tip of paracone
Orientation of mesial fovea on lower molar	Angle formed by line connecting midpoint of foveal basin, tip of protoconid and tip of metaconid
Orientation of distal fovea on upper molar	Angle formed by line connecting center of foveal basin, tip of metacone and tip of hypocone
Orientation of distal fovea on lower molar	Angle formed by line connecting center of foveal basin, tip of entoconid and tip of hypoconulid
Orientation of buccal cusp on upper molar	Angle formed by tip of paracone , line connecting mesial cusps and midline of tooth
Orientation of lingual cusp on upper molar	Angle formed by tip of protocone, line connecting mesial cusps and midline of tooth
Orientation of buccal cusp on lower molar	Angle formed by tip of protoconid, line connecting mesial cusps and midline of tooth
Orientation of lingual cusp on lower molar	Angles formed by tip of metaconid, line connecting mesial cusps and midline of tooth
Orientation of hypoconulid	Angle formed by tip of hypoconulid, tip of hypoconid and tip of entoconid
Orientation of cristid obliqua	Angle formed by prehypoconid cristid, tip of hypoconid and tip of entoconid

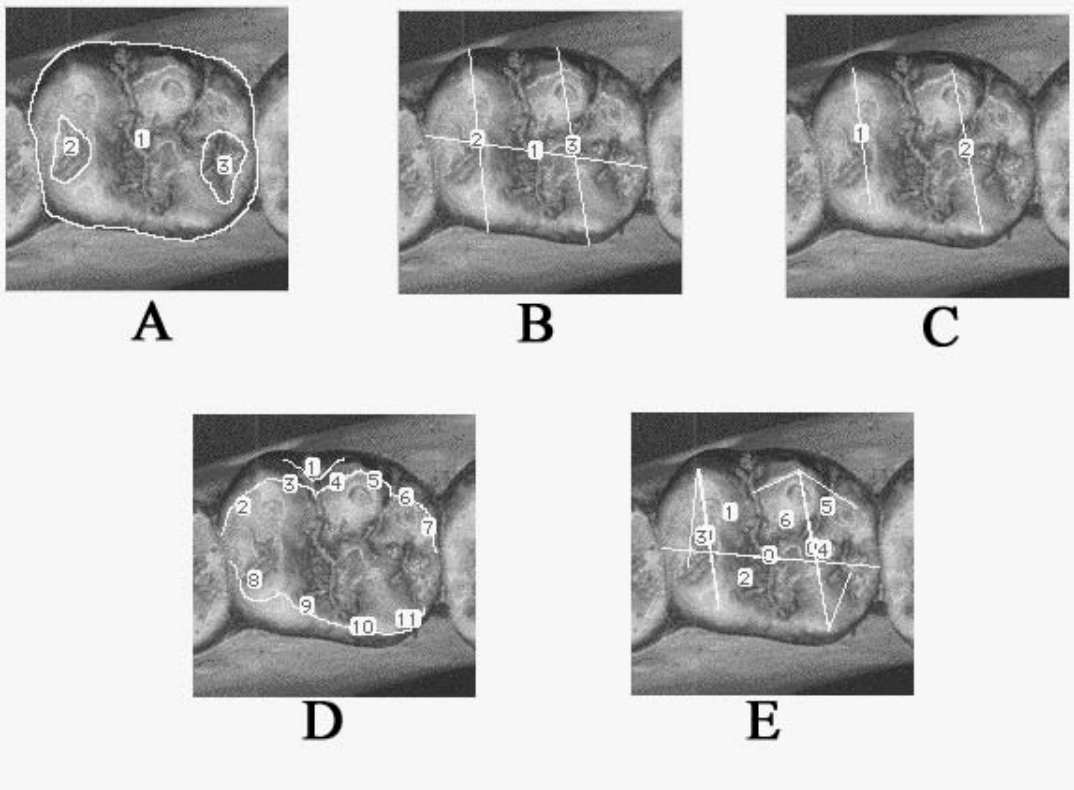


Figure 2.4 Photograph of chimpanzee lower molar showing characters measured using NIH Image. (A) **Areas:** 1. Base area 2. Area of mesial fovea 3. Area of distal fovea (B) **Linear dimensions:** 1.MD 2.BL (mesial cusps) 3. BL (distal cusps)
(C) **Linear dimensions:** 1. BL mesial cusp tips 2. BL distal cusp tips
(D) **Curvilinear lengths:** 1. Buccal cingulum 2. Preprotoconid cristid 3. Postprotconid cristid 4. Prehypoconid cristid 5. Posthypoconid cristid 6. Prehypoconulid cristid 7. Posthypoconulid cristid 8. Premetaconid cristid 9. Postmetaconid cristid 10. Preentoconid cristid 11. Postentoconid cristid
(E) **Angles:** 0. Mesiodistal and buccolingual axes. 1. Position of mesiobuccal cusp 2. Position of distobuccal cusp 3. Position of mesial fovea 4. Position of distal fovea 5. Position of hypoconulid 6. Position of cristid obliqua

Data Analysis

These measurements, taken from digital images and calipers, were then subject to a variety of statistical analyses. The statistical packages SPSS 6.1 for Macintosh, SPSS 10.0 for Windows and SAS 8.2 for Windows were used. Data analysis took place in three stages:

(1) Exploratory data analysis: The variables were examined to see if they were randomly and normally distributed and possible errors in data entry were identified and corrected.

(2) Data transformations: Values were estimated for missing data, and the data were transformed so as to correct for size and shape related differences.

(3) Confirmatory data analysis: Formal univariate and multivariate statistics were applied to the corrected and transformed data.

Exploratory data analysis

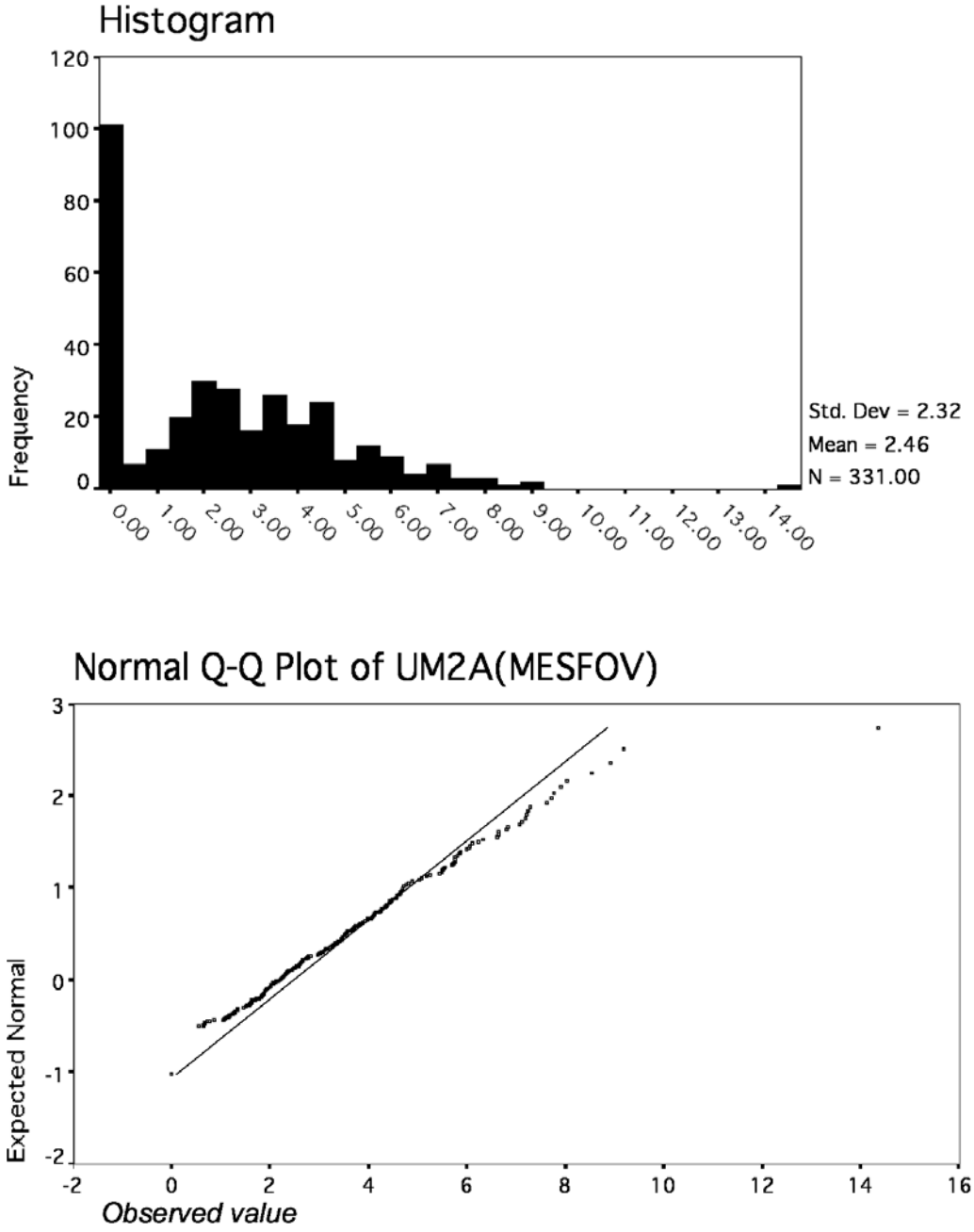
The first step in data analysis was to inspect the data for errors in input. This was done by calculating the frequencies, minimum and maximum values, missing values and outliers for each of the dental variables. When outliers and missing values were found to be due to data entry errors, these were selectively re-measured and corrected. Missing values that were not due to inputting errors were the ones from damaged or missing teeth. These were treated as system-missing values at the exploratory stage of analysis, but were subsequently transformed, as needed, using the missing values analysis, described below.

An initial assumption of all parametric or quantitative statistical procedures

is that the data being analyzed are randomly and normally distributed. The symmetry of distribution of each of the dental variables was explored using descriptive statistics such as mean, median, range, standard deviation, skewness and kurtosis. Graphical procedures such as histograms and Q-Q plots were also used to visually inspect normal distribution, skewness, and kurtosis. Histograms use a bar chart to plot the frequencies with which values occur. Q-Q plots contrast observed quantiles for a variable against the expected normally distributed quantiles and provide correlation coefficients between the observed and expected quantiles. Q-Q plots thus provide a statistic for testing hypotheses of normal distribution.

These statistics revealed that most of the variables had a normal distribution. The following variables were not normally distributed: size and position of mesial and distal foveae, length of cingulum, and length of crista obliqua. These dental characters are variable in their pattern of appearance. Quite frequently they are absent, but when present they are manifest at varying degrees, from very small to very large. Since these characters are both discrete (absent or present) and continuous (occur at varying degrees), it was thought prudent to measure the degree of appearance when manifest. When absent, they were marked with a 0.00, signifying negligible appearance. This measurement technique caused these variables to have a bimodal distribution (Figure 2.5). When viewed as a histogram there was a peak at one end caused by the zeros and a Gaussian curve at

Figure 2.5 Histogram and Q-Q plot showing distribution of area of mesial fovea of UM2 of chimpanzees. The single datum point at the furthest right was re-measured and confirmed as a real value (not a data entry error).



the other end with values in a normal distribution. The range and standard deviation for these characters was relatively large. However, skewness and kurtosis values were not too high, never greater than a positive or negative 3. The Q-Q plots showed that they did not deviate markedly from an expected normal distribution (Figure 2.5), and therefore they were included in all analyses.

Data transformation

Missing Values Analysis

A data set like the present one, where a large number of measurements are taken on each individual and a large sample of individuals is studied, is most effectively analyzed using multivariate methods of analysis. In multivariate statistical methods, however, each variable or measurement contributes to developing a linear function or vector for the individual. The analysis cannot proceed with even a single missing measurement; a missing value causes the entire individual to be excluded from the analysis.

In this study, several strategies were used to avoid the predicament of a dwindling data set due to missing data. So as to maximize sample sizes individuals with missing or damaged teeth were not excluded from the analysis. When a tooth on the right side was found missing, the one on the left side was substituted. If missing on both sides, or if it was too worn or damaged, that tooth type was excluded from study but all other teeth in that individual were studied. The complete data set that included measurements on all types of teeth was then divided into subsets of data for individual teeth. This sorting procedure resulted in a

differing number of individuals studied for each tooth type. For example, the chimpanzee sample size varies from N=331 for UM2s to N=253 for LM3s. If only a small portion of the tooth was damaged, for example due to enamel chipping, all features that were measurable were measured and values for the missing features were estimated. The estimation of missing values is a common procedure in multivariate analysis (Holt & Benfer, 2000) and the commonly available statistical packages such as SAS and SPSS include several methods for estimating missing values.

The Missing Values Analysis toolpack available with SPSS 10.0 was used in this study. The multiple regression method was used to impute missing values. Variables that best explained the variation in the missing data were chosen and using multiple iterations values were randomly selected from a chosen distribution around the regressed value and imputed to the variable (LoPresti, 1998; Albrecht, 1992). Only values missing at random with respect to other variables were estimated using this procedure. These were features missing due to breakage or damage, and accounted for no more than 1% to 2% of any data set. The effect of bias, if any, in the estimated values was considered to be minimal and this approach was used in preference to a lengthy alternative procedure suggested by Holt and Benfer (2000).

Size and shape correction

The effect of allometry or size-correlation was accounted for using the Geometric Mean (GM). GM was calculated by taking the n^{th} root of the product of

n values. All linear measurements were used in calculating the GM and each linear measurement was then divided by the GM for that individual to get a scale-free "shape" variable (Falsetti *et al.*, 1993; Mosimann & James, 1979; Darroch & Mosimann, 1985; James & McCulloch, 1990). Angular measurements, themselves being shape measurements, were not included in the GM, and areas were converted to linear measurements by taking their square roots. All values of zero (for the absent characters mentioned above) were changed to a one to ensure that an error value was not returned when calculating the product of the measurements for the GM. The analyses using raw variables (also called "size and shape variables", Falsetti *et al.*, 1993) were compared and contrasted with the analyses using shape variables so as to ascertain the importance of size and shape (untransformed variables) versus shape alone (transformed variables) in causing separation among groups. The variables were also log transformed (Falsetti *et al.*, 1993) so as compare the results of analyses of log size-and-shape variables (i.e. logged raw variables) with log shape variables (shape variables log transformed). Thus, in all analyses both transformed and untransformed variables were used.

Determining the role of allometry and isometry

The Geometric Mean or the logged Geometric Mean represents overall size. In multivariate analyses, such as discriminant analysis, Pearson's correlations were established between the scores of discriminant functions and the Geometric or logged Geometric Mean so as to determine the role of size in discriminating groups. When raw (untransformed) variables were used in the analysis a high

(above 0.40) and significant (p= 0.01) correlation between the scores of the discrimant function and the Geometric Mean (or logged Geometric Mean) signified the role of size in causing separation. Overall size is called isometric size here because it represents "size and shape", as described by Falsetti *et al* (1993), and is contrasted with "shape", which is corrected for size and is therefore "scale-free". When shape variables were used in the analysis a positive and significant correlation with the GM implied that the separation between groups was of an "allometric" nature – that is, the “shape” separation between the groups was size-related. If there was no significant correlation it signified no change in shape with change in size and therefore “isometry” was invoked to explain this separation (Falsetti *et al*.1993).

Standardizing the variables

Because the variables used in the analyses had different units of measurement (there were linear dimensions measured in millimeters, areas measured in square millimeters and angles measured in degrees), when raw variables were used in multivariate techniques, such as a hierarchical clustering analysis, they were converted to a standardized form. This was done by expressing them as *Z* scores. This ensured that all variables were comparable.

Confirmatory Data Analysis

Several statistical tests were used to analyze these transformed and untransformed data. Univariate statistics such as the chi-square, Student’s t-test, the F-statistic and the one-way analysis of variance were calculated to identify

variables causing group separation. The Levene test for homogeneity of variance was used to test for the violation of the equal variance assumption. The level of significance of this test helped determine whether to use a one-tailed or two-tailed probability for the t-test. If $p < 0.05$, the t-test based on separate variance estimates or the one-tailed probability was used.

For the one-way analysis of variance (ANOVA), the Bonferroni and Scheffé post-hoc tests of comparison were used to test for unplanned comparison of group means. Scheffé analysis is used when groups with variable sample sizes are compared and the Bonferroni test is used when multiple comparisons are made between groups (Howell, 1997).

The coefficient of variation, CV, was calculated to describe within group variation. CV, which is expressed as a percentage of the standard deviation divided by the mean, is very sensitive to sample size. Small samples lead to inflated CV values and an increase in the rate of Type I (incorrect rejection of null hypothesis) and Type II errors (failure to reject null hypothesis). A correction factor suggested by Sokal and Rohlf (1981) was applied in CV calculations for less than 30 individuals. In addition, when comparing groups with unequal sample sizes randomization techniques were used, whereby a sample equal to the smaller of the two groups was randomly and iteratively selected from the larger group.

Range-based statistics were also used to calculate within group variation. Range as a percentage of mean (R%) is the difference between the maximum and minimum value divided by the mean and expressed as a percentage. Because it is

calculated from the maximum and minimum values R% is more prone to type II errors but not type I errors (Martin & Andrews, 1993) and is therefore considered to be a better statistic for comparing variation in fossil samples with that in modern samples. However, it is especially sensitive to sample size, and therefore I used both the CV and R% for comparing ranges of variation.

The main multivariate statistics used were discriminant analysis and heirarchical cluster analysis. Discriminant analysis was used to determine multivariate separation among groups. Based on their scores on the discriminant functions specimens were allocated to predetermined groups (populations, subspecies or species). The percentage accuracy by which individuals were classified into known groups helped confirm (or reject) the preconceived separation of the groups. Squared generalized distances between group means demonstrated the dispersion of the group relative to one another. The loadings of individual variables on the discriminant functions helped identify the variables causing group separation. Only variables having canonical correlations of above 0.40 with the discriminant functions were considered when identifying variables causing group separation. Based on the canonical coefficients a distance matrix was constructed showing squared generalized distances between pairs of groups. This distance matrix showed the interrelationships between groups.

The following options were used for discriminant analysis: the step-wise variable selection procedure based on maximizing the Mahalanobis distance between the two closest groups, all groups assumed to have equal prior

probabilities, the F probability of 0.05 as criterion for entry and 0.10 for removal of variables, and the pooled within-group covariance matrix. The standardized canonical coefficients were used to determine the contribution of variables to the discriminating functions. Pearson's correlation of the score for the discriminant function with the Geometric Mean helped determine the contribution of size in causing variation. The impact of sex and stage of wear in causing group separation was analyzed by conducting separate analyses for the different sex and wear patterns. Only when the results of the sex and wear-pooled samples did not differ from the combined sample analyses, were total sample analyses conducted.

The group means of the transformed and untransformed variables were also subjected to hierarchical cluster analysis techniques. The neighbor-joining method of clustering was used. The squared Euclidean distance was used as the distance measure and *Z* scores were used by way of standardizing the variables. The results of this analysis are presented in the form of a dendrogram graphically representing the morphometric distance between the various groups. The distance between the groups are rescaled to fall within the range of 1 to 25, the smallest distance corresponding to 1 and the largest distance corresponding to 25. Groups that fell together on the same branch had low pair wise distances and were considered to be dentally similar. It should be remembered that the dendrograms represent phenetic distance and do not have phylogenetic intent. Since group means were the primary data used in clustering, sample size difference was not a constraining factor, and the data sets comprising different types of teeth were once again combined into one

large data set.

The qualitative data could not be analyzed using these parametric statistics. These data were initially coded in a MacClade spreadsheet so as to generate cladograms using the MacClade and PAUP computer programs. However, the high degree of dental variation displayed by hominoids poses difficulties when using standard techniques of phylogenetic analyses such as those available with MacClade and PAUP. This is because when individuals are merged into fewer taxa (such as when combining individuals into populations or subspecies), the character states displayed by the individuals are also merged. If a character has multiple states of manifestation within the group, merging the group will result in the character having a polymorphic appearance. Polymorphic characters, as is known, are not informative for phylogenetic analysis and are typically dropped from the analysis. Given a large data set such as the present one, merging taxa leads to an increase in the number of polymorphic characters, and the ultimate outcome is a reduction in the number of informative characters available for determining phylogenetic relationships. To provide an example, when the 341 chimpanzee individuals were clustered into 16 populations, only 2 of the 118 discrete characters prevailed as monomorphic and were therefore considered to be informative.

While one approach to deal with the problem of polymorphism is to arbitrarily assign the most frequently occurring character state to the taxon, or to choose a percentage representation (for example, 65% or higher) to assign a character state to the taxon (*e.g.*, Singleton, 1998), such an approach gives a false

sense of homogeneity to a group that in reality is characterized by a high degree of variability.

So as to preserve the variance within the group, I experimented with distance measures commonly used by dental anthropologists working with human populations. Several such distances statistics are in use (Scott & Turner, 1997). The Mean Measure of Divergence, MMD (Sjovold, 1973) is commonly used with discrete dental traits. It uses the summed difference in mean frequencies of traits in two or more groups to calculate a matrix of morphological distance. A complimentary software program, MMD2, developed by Richard Wright of the University of Sydney was used for standardizing the frequencies of qualitative traits by angular transformations and for calculating a matrix of distances. The use of this statistic requires the use of only binary variables and all multistate variables were recoded for this purpose.

The distance matrix generated using this statistic does not provide a biologically meaningful separation of the groups. In particular, the results of this analysis did not correspond with the results of the quantitative analyses and distances calculated from the quantitative data such as squared Euclidean distances and Mahalanobis distances, which in turn show corroboration with the results of molecular and other types of data. The failure of the MMD to provide a biologically meaningful separation of groups can probably be related to the threshold manner of coding variables as either present or absent. Such an approach imposes an external limit on the diversity present in the African apes. It is possible

that re-defining multistate traits as independent traits rather than multiple manifestations of the same trait would be one solution for preserving this diversity. This would imply that the genotypes for each of the traits are independent, however, an assumption that is precluded by the observed nature of continuous variation in many traits.

Given the difficulty in using traditional distance measures and phylogenetic analyses for studying discrete dental traits in the African apes, I developed a slightly unorthodox method for studying the nature of population differentiation with such data. I calculated an "average character state" for each dental trait by taking the arithmetic mean of the various character states. The discrete character states, although having the nature of nominal data were coded as interval data and these character states (0, 1, or 2) were used in calculating the group means for each of the variables. Since all character states contributed to calculating the group means, means of the groups differed depending on the preponderance of particular character states within the group and based on subtle differences in frequency of states. Thus, groups with a higher frequency of 2s as a character state differed in their means from those with higher frequency of 0s or 1s. These group means were then analyzed using the statistical techniques of hierarchical clustering. A dendrogram graphically summarized the relationship between groups. As will be seen, there is excellent correlation between the dendrograms based on this method and those based on the parametric data.

The mathematical implications of this method have not been critically

evaluated and it should be considered merely as a preliminary approach. The main difficulty is that one is presented with a dendrogram, which is a graphical representation of morphological distance, but this does not provide information regarding the characters responsible for causing group separation (R. Wright pers. comm.). It is clear that there is a need for the development of multivariate methods such as discriminant analysis for use with nonparametric data. Other frequency based methods for studying allele frequencies, for example Nei's distance statistic (Nei, 1972) are also currently being explored for studying these data.

In order to identify the discrete dental traits that cause the differences between populations, a chi-square analysis was used. This helped determine the association between the grouping variable (species, subspecies or population) and frequencies at which dental traits occurred in the different groups. A chi-square probability of 0.001 or less was used. Given that the sample sizes are reduced when analyses are carried out at the level of the population, and the large number of groups compared, this stringent level of significance helped identify only the variables that were most significant in differentiating groups.

CHAPTER THREE
Pan

Introduction

The genus *Pan* is the sister taxon to the genus *Homo*, and it is the only genus within the extant family Hominidae that is generally accepted to have more than one living species. Because of these two unique characteristics chimpanzees are useful for understanding patterns of inter-specific variation in taxonomic analyses of extinct hominids and hominoids, and in assessing the position of *Homo* and the great apes in phylogenetic analyses. Consequently, several studies have examined the patterning of variation in aspects of ecology, behavior, morphology and genetics, and based on these studies the taxonomy and phylogeny of the genus has been repeatedly reevaluated.

The species level taxonomy with one genus (*Pan*), and two species (*Pan troglodytes* and *Pan paniscus*) is well established using several independent sources of data and methodologies. The taxonomy at the infraspecific level is presently in a state of flux. Ongoing studies have made it increasingly clear that the three commonly recognized subspecies of *P. troglodytes* (*P. troglodytes troglodytes, P. t. schweinfurthii* and *P. t. verus*) do not adequately represent the nature of the structure within chimpanzee populations. Surprisingly, geographical variation, namely the "occurrence of differences in spatially segregated populations of a species," (Mayr, 1963: 297) has not been studied in any great detail in chimpanzees. This lapse in chimpanzee studies is remarkable considering that geographic variation has been studied in the other great apes (Groves, 1970b;

Jacobshagen, 1979) and geographic variation is considered to be the cornerstone of evolutionary studies (Albrecht & Miller, 1993, and references therein).

In this chapter I describe the patterns of variation in dental morphology in populations, subspecies and species of chimpanzees. Using quantitative and qualitative dental characters, I undertook an analysis of geographic variation in chimpanzees. I sampled dental material from the entire range of distribution of the genus and studied the patterns of variation within and among populations. Such an approach helps to identify clusters of populations that are similar in dental morphology. I then compared these clusters with groupings of chimpanzees recognized by other studies. Such a comparison, while evaluating the utility of dental morphology for recognizing population structure also helps to evaluate the validity of traditionally recognized groupings, such as the subspecies and species of chimpanzees. Subsequent to analyzing dental variation in populations, I compared the patterns of variation in the four commonly recognized subgroups: the three subspecies of *P. troglodytes* (*P. t. verus, P. t. troglodytes, P. t. schweinfurthii*) and *P. paniscus*. Finally, I compared dental variation in the two species, *P. troglodytes* and *P. paniscus*. Examining variation in such a nested hierarchy facilitates an understanding of how variation is partitioned within the genus and helps to document the process of speciation.

The chapter begins with a review of previous studies that have examined variation in species, subspecies and populations of chimpanzees. The conclusions that are pertinent to the present study are highlighted. Based on the problems raised

in previous studies, the questions to be addressed in this study are formulated. The study sample and the statistical analyses are then discussed. Finally, the results are put in perspective within the framework of chimpanzee systematics, and the patterns of variation are explored within the context of size, diet and genetic drift.

Background

Distribution and taxonomy

Chimpanzees have a wide distribution in Equatorial Africa. They are found from Senegal in West Africa to Tanzania and Uganda in East Africa, from about 14^0 N, 15^0 W to 4^0 S, 29^0 E. They are also found along the southern bank of the Congo River between 16^0 E, 1^0 N to 25^0 E, 4^0 S (Wolfheim, 1983; figure 3.1). In West Africa the distribution of the genus is patchy – localized populations are found from Senegal to Ghana. The area between Ghana, Togo and Benin (about 3^0 W to 3^0 E), an arid zone called the Dahomey Gap marks a break in chimpanzee distribution. From the eastern edge of the Dahomey Gap chimpanzees occur throughout Equatorial Africa up to the southwestern margin of Tanzania.

The Congo River apparently constitutes the most important barrier for the dispersal of chimpanzees – populations on either side are designated as distinct species: *P. troglodytes* (chimpanzees) on the north of the river and *P. paniscus* (bonobos) on the south. The rivers Niger and Ubangi are also considered to be biogeographic barriers, but less effective than the Congo. Chimpanzee populations demarcated by these rivers are designated as subspecies of *P. troglodytes*:

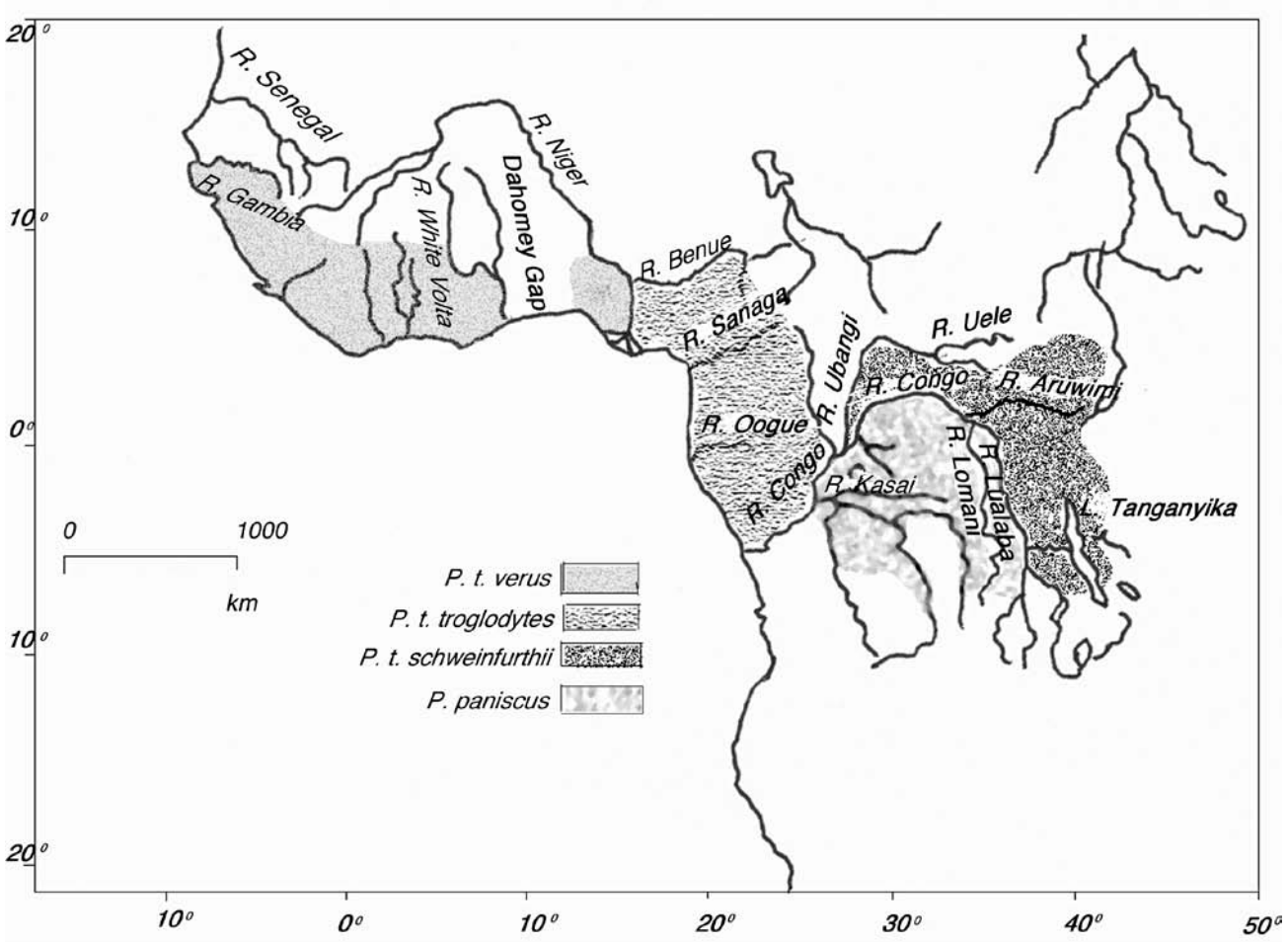


Figure 3.1 Distribution of chimpanzees in Africa (adapted from Groves *et al*., 1992).

P. t. verus to the west of the River Niger, *P. t. troglodytes* between the rivers Niger and Ubangi, and *P. t. schweinfurthii* to the east of the River Ubangi (Figure 3.1). As reviewed below, recent research has questioned the effectiveness of the rivers Niger and Ubangi as barriers to chimpanzee dispersal.

Previous Studies

Species

The Congo River is considered to be an excellent faunal barrier not only for the genus *Pan* but several other taxa (Grubb, 1990). *Pan troglodytes* on the north of the river has a wide distribution covering a distance of more than 5000 km (Figure 3.1). The distribution of *P. paniscus* is more restricted, only about 900 km west to east (Kano, 1992). Commensurate with this range of distribution the two species exhibit remarkable differences in ranges of variation. *Pan troglodytes*, with at least three recognized subspecies, is extremely variable, while *P. paniscus*, with no geographic variants, is relatively less variable. This difference in range of variation is seen in the ecology, behavior, morphology, and genetics of the two species. *Pan troglodytes* occupies a wide variety of habitats from closed forest to open woodland, but *P. paniscus* is confined to a swamp forest zone (Kano, 1992; Wrangham *et al.*, 1994). In blood group polymorphisms, *P. paniscus* is relatively monomorphic, while *P. troglodytes* exhibits a diversity of blood types (Socha, 1984; Table 3.1). Genetic variability within *P. troglodytes* is substantially greater than in *P. paniscus* as indicated by DNA-DNA hybridization studies and mtDNA sequence studies (Kocher & Wilson, 1991; Sibley & Ahlquist, 1984; Caccone &

Powell, 1989; Morin *et al.*, 1994; Ruvolo *et al.*, 1994). In several dental features, *P. troglodytes* exhibits greater variability than *P. paniscus* (Kinzey, 1984; Uchida, 1996). For example, in *P. paniscus* the second molar is most frequently the longest molar, but in *P. troglodytes* the relative size of molars is variable (Kinzey, 1984). In body size and skeletal dimensions, some populations of *P. troglodytes* are smaller, on average, than *P. paniscus* (for example, the population of *P. t. schweinfurthii* from Gombe National Park, Tanzania), but others are larger (Morbeck & Zihlman, 1989; Jungers & Susman, 1984).

Differences between the two species are also seen in behavioral strategies. The diet of *P. troglodytes* predominantly consists of ripe fruits (Mitani *et al.*, 2002). Meat, insects and foliage supplement the diet when fruit is scarce. However, the preference for ripe fruit is more persistent year-round than in sympatric gorillas (Kuroda *et al.*, 1996). The bonobo diet differs somewhat because bonobos consume a greater proportion of tough terrestrial herbs (Malenky & Stiles, 1991). Wrangham (1986) has suggested that the bonobo preference for tough herbaceous foods provides an ecological explanation for the differences in social organization and feeding behaviors of the two species, as described below.

Chimpanzee social organization is described as "fission-fusion" (Kortlandt, 1962; Goodall, 1986). Large multi-male, multi-female groups are formed and they split into subgroups of the same sex (all males, all females, females and infants) or mixed sex (estrus females and males) for foraging. Bonobo subgroups are larger and more cohesive during feeding, and typically contain multiple adult males and

females (White, 1996).

In both species, males are generally dominant over females individually. Grooming and affiliative behaviors differ between the species. In chimpanzees, grooming and bonding behaviors are more common among males, while in bonobos affiliative behaviors, including grooming and homosexual behaviors, are commonly observed between females (Mitani *et al.*, 2002).

Intergroup encounters are hostile in chimpanzees and larger groups aggressively attack and supplant smaller groups during foraging. Males are commonly seen patrolling chimpanzee territory (Wrangham *et al*., 1994; Mitani *et al.*, 2002). Bonobo intergroup encounters are not as aggressive and mostly consist of vocal contests and avoidance (White, 1996).

In dispersal patterns, however, the two species do not differ (White, 1996). Chimpanzee dispersal patterns are characterized by male philopatry. Females emigrate from the natal group so that the core of the group consists of related males. Male dispersal is not very common but is sometimes seen (Sugiyama, 1999). Secondary female transfer appears to be rare in chimpanzees (Mitani et al., 2002).

The differences between the two species are summarized in Table 3.1. Many of the morphological differences are related to overall size. Bonobos, on average, are smaller than chimpanzees in cranial, dental, and several body dimensions, but they have longer hindlimbs. Shea (1981, 1983a, 1983b, 1983c, 1984) studied the size-related differences from the perspective of ontogenetic allometry. He attributes the smaller dimensions in skull and postcranials in bonobos

Table 3.1 Differences between *Pan paniscus* and *Pan troglodytes* (summarized from Coolidge, 1933; Schultz, 1969; Johanson, 1974; Cramer, 1977; Kuroda, 1979; Kano, 1980; 1983; 1992; Shea, 1983a; 1983b; 1984; Jungers & Susman, 1984; Socha, 1984; Shea & Groves, 1987; Morbeck & Zihlman, 1989; Uchida, 1996; White, 1996; Mitani *et al.*, 2002).

Character	*Pan paniscus*	*Pan troglodytes*
Habitat	Closed forest	Closed forest, open grassland, dry woodland
External appearance	Body hair black, head hair centrally parted, small ears, pink lips, hardly any chin beard, clitoris ventrally placed, large sexual swelling	Body hair black turning brown to gray in adulthood, no central partition on head, ears large, lips not markedly pink, white chin beard in adults, clitoris more dorsally placed, smaller sexual swelling
Inter-group encounters	Less inter group aggression	Substantial inter group aggression
Diet	A high proportion of tough herbaceous foods	Mostly fruit
Affiliative behavior	More between-sex affiliative behaviors during feeding	Few affiliative behaviors overall
Sexual dimorphism	Reduced dimorphism compared to chimpanzees, except in canine size	Greater dimorphism than in bonobos
Postcranials	Shorter arms, longer legs, shorter clavicles, narrower pelves, narrower thorax, more horizontal vertebral column	Longer arms, shorter legs, longer clavicles, broader pelves, braoder thorax, more upright vertebral column
Cranium	Small head, tall forehead, no marked supraorbital torus	Larger head, relatively low forehead, supraorbital torus quite marked
Teeth	Heavy incisor wear, reduced lateral incisors, narrower LP3 many with metaconid, shorter LP4, molars with sharper cusps, C6 and C7 rarely present, larger protocone, smaller hypocone, larger metaconid	Incisor wear relatively reduced, broader LP3 without metaconid, longer LP4, molar cusps not as sharp, frequency of C6 and C7 high, smaller protocone, larger hypocone, smaller metaconid
Blood types	Monomorphic: Of A-B, only A, of M-N, M; of V-A-B-D, D; of R-C-E-F, R_{ab}CE	Polymorphic: Of A-B, A or O; of M-N, M or MN; of V-A-B-D 16 types; of R-C-E-F at least 24 types

to paedomorphism – the retention of juvenile features into adulthood. Charting the developmental pathways of the two species, he has demonstrated that the differences in size occur through heterochronic processes of ontogenetic development, whereby bonobos have an extended juvenile-like period compared to chimpanzees, culminating in an adult size similar to subadult chimpanzees. In external appearance too, bonobos retain several characteristics seen in juvenile chimpanzees. For example, body hair in bonobos remains black right through adulthood while in chimpanzees it turns brown or gray in later years. In addition, the bonobo head does not go bald as in chimpanzees (Kano, 1992).

The phenotypic and behavioral differences are considered to be so overwhelming that, on the whole, molecular systematists have not dwelt on re-evaluating the taxonomy and separation of *P. paniscus* from *P. troglodytes*. Rather, the two species are taken as well-established and the genetic distance between them is often held up as a standard against which to measure genetic distances between gorilla and orangutan subspecies and gibbon species (e.g., Ruvolo *et al.,* 1994; Morin *et al.,* 1994).

Subspecies

Prior to 1934 there were approximately 35 nomina associated with *P. troglodytes* (reviewed in Allen, 1925; Stiles & Orleman, 1927; Hill, 1967, 1969; Groves, 1986; Jenkins, 1990). Schwarz (1934) simplified the taxonomy and lumped all prior taxa into one species, called *Pan satyrus*, and four subspecies: *P. s. verus, P. s. satyrus, P. s. schweinfurthii* and *P. s. paniscus*. Later, Hill (1967; 1969)

recognized *Pan paniscus* as a distinct species, and adopted the name *Pan troglodytes* following the suppression of *Simia satyrus* Linnaeus by the *International Commission on Zoological Nomenclature* (ICZN, Opinion 114, 1929). Hill also reinstated the subspecies *P. t. koolakoomba*, but several subsequent studies have demonstrated that this subspecies is synonymous with *P. t. troglodytes* (Johanson, 1974; Cousins, 1980; Shea, 1984; Shea & Coolidge, 1988). Recent research has also suggested that *P. t. verus*, in particular, is more divergent than the other two subspecies. Following is a summary of the molecular and morphological studies that illustrate the distinctiveness of *P. t. verus*:

1. In a short segment of the cytochrome b region and a longer segment from the control region of mtDNA, Morin *et al.* (1994) found *P. t. verus* to be so widely separated from the other two subspecies, that they suggested elevating it to the rank of a species (*Pan verus*). Jolly *et al.* (1995), criticizing Morin's suggestion, pointed out that the seemingly greater separation Morin encountered could have occurred due to a sampling hiatus – a distance of about 1700 km between *P. t. verus* and *P. t. troglodytes* was left unsampled in Morin's analysis.
2. Gonder *et al.* (1997) sequenced the mtDNA control region of 12 individuals from both sides of the Niger River, thus sampling a geographic area neglected by Morin *et al.* (1994). They found that the 12 individuals, although traditionally placed in two distinct subspecies, formed a tight cluster that was most closely allied with *P. t. verus*, but that differed at least as much from *P. t. verus* as *P. t. troglodytes* and *P. t. schweinfurthii* differ from each other. Gonder

et al. suggested either placing the Nigerian chimpanzees within *P. t. verus*, thus making it a subspecies with higher levels of diversity than the other two, or recognizing this population as a fourth subspecies. They suggested using a previously assigned name, *P. t. vellerosus*, for this subspecies.

3. In a subsequent nuclear DNA study using single tandem repeat sequences, Gonder (2000) demonstrated that the population from the east of the Niger River showed closest affiliation with populations from Northern Cameroon, not with the west Niger populations. Thus, while the mtDNA study questioned the effectiveness of the Niger River in maintaining genetic discontinuity, the nuclear DNA study supported it. Both types of data suggested that the Sanaga River plays a strong role as a biogeographic barrier.
4. Groves (2001) studied the configuration of bones of the medial orbital wall and concurred with Gonder regarding the distinctiveness of the Nigerian chimpanzees. However, Groves found the Nigerian population to be most closely related to *P. t. troglodytes*, not *P. t. verus* as suggested by Gonder *et al.*'s mtDNA study.
5. Uchida (1992) measured areas of the cusps of molars and found that in both upper and lower molars, in linear dimensions, shape indices and cusp areas, *P. t. verus* is clearly separated from the other *Pan troglodytes* populations. Using *P. paniscus* as an outgroup Uchida also conducted a phylogenetic analysis using Johanson's (1974) data on non-metric dental features and found that although the three subspecies form an unresolved trichotomy, *P. t. verus* has a

much longer branch length, and is therefore more divergent than the other subspecies.

6. Braga (1995,1998) reiterated Uchida's conclusion and found that in cranial and palatal morphology *P. t. verus* is most widely separated from the other two subspecies of *P. troglodytes*.
7. Reviewing behavioral observations, Wrangham *et al.*(1994) found that in at least two aspects of behavior, *P. t. verus* is quite different from the other two subspecies: *P. t. verus* at Bossou and Taï show strong patterns of female affiliation, a behavior not observed in the other subspecies, and nut cracking behavior was found to occur in some populations of *P. t. verus*, but this behavior is not seen in any population of *P. t. troglodytes* or *P. t. schweinfurthii* despite years of study, and the availability of suitable raw materials at these sites.

P. t. verus, however, is not the only traditional subspecies whose status is being challenged. In a craniometric study Groves *et al.* (1992) identified *P. t. schweinfurthii* as the subspecies with the greatest within group variation. Dividing each of the subspecies into populations they examined the nature of variation within and between the three subspecies. *P. t. schweinfurthii* was divided into four localities, and in some of the analyses, two geographic samples within *P. t. schweinfurthii* were at least as well separated as the three subspecies. *P. t. verus,* however, was represented by just one locality, while *P. t. troglodytes* like *P. t. schweinfurthii* was sampled from four localities.

Several other studies have demonstrated the high levels of within group variation in *P. t. schweinfurthii*. Jungers & Susman (1984), and Shea (1981; 1984; and references mentioned therein) have demonstrated that ranges for body weight and skeletal dimensions within *P. t. schweinfurthii* are higher than the other two subspecies. The population from Gombe National Park, Tanzania, in particular, increases the range of the subspecies.

It remains to be mentioned that at least three craniometric studies (Shea & Coolidge, 1988; Shea & Groves, 1987; & Shea *et al.*, 1993) and one odontometric study (Johanson, 1974), while supporting the tripartite classification of *P. troglodytes*, did not propose any one subspecies to be more distinct than the others. Shea & Coolidge (1988) found that Mahalanobis D^2 values, or the intergroup centroid distances separating the three subspecies were lower than that separating the subspecies of *Gorilla gorilla* and *Pongo pygmaeus* as studied earlier by Groves (1970) & Jacobshagen (1979), respectively. They propose that this could mean there is extensive gene flow between chimpanzee subspecies, a suggestion supported by mtDNA studies (Morin *et al*, 1994).

A tabulation of dental trends in Johanson's (1974) odontometric analysis (table 129, Johanson, 1974: 322) showed that both *P. paniscus* and *P. t. verus* are distinct (also shown by Uchida, 1992, using his data), but Johanson (p. 339) commented only on the distinctiveness of *P. paniscus*.

In conclusion, unlike the two species classification of *Pan*, which is widely accepted, the subspecies classification of *P. troglodytes* is unresolved. Several

studies indicate that *P. t. verus* is distinct from the other two subspecies, and that *P. t. schweinfurthii* is more variable than the other subspecies. Yet, the three subspecies are more closely related to each other, and form a trichotomy when compared to *P. paniscus* (Braga, 1995; Uchida, 1996).

Another point raised by these studies concerns the biogeographic boundary between the western and central African subspecies. Gonder (2000) studied the patterning of variation in mtDNA in a large sample of *P. troglodytes* and found support for only two major lineages of chimpanzees in Africa, which converge at the Sanaga River in Cameroon. Her study indicates that the central and east African chimpanzees (*P. t. troglodytes* and *P. t. schweinfurthii*, respectively) are a closely related ancient lineage with high within-group variation, while the north Cameroon and west African lineage is more recent and characterized by a lesser degree of variation. The study implies that the Rivers Niger and Ubangi, traditionally considered to be important boundaries for maintaining subspecies distinctions, may not be effective as barriers to gene flow as the River Sanaga. Clearly, the inter-population relationships of *P. troglodytes* needs to be reinvestigated so as to critically examine the boundaries at which populations become distinct enough to be called subspecies.

Populations

Although there has not been a thorough investigation of the overall patterns of geographic variation in chimpanzees, the nature of variation within and between populations of chimpanzees has been studied from several localities. Most of the

population studies stem from the behavioral research that has been carried out at more than 40 localities across Africa (Wrangham *et al.*, 1994). At least five chimpanzee populations (Gombe, Mahale, Kibale, Taï and Bossou) have been monitored for several decades now and provide excellent information on variation in life history patterns, behavior, ecology, genetics and morphology at these localities (Goodall, 1986; Nishida et al., 1990; Wrangham *et al*., 1992, 1996; Boesch & Boesch, 2000; Sugiyama, 1994). In addition, two cranial collections from the Senckenberg Museum in Frankfurt, Germany, and the Peabody Museum at Harvard University, USA, of populations from Liberia have provided information on intra- and inter-population variation in crania and teeth.

Following is a summary of the population studies that provide an understanding of within and between population variation in chimpanzees:

(1) Schuman & Brace (1954; 1955) studied the nature of dental variation in a population of chimpanzees from western Liberia, and recently Swindler *et al.* (1998) mirrored their study with a population from central Liberia. They found that the Coefficient of Variation (CV) of dental dimensions was quite low in both populations. Comparing the two populations, Swindler *et al.* (1998) found that the CVs for the same teeth in both localities were about the same, and the values did not increase when the two populations were combined. Comparing the CVs from these two localities with CVs for the same teeth for the entire species, they found that these populations did not follow the expected pattern of increasing variation from population to species – although CV values were

slightly higher at the level of the species, it was only for the M3 that they were almost double.

(2) Eckhardt & Protsch (1988) documented the frequencies for different nasal region morphologies in 124 individuals from a population of *P. t. verus* in Liberia. They found that a morphological configuration which Olson (1985a, 1985b) suggested is absent in *Pan*, was actually manifest at a fairly high frequency (28%). Of greater relevance to the present study was their finding, based on comparisons with the results of an earlier study (Eckhardt, 1987), that the frequency of this morphological variant was higher within the population than within the species. The frequency of the trait was about 17% in the species.

(3) Morin *et al*., (1994) calculated the allele frequencies for eight nuclear DNA loci in 43 individuals from the Gombe population and found that there is a lower frequency of heterozygotes than expected under the assumption of Hardy-Weinberg equilibrium. This suggested to them a non-random mating pattern, which they explained by the chimpanzee social structure of male philopatry. Sequencing mtDNA they found that there is a high within-community genetic variation in the control region of mtDNA, indicating that, due to female dispersal, there is a significant amount of gene flow between communities.

(4) A comparison of body weight of a population of chimpanzees from Mahale National Park, Tanzania with weights recorded for Gombe and another population from eastern Zaire revealed that there was a high range of diversity

between populations, especially in the weight of females (Uehara & Nishida, 1987). The three populations belong to the same subspecies but the population from Gombe had a lower average body weight than the other two, a finding repeated by Morbeck & Zihlman (1989).

(5) Morbeck & Zihlman (1989) measured attributes such as dental dimensions, cranial capacity, body weight, and limb bone proportions from Gombe and compared these with values for the subspecies and species of chimpanzees. They found that mean values for tooth size and cranial capacity are the same as in *P. troglodytes*, but the range of variation, based on the maximum and minimum values reported are lower for the Gombe population, and fall within the range for *P. t. schweinfurthii* and *P. troglodytes*. Mean long bone length and body weight, however, was found to be significantly lower than *P. t. schweinfurthii*, *P. troglodytes* and even *P. paniscus*. They discuss the implication of this for both the Gombe population and *P. paniscus*. It is significant that apart from long bone length and body weight, variation within the Gombe population was lower than the subspecies and species.

(6) Wrangham (1986, 1987), Ghiglieri (1987), Wrangham et al., (1994), and McGrew et al., (1996) compared behavioral observations at different localities and found a high degree of behavioral variation between populations, even between neighboring populations within the same subspecies (Wrangham, 1986; Boesch & Boesch, 2000). Boesch & Boesch (1990, 2000) suggest that the diversity could be attributed to the inherently varied behavioral repertoire of

chimpanzees, related to more elaborate cognitive abilities and a higher learning capacity.

From these studies no clear consensus can be drawn regarding patterns of variation in chimpanzee populations. In populations of *P. t. verus* from Liberia and *P. t. schweinfurthii* from Tanzania, CV of dental dimensions suggest that within-population variation is low. However, variation does not increase substantially as one goes from population to subsequently higher taxonomic levels. In nasal region morphology in a Liberian population, and mtDNA in the Gombe population, on the other hand, variation was higher within the population than the subspecies and species. In body weight and long bone dimensions in Gombe, variation was substantially lower. In comparing behavioral patterns and body weight, between-population variation was found to be high. In conclusion, based on the available studies, it appears that patterns of population variation in chimpanzees are complex and do not follow the predicted pattern of increasing variation from the level of the Mendelian population to the species (Mayr, 1963; 1969; Endler, 1977; Albrecht & Miller, 1993). A study of geographic variation, while using these studies to formulate initial hypotheses, will illuminate the pattern of variation in chimpanzees.

This Study

Based on the review of variation in chimpanzees, the following testable hypotheses can be formulated:

(1) The two species of chimpanzees are well separated morphologically and clearly diagnosable.

(2) The three subspecies of *P. troglodytes* are not so well differentiated. *P. t. verus* is more distinct from the other two subspecies.

(3) Chimpanzees from both sides of the Niger River are closely associated and are distinct from both *P. t. verus* and *P. t. troglodytes*.

(4) *P. t. troglodytes* and *P. t. schweinfurthii* have high intra-group variation, but *P. t. verus* does not.

(5) Populations from the north of the Sanaga River share greater similarity with west African chimpanzees than with populations from the south of the river.

(6) The population from Gombe National Park, Tanzania, is distinguishable from other populations of *P. t. schweinfurthii*.

(7) The range of variation within chimpanzee populations is high but variation is higher within subspecies and species.

(8) Chimpanzee populations are distinct from one another and between-population variation is high.

The study sample used to test these hypotheses is outlined in Table 3.2. The localities included within each of the 16 populations are listed in Chapter 2. The sample sizes for some of the populations are clearly quite small and the sex ratios

imbalanced. Despite this limitation these populations were not combined with other populations because phylogeographic studies (*e.g.*, Grubb, 1990) dispute their traditional affinities. Discriminant scores from the larger sample analyses were used in posthoc discriminant analyses to classify these populations and establish their affinity. Unfortunately, individuals from Gombe National Park were not included within the study sample, so hypothesis 6 could not be tested.

Table 3.2 Chimpanzee material used in this study

Group	*N*	**Male%, Female%**
Pan	**341**	**47, 53**
Pan troglodytes verus	**64**	**47, 53**
Population 1	51	43, 57
Population 2	10	50, 50
Population 3	3	100, 0
Pan troglodytes troglodytes	**152**	**46, 54**
Population 4	9	56, 44
Population 5	47	47, 53
Population 6	71	42, 58
Population 7	14	57, 43
Population 8	11	46, 54
Pan troglodytes schweinfurthii	**79**	**52, 48**
Population 9	6	50, 50
Population 10	20	35, 65
Population 11	18	61, 39
Population 12	16	50, 50
Population 13	19	63, 37
Pan paniscus	**46**	**39, 61**
Population 14	4	25, 75
Population 15	39	38, 62
Population 16	3	67, 33

Populations

Sexual dimorphism

I used a one-way Anova with a $p<0.01$ to test for the differences between the two sexes in linear dimensions of molars. I found that molar dimensions do not differ significantly between the sexes in any of the populations of *Pan*. When transformed into shape variables no sexual dimorphism was noted in molar dimensions. Thus, on the whole sexual dimorphism is not very significant in molar dimensions in *Pan*. In the multivariate analyses of molars described below the sexes were combined.

From the qualitative set of dental traits the only traits that differed significantly between the sexes (chi-square probability < 0.05) were: mesial and lingual groove on the UC, enamel extension on UP3, mesiolingual tubercle on UP3, and lingual and distal groove on LC.

Distribution of dental variation in populations

The 341 chimpanzee individuals were divided into 16 populations taking care to treat individuals from either side of the above geographical features as part of separate populations. A step-wise discriminant analysis was performed on each of the molars using both raw and shape variables and the canonical scores were used to generate generalized squared distances between all pairs of populations. The means of the D^2 values for the upper and lower molars were calculated so as to show the average distance between population pairs. These distance values are shown in Tables 3.3A and 3.3B. A full data matrix is presented so as to facilitate

reading both horizontally and vertically. Figure 3.2 shows the distances between populations on a map of Equatorial Africa.

Two major observations emerge from the data matrix:

(1) Populations from adjoining localities show a close association. This is best seen in the analyses using raw variables by identifying the closest affiliate for every population (Table 3.3 A). Population 5, 6, 10, 11, 12, 14, 15 and 16, and to a lesser extent 13, 1 and 2 show greatest similarity with an adjacent population (Figure 3.3).

(2) This pattern of similarity between adjoining populations is not true for all populations. For example, population pairs 4 and 5, 6 and 9, 8 and 16, and 11 and 15 are in close geographical proximity (Figure 3.2), yet their intergroup centroid distances are relatively large.

Arguments of vicariance biogeography (Rosen, 1978) suggest that populations that share low intergroup centroid distances exchange genetic material and have a closer phylogenetic affinity (and possibly a shared history), whereas populations from adjacent localities that are divergent in their centroid distances have a barrier inhibiting genetic exchange and are phylogenetically separated.

Based on these patterns of interrelationships, four major clusters of chimpanzee populations can be recognized: Cluster A formed by populations 1 and 2 in west Africa, cluster B made up of populations 5, 6, 7 and 8 in the western part of central Africa, cluster C formed by populations 9, 10, 11, 12 and 13 in central and east Africa, and cluster D formed by populations 14, 15 and 16 on the southern bank of the Congo River. These clusters correspond with the four traditional

Table 3.3 Mean generalized squared distances between chimpanzee populations. The bold type shows the lowest D^2 value for the population mentioned at the head of the column.

A. Raw variables

POP	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	0	3.94	3.00	7.07	4.31	4.74	5.42	4.41	5.82	4.35	3.92	4.46	5.12	20.53	10.84	17.83
2	3.94	0	3.22	9.16	4.68	5.53	5.40	6.06	5.79	5.18	5.49	5.20	6.99	24.93	14.62	20.08
3	**3.00**	**3.22**	0	5.03	3.40	3.58	**2.51**	4.31	3.64	2.35	2.60	2.45	3.14	12.08	6.78	9.38
4	7.07	9.16	5.03	0	4.66	4.97	6.90	4.57	6.39	6.15	6.08	5.98	4.66	15.03	8.74	13.17
5	4.31	4.68	3.40	4.66	0	**0.88**	3.34	**2.24**	4.01	2.43	2.62	1.87	2.72	15.41	7.38	12.76
6	4.74	5.53	3.58	4.97	**0.88**	0	2.88	2.31	4.29	3.22	3.16	2.34	3.57	14.23	6.16	11.89
7	5.42	5.40	2.51	6.90	3.34	2.88	0	3.37	4.82	4.29	4.37	3.09	4.99	15.60	8.10	12.78
8	4.41	6.06	4.31	**4.57**	2.24	2.31	3.37	0	4.58	3.76	3.43	2.94	3.11	14.16	6.59	10.69
9	5.82	5.79	3.64	6.39	4.01	4.29	4.82	4.58	0	3.43	3.13	3.69	4.11	22.83	11.89	17.30
10	4.35	5.18	**2.35**	6.15	2.43	3.22	4.29	3.76	3.43	0	**1.01**	1.78	**1.88**	19.02	9.60	15.17
11	3.92	5.49	2.60	6.08	2.62	3.16	4.37	3.43	**3.13**	**1.01**	0	**1.60**	2.20	18.91	9.77	15.20
12	4.46	5.20	2.45	5.98	1.87	2.34	3.09	2.94	3.69	1.78	1.60	0	2.07	17.06	8.44	13.19
13	5.12	6.99	3.14	4.66	2.72	3.57	4.99	3.11	4.11	1.88	2.20	2.07	0	16.57	7.94	12.57
14	20.53	24.93	12.08	15.03	15.41	14.23	15.60	14.16	22.83	19.02	18.91	17.06	16.57	0	5.50	5.69
15	10.84	14.62	6.78	8.74	7.38	6.16	8.10	6.59	11.89	9.60	9.77	8.44	7.94	**5.50**	0	**4.05**
16	17.83	20.08	9.38	13.17	12.76	11.89	12.78	10.69	17.30	15.17	15.20	13.19	12.57	5.69	**4.05**	0

Table 3.3 B. Mean generalized squared distances between chimpanzee populations. The bold type shows the lowest D^2 value for the population mentioned at the head of the column.
Shape variables

POP	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	0.00	4.19	3.28	6.83	4.70	4.56	5.54	3.62	5.38	4.84	4.78	5.31	5.31	8.50	5.40	10.63
2	4.19	0.00	3.21	7.38	4.19	4.32	4.91	3.56	5.04	5.17	5.23	4.58	5.57	11.50	7.22	10.90
3	**3.28**	**3.21**	0.00	**4.13**	3.22	2.88	**2.04**	3.31	3.02	2.17	2.39	2.28	2.59	4.34	**2.57**	**3.66**
4	6.83	7.38	4.13	0.00	4.26	4.99	6.95	4.25	5.52	5.70	5.54	5.60	4.46	8.91	6.79	11.04
5	4.70	4.19	3.22	4.26	0.00	**0.78**	3.30	**1.56**	3.41	2.26	2.66	1.90	2.59	5.97	3.62	7.40
6	4.56	4.32	2.88	4.99	**0.78**	0.00	3.34	2.14	3.81	3.20	3.34	2.64	3.60	6.36	3.75	8.35
7	5.54	4.91	**2.04**	6.95	3.30	3.34	0.00	3.46	4.14	4.17	4.58	3.41	5.22	6.59	4.67	8.48
8	3.62	3.56	3.31	4.25	1.56	2.14	3.46	0.00	**2.68**	3.03	2.39	2.61	2.78	7.34	4.52	7.85
9	5.38	5.04	3.02	5.52	3.41	3.81	4.14	2.68	0.00	3.17	2.81	3.52	3.09	8.43	4.92	8.08
10	4.84	5.17	2.17	5.70	2.26	3.20	4.17	3.03	3.17	0.00	**1.23**	2.02	**1.82**	7.78	5.51	9.00
11	4.78	5.23	2.39	5.54	2.66	3.34	4.58	2.39	2.81	**1.23**	0.00	**1.79**	1.88	7.55	5.34	7.95
12	5.31	4.58	2.28	5.60	1.90	2.64	3.41	2.61	3.52	2.02	1.79	0.00	2.27	7.13	4.76	7.26
13	5.31	5.57	2.59	4.46	2.59	3.60	5.22	2.78	3.09	1.82	1.88	2.27	0.00	8.41	5.15	8.51
14	8.50	11.50	4.34	8.91	5.97	6.36	6.59	7.34	8.43	7.78	7.55	7.13	8.41	0.00	4.23	7.18
15	5.40	7.22	2.57	6.79	3.62	3.75	4.67	4.52	4.92	5.51	5.34	4.76	5.15	**4.23**	0.00	5.09
16	10.63	10.90	3.66	11.04	7.40	8.35	8.48	7.85	8.08	9.00	7.95	7.26	8.51	7.18	5.09	0.00

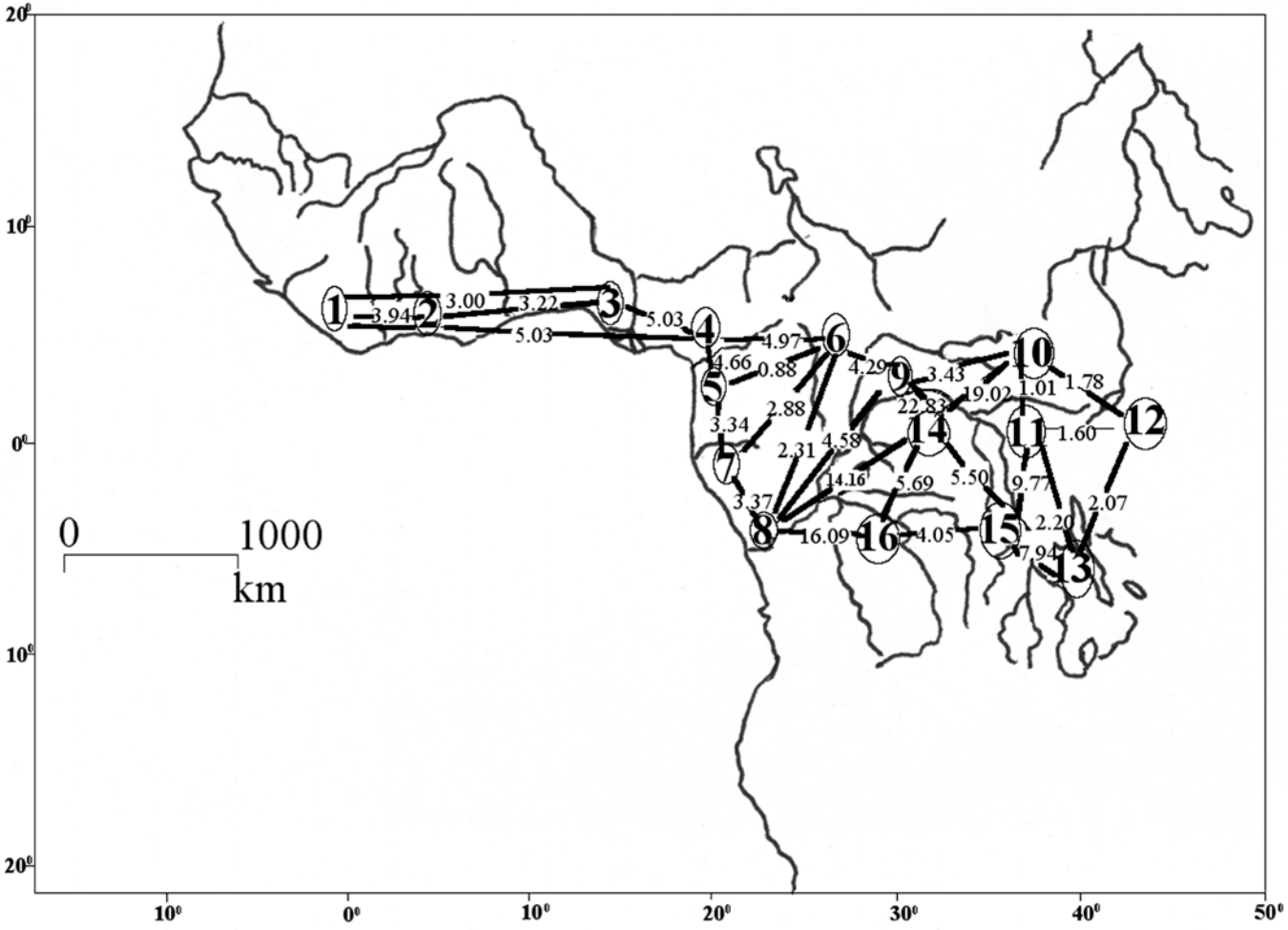


Figure 3.2 Squared generalized distances between chimpanzee populations (after Groves, 1970).

subgroups of chimpanzee and thus provide partial support for these subdivisions.

Populations 14, 15 and 16, belonging to *P. paniscus,* are characterized by the highest intergroup centroid distances and are the most widely separated from all other populations. Mahalanobis D^2 values between these three populations and all others range from 6.16 to 24.93 (Table 3.3A). This is not surprising given their location along the south of the Congo River and the known role of the river as a major faunal barrier (Grubb, 1990; Oates, 1996). Although these three populations are the most closely associated with each other, they are also separated from each other by distances comparable to that separating populations from the west and east African clusters on the north of the Congo River. The D^2 values for populations 14/15 are 5.50, 15/16 are 4.05 and 14/16 are 5.69 in the raw variable analysis. In contrast, values for populations hailing from the two markedly distinct subspecies, *P. t. verus* and *P. t. troglodytes,* are 4.31 for 1/5, and 4.68 for 2/5 (Table 3.3A). This could imply that there are hitherto unrecognized geographic variants within *P. paniscus,* separated by the rivers Lomani and Kasai. Localities demarcated by these rivers are considered to be Centers of Species Endemism (Grubb, 1990). Colyn (1988) has recognized several endemic subspecies from the Lomani center. However, caution must be exercised when making proposals regarding geographic variants within *P. paniscus* because only 3 individuals each were sampled from the populations 14 and 16 in this study.

The lack of adequate sample sizes also prohibits drawing firm conclusions

regarding the position of population 3. Gonder *et al.* (1997) have suggested that in mtDNA this population, from the west bank of the Niger River, is most closely allied with the population from the east bank (population 4 here) and not with *P. t. verus*. In this study only three individuals represent this population, and only maxillary teeth could be studied. The affiliation of the individuals changed depending on the tooth type studied. At times the population was associated with populations of *P. t. verus,* at other times with populations of *P. t. troglodytes*. The average D^2 value shows its closest affiliate to be population 10 in the raw variable analysis (Table 3.3A), and population 7 in the shape analysis (Table 3.3B). Given the high range of variation within the species, *P. troglodytes*, no great significance can be attached to the overall pattern of relationship displayed by the three individuals. It is noteworthy, however, that these individuals are not closely associated with individuals from population 4 on the east of the Niger. In fact, the intergroup distances between these two populations are very divergent, second only to the distance of population 3 from populations 14, 15 and 16 of *P. paniscus.*

Gonder *et al.* (1997) proposed that in mtDNA individuals from both sides of the Niger River are closely related, and together they are distinct from the other subspecies of *P. troglodytes*. This finding, based on the study of the control region of mtDNA could not be sufficiently supported by nuclear DNA data (Gonder, 2000), partly because of the lack of adequate samples. Groves (2001) found support for Gonder *et al.*'s (1997) proposal in nonmetric cranial characters, but once again

with small sample sizes. This study, albeit with a small sample, would indicate that the populations from either side of the Niger are not closely related in dental metrics but share affiliation with populations both to the west and the east.

Population 4 from eastern Nigeria is represented by a larger sample size of nine individuals. Mahalanobis distances between this population and all others shows that it is distinct from the west African populations 1 and 2 and the central and east African populations 5 to 13 (Table 3.3A). D^2 values between this population and all others are greater, on the whole, than the distance separating populations of *P. t. troglodytes* from *P. t. schweinfurthii*. This supports Gonder's (2000) claim that the Sanaga River exerts a greater influence in separating chimpanzees than the Ubangi River in central Africa and could indicate the presence of a distinct subspecies, *P. t. vellerosus*, in this region. Contrary to its affiliation in mtDNA and nuclear DNA (Gonder *et al.*, 1997; Gonder, 2000), however, in dental metrics population 4 is more closely related to *P. t. troglodytes* than the west African *P. t. verus*. The Mahalanobis distances between population 4 and population 1 and 2 of *P. t. verus* are 7.07 and 9.16, respectively, while the distances to populations 5 to 13 (*P. t. troglodytes* and *P. t. schweinfurthii*) range from 4.57 to 5.98. The closest affiliate of population 4 is population 8 (D^2 4.57) in southern Gabon. Groves (2001) likewise found this population to have greater affinity with *P. t. troglodytes* rather than with *P. t. verus*.

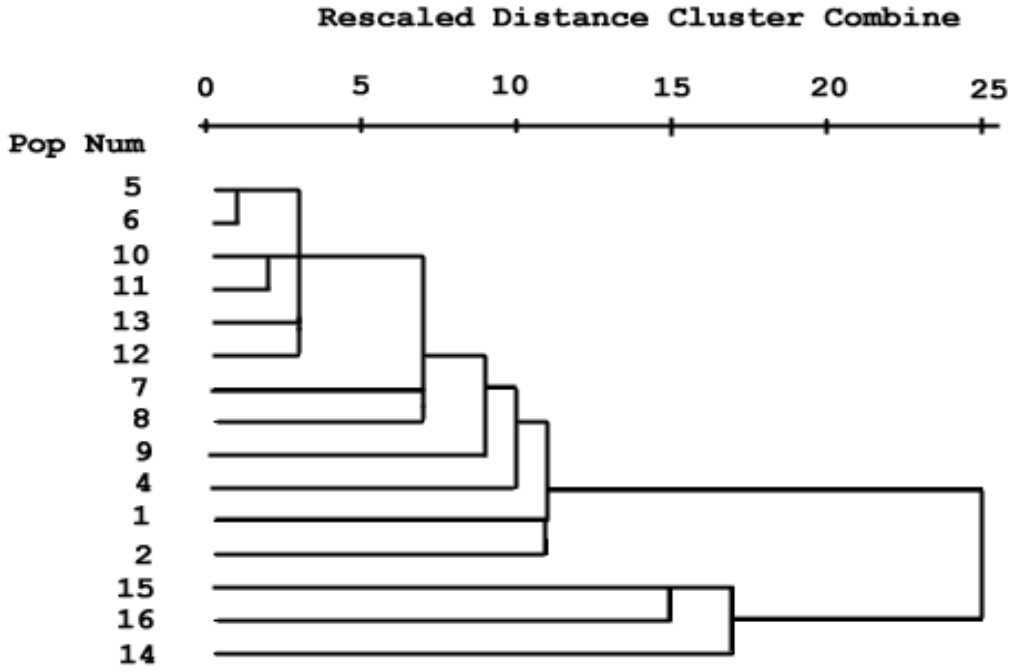
The study of population substructure reveals that populations of *P. t. troglodytes* and *P. t. schweinfurthii* are closely associated with each other. On the whole, distances between populations 5 to 13 are small compared to distances to populations of *P. t. verus* (population 1 and 2) or *P. paniscus* (populations 14, 15, 16) as seen in Table 3.3 A and B. D^2 values between populations 5 to 13 range from 0.88 to 4.99, while distances to populations 1 and 2 range from 4.31 to 6.99 and distances to populations 14, 15 and 16 range from 6.16 to 22.83 in the raw variable analysis. This relationship is illustrated most clearly in the dendrogram in Figure 3.3. It shows the results of a hierarchical cluster procedure. The group means of dental variables were used to examine the affinity between populations and the dendrogram was constructed using a centroid-clustering method (so as to be comparable with the Mahalanobis distance matrix). Population 3, which comprised only maxillary material, was not included in this analysis.

That the Ubangi River still has a modest influence in maintaining genetic discontinuity is evident when distances between adjacent populations 6 and 9 are compared (Table 3.3). Population 6, although in close geographical proximity to population 9 (Figure 3.2) shows greater affinity with populations 5, 7 and 8 from the west of the Ubangi, while population 9 most closely approximates populations 10, 11 and 12 from the east of the river (Table 3.3).

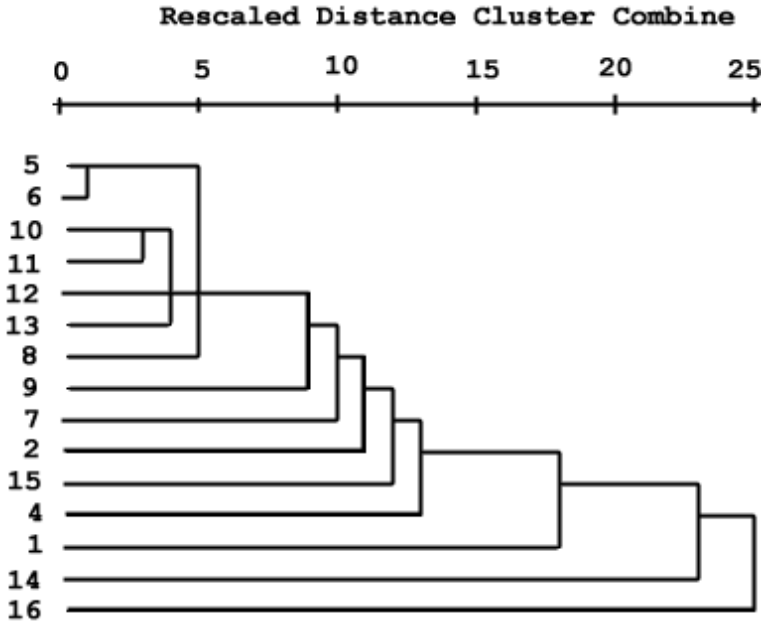
The non-metric dental characters show similar patterns of geographic variation as the metric variables. Figure 3.4 is a dendrogram graphically

Figure 3.3 Dendrogram showing relationship between chimpanzee populations.

A. Raw Variables



B. Shape Variables



illustrating the results of a hierarchical cluster analysis of the group means of the qualitative variables. Predictably, populations 14,15 and 16 of *P. paniscus* form a cluster, and so do populations 5 and 6 (*P. t. troglodytes)*, 10 and 11 (*P. t. schweinfurthii*) and 1 and 2 (*P. t. verus*). Just as in the metric variable analysis, population 4 (*P. t. vellerosus*) clusters with populations 7 and 8 of *P. t. troglodytes*, not with *P. t. verus* as suggested by mtDNA (Gonder *et al.*, 1997). And populations of *P. t. troglodytes* and *P. t. schweinfurthii* are closely affiliated: populations 5 and 6 with 10, 11, 12 and 13. The only novel finding that emerges from the non-metric variable analysis is the distinctiveness of population 9. This population is located on the east of the Ubangi River (Figures 3.2 and 2.1), an area identified by Grubb (1990) as a Center of Species Endemism. In the metric variable analysis population 9 is distinctly divergent from population 6 on the west bank of the Ubangi and closer to populations 10, 11, 12 and 13 (Table 3.3). Mahalanobis distances separating it from populations 10, 11, 12 and 13 are slightly higher than that separating 10, 11, 12 and 13 from each other. It should be reiterated, that because of the small samples studied (six individuals) observations regarding the singularity of this population (and others proposed here) are preliminary.

Based on the results of the discriminant analyses, the intergroup centroid distances, and the hierarchical cluster analysis of the metric and non-metric variables, this study concurs with molecular studies (Gonder *et al.*, 1997; Gonder, 2000) regarding the role of the Sanaga River in providing a biogeographical barrier for chimpanzees. Support is also found for Gonder's (2000) proposal that the

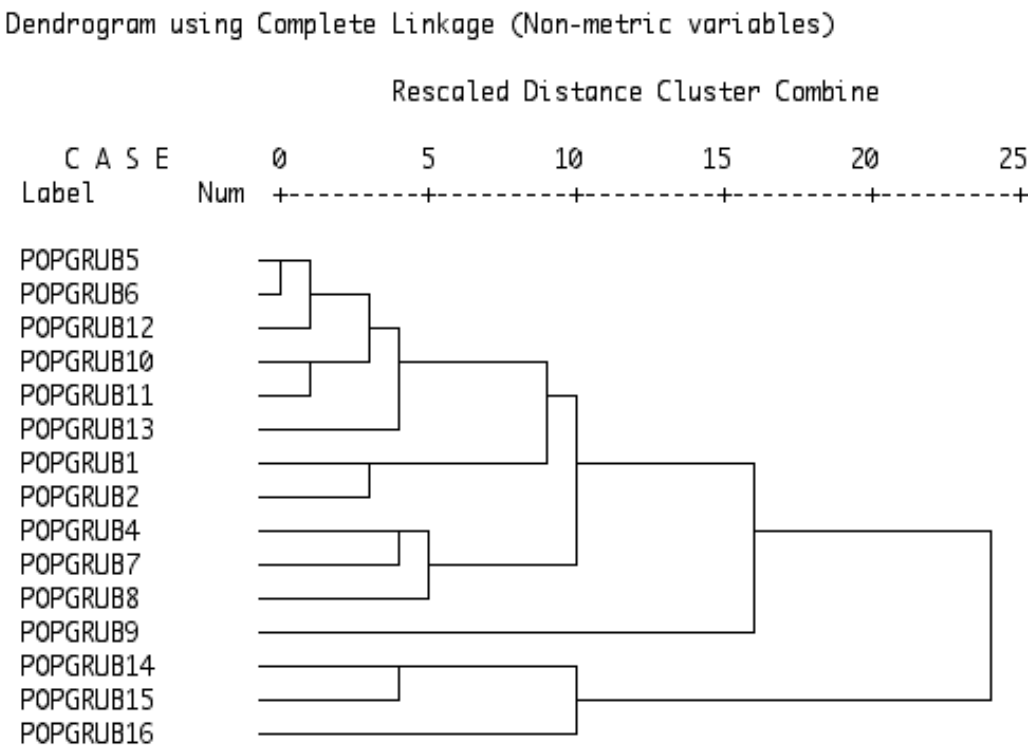


Figure 3.4 Dendrogram showing interrelationships of chimpanzee populations based on hierarchical cluster analysis of qualitative non-metric variables

central and east African chimpanzees are closely related. However, the Dahomey Gap may not exert a strong influence in separating the west and central African chimpanzees. Populations 1 and 2 on the west of the Dahomey Gap are similar to population 3 on the east of the Gap. It suggests instead that the Niger River separates *P. t. verus* from *P. t. vellerosus*. This study also suggests that the River Ubangi does separate the central and east African chimpanzees, *P. t. troglodytes* and *P. t. schweinfurthii*, although these two subspecies are closely related. In addition, the Rivers Kasai and Lomani may play a role in separating populations on either banks, but this will have to be reaffirmed using larger samples.

Subspecies differences

In order to examine the patterning of variation at a higher taxonomic level I divided the populations into the four subgroups – three traditionally recognized subspecies of *P. troglodytes* and *P. paniscus.* I performed discriminant analyses using both raw and shape variables. Mean generalized squared distances (Mahalanobis distances) between group centroids addressed the separation of the groups relative to one another.

When raw variables were used, average classification accuracy was about 73% for the four taxa (Table 3.4). Classification accuracy for *P. paniscus* was fairly high at about 95% and *P. t. verus* had a classification accuracy of about 79%. Classification accuracy for *P. t. troglodytes* and *P. t. schweinfurthii* was lower at 59% and 62%, respectively. As is to be expected from the population-level

analysis, *P. paniscus* is clearly separated from each of the subspecies – D^2 values separating *P. paniscus* from each of the subspecies of *P. troglodytes* were high (Table 3.5). The intergroup centroid distances (Table 3.5), and the specimens from each group misclassified into the other, also reveals a close affinity between *P. t. troglodytes* and *P. t. schweinfurthii*.

The first discriminant function, which separates *P. paniscus* from the subspecies of *P. troglodytes* is correlated with overall size. Pearson's correlation of the DF1, which accounts for about 60% of the variance, with the Geometric Mean was 0.7524 for LM3, 0.6385 for UM1, and 0.7650 for the UM2, $p<0.0001$. When discriminant analysis was carried out using shape variables, thus expressly reducing the effect of isometric size (or overall size), the average overall classification accuracy dropped to 64% (Table 3.4). The group contributing most strongly to this difference was *P. paniscus*, which declined by 25% in classification accuracy. Classification accuracy for *P. t. verus* also changed slightly (from 79% to 67%), but the number of specimens correctly assigned to *P. t. schweinfurthii* and *P. t. troglodytes* remained virtually unchanged. In addition, when shape variables were used, the four subgroups show comparable ranges of variation, as is apparent from the accuracy of classification and the number of specimens from each group misclassified into the other three groups.

Table 3.4 Classification accuracy for subspecies using discriminant analysis on raw and shape transformed measurements

RAW					
	Cases	*P. t. v.*	*P. t. t.*	*P. t. s.*	*P. p.*
P. t. v.	53	42	5	5	1
		79.25%	9.43%	9.43%	1.89%
P. t. t.	128	16	75	26	11
		12.50%	**58.59%**	20.32%	8.59%
P. t. s.	65	9	12	40	4
		13.85%	18.46%	**61.54%**	6.15%
P. p.	37	0	1	1	35
		0%	2.70%	2.70%	**94.60%**
Overall classification accuracy: 73.50%					

SHAPE					
	Cases	*P. t. v.*	*P. t. t.*	*P. t. s.*	*P. p.*
P. t. v.	53	36	7	5	5
		67.17%	13.17%	9.72%	9.4%
P. t. t.	128	15	73	24	16
		11.72%	**57.03%**	18.75%	12.5%
P. t. s.	65	6	11	41	7
		9.23%	16.92%	**63.08%**	10.77%
P. p.	37	3	4	4	26
		8.11%	10.81%	10.81%	**70.27%**
Overall classification accuracy: 64.39%					

Table 3.5 Generalized squared distances to subspecies using raw and shape transformed measurements.

RAW				
	P. t. v.	*P. t. t.*	*P. t. s.*	*P. p.*
P. t. v.	0			
P. t. t.	4.11	0		
P. t. s.	4.06	2.09	0	
P. p.	12.32	7.21	9.53	0

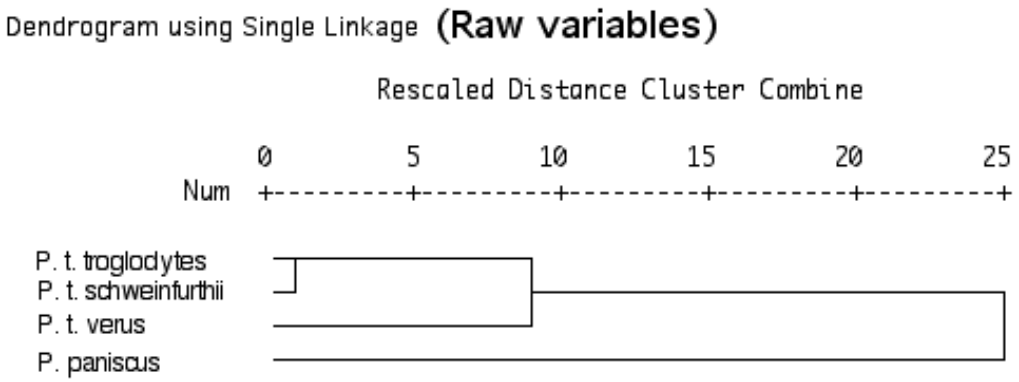
SHAPE				
	P. t. v.	*P. t. t.*	*P. t. s.*	*P. p.*
P. t. v.	0			
P. t. t.	3.69	0		
P. t. s.	4.04	1.84	0	
P. p.	5.73	3.39	4.27	0

Mahalanobis distances separating *P. paniscus* from the subspecies of *P. troglodytes* were reduced considerably when shape variables were used (Table 3.5). This is understandable considering that the effect of isometric size was reduced in the shape analysis. Nevertheless, the two species were still well separated. Of greater relevance for the recognition of subspecies differences, however, were the Mahalanobis distances showing the marked divergence between *P. t. verus* and the two other subspecies of *P. troglodytes* following the use of shape variables. When size differences between the subgroups were reduced, *P. t. verus* stood out as being distinct from the other two subspecies of *P. troglodytes*.

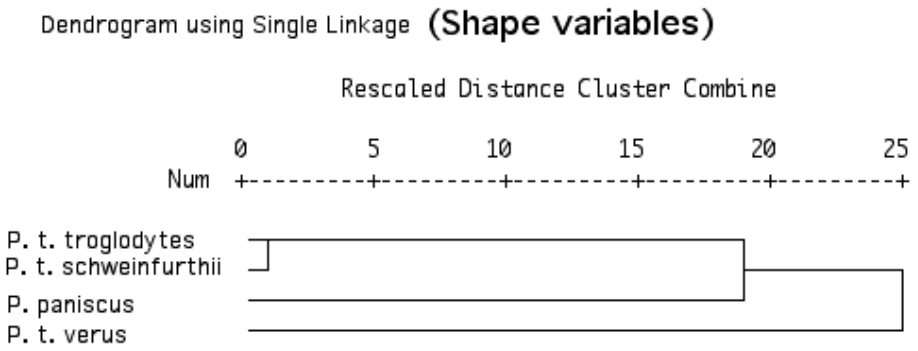
So as to further explore the interrelationships between the four taxa, and the position of *P. t. verus* vis-à-vis the other subspecies of *P. troglodytes,* I used the group means of the variables used in the discriminant analysis to complete a hierarchical cluster analysis using the neighbor-joining method. Figure 3.5 is a dendrogram graphically summarizing the clustering procedure for the raw (Figure 3.5 A) and shape transformed (Figure 3.5B) variables. As is evident from the discriminant analysis and the intergroup centroid distances, *P. t. troglodytes* and *P. t. schweinfurthii* cluster together most closely (Table 3.4 and Table 3.5). In the raw variable analysis (Figure 3.5 A) the cluster formed by *P. t. schweinfurthii* and *P. t. troglodytes* was joined first by *P. t. verus* and next by *P. paniscus*. Due to similarity in size *P. t. verus* is not as widely separated from the other subspecies of *P. troglodytes* as *P. paniscus*, but there is nevertheless a marked divergence. However, when the dendrogram was constructed using shape variables (Figure 3.5 B), the

Figure 3.5. Dendrogram showing hierarchical clustering solution of four subspecies. A. Group means of raw variables. B. Group means of shape variables.

A.



B.



cluster formed by *P. t. troglodytes* and *P. t. schweinfurthii* was combined first with *P. paniscus* and subsequently with P. *t. verus*, suggesting a slightly greater dental similarity between *P. paniscus* and the other two subspecies of *P. troglodytes* than between them and *P. t. verus*.

This distinctiveness of *P. t. verus* has been noted previously and was one of the hypotheses I set out to test in the present study. Molecular, behavioral, craniometric and dental data have indicated strong separation of this subspecies (Morin *et al.*, 1994; Wrangham *et al.*, 1994; Braga, 1995; Johanson, 1974; Uchida, 1996). The dental measurements used in this study confirm that *P. t. verus* is distinct from *P. t. troglodytes* and *P. t. schweinfurthii* both in size dependent and non-size dependent characters. The canonical correlations between the discriminant functions and discriminating shape variables are summarized in Table 3.6. Only variables with correlations of 0.40 or higher are included.

The variables that have high canonical correlations with the discriminant functions also have higher F-statistics and help differentiate the four groups. These differences are summarized in Table 3.7.

Discriminant analyses, intergroup centroid distances and hierarchical cluster analyses of both raw and shape data also reveal that *P. t. troglodytes* and *P. t. schweinfurthii* are closely allied. This strong affinity has not been noted previously using morphological data. Shea *et al.*'s (1993) craniometric data link *P. t. verus* and *P. t. troglodytes* in both regression-corrected and non-regression-corrected analyses, and Shea & Groves (1987) indicate a resemblance between *P. t.*

schweinfurthii and *P. paniscus*. In Shea & Coolidge's (1988) analysis the intercentroid distances between *P. t. schweinfurthii* and *P. t. troglodytes* are closest, but this distance is not substantially lower than the distance separating *P. t. schweinfurthii* and *P. t. verus*. It is possible that the choice of dental variables used in this study reveals an affinity between the two subspecies that is not seen using other types of data. It is also possible that the absence of individuals from the Gombe population, considered to be distinct from other populations of *P. t. schweinfurthii* (Morbeck & Zihlman, 1989; Uehara & Nishida, 1987; Jungers & Susman, 1984; Goodall, 1986), causes a spurious association. In dental size, however, the Gombe population was found to be similar to the subspecies *P. t. schweinfurthii* and the species *P. troglodytes* (Morbeck & Zihlman, 1989), thus questioning the likelihood that this population would increase the variation within *P. t. schweinfurthii* in this study.

The only other study that revealed a close association between the subspecies *P. t. troglodytes* and *P. t. schweinfurthii* was a molecular study by Gonder (2000). Her genetic diversity study implied that the central and east African chimpanzees (*P. t. troglodytes* and *P. t. schweinfurthii*) are a closely related lineage distinct from the north Cameroon and west African lineage. These findings are borne out by the dental metric data in this study. Tables 3.7 and 3.8 summarize the differences between the four taxa in metric and nonmetric characters. It is seen that *P. t. troglodytes* and *P. t. schweinfurthii* have several similarities in dental characters especially when compard with *P. t. verus*. Gonder has suggested that the

Table 3.6 Pooled within-groups correlations between discriminating variables and canonical discriminant functions. Variables ordered by size of correlation within function (only variables with correlations of 0.40 or higher are shown).

	Func 1	Func 2	Func 3		Func 1	Func 2	Func 3		Func 1	Func 2	Func 3
UM1				**UM2**				**UM3**			
SHUM1PRP	0.50		0.45	SHUM2PR1	0.49			SHUM3LCO	-0.53		
				SHUM2PO1	0.48						
								SHUM3LCI		-0.58	
SHUM1PR1		0.59		SHUM2PRP		0.69		SHUM3MFO		-0.51	
SHUM1LMC		0.50		SHUM2PRH		-0.53		SHUM3PRP		0.48	
SHUM1PO1		0.50		SHUM2BLM		0.50	0.47	SHUM3LMC		0.47	
SHUM1MD		0.44						SHUM3PO1		0.41	
SHUM1BLM		0.44		UM2POS_M			0.42				
				SHUM2LCO			-0.41	SHUM3MD		0.46	
SHUM1LDC			0.48					SHUM3BLD			-0.44
UM1AN_LC			0.42					SHUM3LDC			-0.43
UM1AN_BC			-0.42								
LM1				**LM2**				**LM3**			
SHLM1BLD	0.62			SHLM2BLM	0.65			SHLM3LPO	0.59		
SHLM1MD	0.50			SHLM2LMC	0.50			LM3AN_CR	0.50		
SHLM1LDC	0.50			SHLM2BLD	0.47			SHLM3BLM	0.49		
SHLM1BLM	0.50			SHLM2LPO	0.47	-0.43		SHLM3LMC	0.40		
SHLM1LMC	0.44										
SHLM1LCI	-0.41			LM2AN_HY		0.43		SHLM3LP4		-0.41	
SHLM1LPR	0.40			SHLM2LP4		-0.40					
								LM3AN_BC			0.40
LM1AN_HY		-0.49		SHLM2LPE			-0.44				
				LM2AN_BC			0.42				
SHLM1LPO			0.44								

Table 3.7 Differences between chimpanzee subspecies as compiled from canonical scores of step-wise discriminant analysis. Characters distinguishing subspecies are marked in bold. F statistic p<0.01

Character	*P. t. v.*	*P. t. t.*	*P. t. s.*	*P. p.*	F statistic
UM1 width distal	**Very wide**	Narrow	Narrow	Narrow	F(3, 289)= 8.0190
UM3 crista obliqua	**Often absent**	Often present	Often present	Often present	F(3, 280)= 7.9143
LM1 length	**Long**	Short	Short	Much shorter	F(3, 249)= 22.3142
LM1 width at mesial end	**Wide**	Narrow	Narrow	Very narrow	F(3, 249)= 19.6391
LM1 mesial cusps	**Widely spaced**	Closely spaced	Closely spaced	Closely spaced	F(3, 249)= 20.2786
LM1 width at distal end	**Wide**	Narrow	Narrow	Very Narrow	F(3,249)= 35.8140
LMI distal cusps	**Widely spaced**	closely spaced	closely spaced	Closely spaced	F(3, 249)= 25.8556
LM1 cingulum compared to buccal length	**Short**	Long	Long	Much longer	F(3, 249)= 10.4628
LM2 width mesial	**Very wide**	Narrow	Narrow	Narrow	F(3, 279)= 39.7382
LM2 mesial cusps	**Very wide**	Narrow	Narrow	Narrow	F(3, 279)= 25.3797
LM2 BL distal	**Very wide**	Narrow	Narrow	Narrow	F(3, 279)= 23.9321
LM2 postprotocristid	**Very long**	Short	Short	Short	F(3, 279)= 30.7254
UM1 length	Long	**Very short**	Long	Long	F(3, 289)= 7.9257
UM1 width mesial	Long	**Very short**	Long	Long	F(3,289)= 6.0757
UM1 mesial cusps	Widely spaced	**Closely spaced**	Wide space	Wide space	F(3, 289)= 8.4921
UM1 preprotocrista	Long	**Very short**	Long	Long	F(3, 289)= 10.4725
UM2 preprotocrista	Long	**Very short**	Long	Long	F (3, 327) = 10.3889
UM1 postprotocrista	Long	**Very short**	Long	Long	F(3, 289)= 7.2006
UM2 postprotocrista	Long	**Very short**	Long	Long	F (3, 327)= 8.4828
UM3 preparacrista	Long	**Short**	Long	Long	F(3, 280)= 7.4772

Table 3.7. continued

Character	*P. t. v.*	*P. t. t.*	*P. t. s.*	*P. p.*	F statistic
UM3 postprotocrista	Long	**Short**	Long	Long	F(3, 280)= 3.9932
UM3 lingual cingulum compared to lingual side	Short	**Long**	Short	Very short	F(3, 280)= 8.2385
UM3 mesial cusps	Widely spaced	**Closely spaced**	Widely spaced	Widely spaced	F(3, 280)= 5.3718
UM3 length	Long	Short	**Very long**	Short	F(3, 280)= 8.0133
UM1 preparacrista	Long	Short	**Very short**	Very long	F (3, 289)= 25.1940
UM2 preparacrista	Long	Short	**Very short**	Long	F (3, 327)= 13.0894
Placement of LM1 hypoconulid	Lingual	Slightly buccal	**Very buccal**	Very lingual	F(3, 249)= 12.2628
UM2 prehypocrista	Short	Long	**Very long**	Short	F (3, 327)= 6.1779
UM2 BL mesial	Long	Short	**Very short**	Long	F (3, 327)= 6.9088
LM2 preentoconid cristid	Short	Short	**Very long**	Short	F(3, 279)= 11.7908
UM3 distal cusps	Long	Short	Long	**Very short**	F(3, 280)= 4.3420
UM3 mesial fovea	Small	Large	Small	**Very small**	F(3, 280)= 5.8195
LM1 preprotocristid	Long	Short	Short	**Very short**	F(3, 249)= 17.7570
LM1 length of postprotocristid	Short	Very short	Long	**Very long**	F(3, 249)= 16.6097
LM3 postprotocristid	Long	Short	Very short	**Very long**	F(3, 252)= 14.4835
LM3 postmetaconid cristid	Very short	Long	Short	**Very long**	F(3, 252)= 8.3516
LM2 postmetaconid cristid	Long	Very short	Short	**Very long**	F(3, 279)= 11.0334
Placement of LM2 hypoconulid	Lingual	Buccal	Buccal	**Very lingual**	F(3, 279)= 18.0744
Placement of LM3 cristid obliqua	Buccal	Slightly lingual	Very lingual	**Very buccal**	F(3, 252)= 10.1429
LM3 BL mesial	Wide	Narrow	Narrow	**Wide**	F(3, 252)= 10.3109

River Ubangi, which constitutes the traditional boundary between the two subspecies may not be as effective a barrier to gene flow as previously thought. The population patterns studied above suggest that the Ubangi may not be as effective as the Niger or Sanaga rivers, but it does exert some influence as a biogeographic barrier.

Another relationship of note is that between *P. paniscus* and *P. t. troglodytes*. As summarized by the D^2 values in Table 3.5, in both raw and shape variable analyses, when averaged over all tooth types, *P. paniscus* most closely resembles *P. t. troglodytes*. Of the six molar types studied, this association was found to occur in four molars (UM1, UM2, LM1, LM3) when untransformed dental variables were used and in three molars (UM1, LM1 and LM3) when the variables were shape transformed. This relationship may be due to similarity in dental size – most dental dimensions in *P. t. troglodytes* are smaller than the other two subspecies. This could imply a shared primitive retention and a possibility of a dispersal corridor between West Africa and the south of the Congo River. In cranial growth patterns, however, Shea & Groves (1987) found *P. t. schweinfurthii* to most closely resemble *P. paniscus*.

Non-metric dental characters reinforce the patterning of variation encountered using metric characters. Chi-square statistics with associated *p* values of less than 0.001 were used to identify discrete dental characters that significantly differ in the four taxa. Table 3.8 summarizes these differences. The most relevant differences are the ones where only one of the four groups varies in the

Table 3.8 Differences between subspecies in non-metric characters. Character states and frequencies distinguishing the groups are marked in bold. Chi-square p<0.01.

Character	P. paniscus	P. t. sch	P. t. trog	P. t. ver
UI1 lingual pillar median	**0%**	54%	49%	60%
LI1 lingual pillar median	**37%**	70%	68%	81%
LI2 lingual pillar median	**43%**	76%	83%	85%
LI1 mesial notch	**0%**	21%	41%	44%
LI2 mesial notch	**0%**	37%	47%	57%
UP3 distolingual tubercle	**74%**	47%	43%	34%
Enamel extension on UP3	**57%**	96%	86%	99%
UP4 transverse ridge	**54%**	76%	81%	81%
UM2 anterior transverse crest	**43%**	84%	92%	74%
UM2 sulcus obliquus	**74%**	96%	98%	99%
LM1 mesiobuccal dev. groove wide notch	**89%**	45%	57%	55%
LM2 tuberculum sextum	**2%**	26%	37%	39%
LM3 lingual dev groove	**50%**	90%	86%	95%
UP3 mesial cingulum	85%	**66%**	81%	91%
UP3 distal cingulum	62%	**24%**	73%	82%
UM1 paraconule	5%	**36%**	13%	1%
UM1 protoconule	47%	**66%**	33%	46%
UM2 paraconule	2%	**24%**	11%	7%
UP4 mesial cingulum	49%	61%	**82%**	61%
UC mesial groove	82%	73%	64%	**43%**
UM1 crista obliqua	93%	94%	93%	**69%**
UI1 cingulum	**continuous 18%, continuous & bulge 6%, bulge 76%**	bulge tapering towards apex 94%	bulge tapering towards apex 95%	continuous 29%, continuous & bulge 13%, bulge 58%
UI2 cingulum	**continuous 53%, both 3%, bulge 44%**	continuous 11, both 7%, bulge 70%	continuous 15%, both 1 %, bulge 77%	continuous 48%, both 4%,bulge 36%
UP3 transverse ridge	**straight 34% or V-shaped 38%**	straight 39% or mesially curved 27%	straight 41% or mesially curved 26%	straight 46%or mesially curved 40%
UM1 cta mesially oriented	**33%**	69%	70%	24%
UM1 cta buccally oriented	**54%**	28%	24%	73%
UM2 cta buccally oriented	**9%**	22%	26%	8%

Table 3.8. continued				
Character	P. paniscus	P. t. sch	P. t. trog	P. t. ver
UM3 cta	**29%**	63%	61%	48%
UP4 mesiobuccal tubercle	32%	**48%**	13%	7%
UP4 distobuccal tubercle	65%	**82%**	46%	43%
LC distal groove	95%	**80%**	53%	56%
UM3 protoconule	15%	**45%**	20%	36%
UM2 protoconule	37%	66%	**33%**	62%
LM1 trigonid crest	41%	45%	**24%**	70%
LM3 trigonid crest	69%	65%	**44%**	78%
UM3 distoconule	33%	62%	56%	**31%**
LM1 trigonid crest twinned interrupted	21%	6%	8%	**38%**
LM2 mesiobuccal dev groove wide notch	86%	42%	51%	**75%**
LM3 tuberculum sextum	16%	47%	55%	**28%**

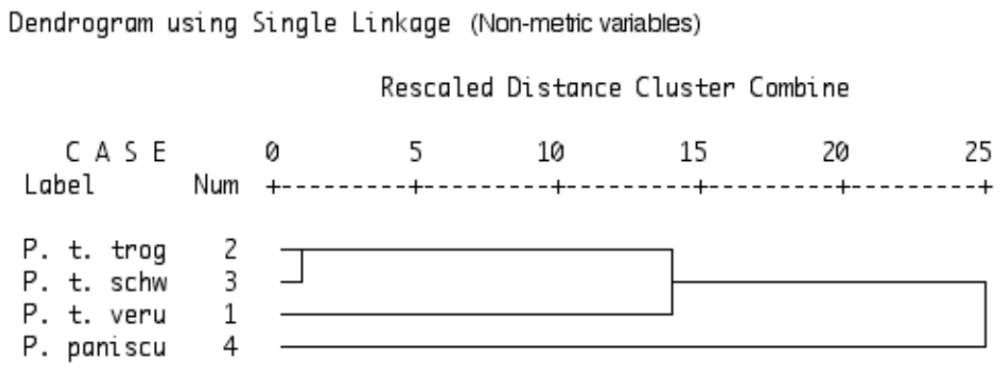
manifestation of a character, with the other three being invariable. Most of the differences between *P. paniscus* and the subspecies of *P. troglodytes* are of this type. The differences between the subspecies of *P. troglodytes* are far fewer and of degree rather than kind, often with one of three being similar to *P. paniscus*.

When comparisons were made between frequencies for morphological characters recorded in this study and other such studies, several differences were found. For example, the presence of the distoconule was recorded at significantly higher frequency in this study compared to Johanson (1974). This was also the case for the incidence of the seventh cusp (tuberculum intermedium). The frequency of the crista obliqua on the upper molars, however, was the same. Swindler *et al.* (1998), when comparing the results of their study with the results of Schuman and Brace (1954) and Johanson (1979) similarly found their results to be significantly different. Johanson (1974) likewise reported differences between his findings and

that of Schuman and Brace (1954). These differences could be due to different samples studied or could reflect regional differentiation. The significantly higher frequency recorded by Johanson (1974) for the distoconule of *P. t. troglodytes* from the Powell-Cotton collection from Cameroon compared to the Berlin and Cleveland collection, which also came from Cameroon, makes this seem likely. Swindler *et al*. (1998) have suggested, however, that differing methodological criteria employed in scoring characters causes the difference. In this study, for example, because of the difficulty in defining and delineating homologous characters, any cuspule located between the hypoconulid and entoconid was defined as tuberculum sextum, whereas Johanson using a stricter definition demarcated the cuspule by well developed grooves from the adjoining cusps and excluded cusps resulting from a split hypoconulid. No methodological differences were recorded in defining and scoring the distoconule and the seventh cusp in the two studies.

The discrete data were also used in examining the interrelationships between the four subgroups. Group means were calculated for each of the taxa for the qualitatively coded characters and these were used in a hierarchical cluster analysis. The results of this analysis presented in the form of a dendrogram (Figure 3.6) reveal a close association between *P. t. troglodytes* and *P. t. schweinfurthii*. *P. t. verus* was clearly separated from these two subspecies and *P. paniscus* was found to be distinct from all three. Thus, the pattern of relationships based on qualitative, non-metric characters is the same as that found using quantitative metric variables.

Figure 3.6 Dendrogram showing hierarchical clustering solution of four subspecies using qualitative data.



As seen in Tables 3.7 and 3.8 there is a high degree of overlap in dental morphology, in particular between the West and Central African chimpanzees. The following dental traits, which occur at significantly different frequencies in each, and can be used to characterize the four taxa:

P. paniscus: In dental metrics the smallest of the four taxa. Incisors with median lingual pillar absent or at low incidence, mesial notch on lingual side of incisors absent or low incidence, upper incisor often with lingual cingulum forming continuous ledge along cervical margin, high incidence of distolingual tubercle on UP3 but low incidence of enamel extension, UP3 transverse ridge often V-shaped, UP4 transverse ridge often absent, UM1 anterior transverse crest often meets protocone, UM2 and UM3 anterior transverse crest often absent, UM2 sulcus obliquus often absent, LM1 and LM2 quite large, larger than *P. t. troglodytes* and *P. t. schweinfurthii*, LM1 preprotocristid very short, postprotocristid very long,

LM2 and LM3 postmetaconid cristid very long, LM3 postprotocristid very long, LM2 hypoconulid very lingually placed, LM3 cristid obliqua very buccally placed.

P. t. verus: Dentally the largest of the four taxa. Low incidence of UC mesial groove, UM1 crista obliqua, UM3 distoconule and tuberculum sextum on LM3. LM1 trigonid crest often twinned and interrupted, LM2 mesiobuccal developmental groove often a wide notch, LM1 and LM2 length and width longer than other subspecies, lower incidence of cingulum and additional cuspules like pericone.

P. t. troglodytes: Smaller teeth than other subspecies of *P. troglodytes*, especially UM1 length, width, distance between cusps, and length of preprotocrista. Also UM2 preprotocrista and postprotocrista and UM3 preparacrista, postprotocrista and distance between mesial cusps. Higher incidence of cingulum on UP4 and UM3, and low incidence of trigonid crest on LM1 and LM2.

P. t. schweinfurthii: Teeth about same size as *P. t. troglodytes*. UP3 mesial and distal cingulum not common, UM1 and UM2 have short preparacrista, UM2 prehypocrista longer than other three subspecies, also UM3 length, UM2 mesial width short, higher incidence of cingulum on UP3, higher incidence of additional tubercles such as paraconule on UM1 and UM2, protoconule on UM1 and UM3, mesiobuccal and distobuccal tubercles on UP4, and distal groove on LC, LM1 hypoconulid buccally placed, LM2 preentoconid cristid long.

Species differences

To study the nature of the difference between the two species in dental traits, I divided the sample into the two traditionally recognized species, *P.*

troglodytes and *P. paniscus*, and carried out a two-sample discriminant analysis. Separate analyses were conducted on the raw measurements and the shape variables.

The results of these analyses revealed that raw, untransformed, dental measurements are able to classify the two species with an accuracy of 91%, when averaged over all tooth types (Table 3.9). The single discriminant function (DF 1), which is highly significant (p=0.0001), accounts for, on average, 70% of the observable variation. Furthermore, in the case of the UM1, UM2, UM3 and LM3 the discriminant scores for this function are strongly correlated with size, represented by the Geometric Mean (r = 0.7424, 0.7321, 0.6518, and 0.7211, respectively, p = 0.0001). This demonstrates that overall dental size marks the predominant difference between chimpanzee species. This has been reported previously (Shea, 1983; 1984), even using dental data (Johanson, 1974; McHenry & Corrucini, 1981; Kinzey, 1984; Uchida, 1996).

Comparing mean linear dental dimensions in both species, I found that UP3s are only 11% larger in *P. troglodytes*, LM1s are only about 10% larger, but both upper and lower canines are more than 30% larger (Table 3.10). In other words, bonobos have relatively large UP3s and LM1s but relatively small canines compared to chimpanzees. Sexual dimorphism in canines, measured using a ratio of female to male canine dimensions, however, was found to be similar in both species. The average difference between the two species in linear dental dimensions was 18%.

Table 3.9 Summary of two species discriminant analysis using raw, shape, and log shape variables. Standardized canonical coefficients shown.
* Pearson correlation between DF and Geomean

Raw variables	Shape variables
UM1 (N=293)	
Accuracy 95.90% Canonical correlation 0.75 UM1MD .84549 UM1BLMES .29943 IUM1L_MC -.26126 IUM1L_DC .60260 UM1LPREP -.48677 UM1LPRE1 -.23724 UM1LPREH .17902 UM1LPOS2 .18829 UM1AN_LC .19707 * r = 0.7424	Accuracy: 87.03% Canonical correlation 0.59 SHUM1MD -1.16658 SHUM1BLM -.43788 SHUM1BLD 1.57495 SHUM1LMC .65952 SHUM1LDC -.88003 SHUM1PRP .65379 SHUM1PRM .29632 SHUM1PRH -.37946 SHUM1POH -.27303 UM1AN_BC .34927 * r = -0.3675
UM2 (N=331)	
Accuracy 91.84% Canonical correlation 0.65 UM2MD .48054 UM2BLMES .56894 UM2LPREP -.20475 UM2LPOS1 .19706 UM2LPREH .18534 UM2LPOS2 .20883 UM2POS_D -.19463 * r = 0.7321	Accuracy: 68.58 Canonical correlation 0.33 SHUM2MFO .48596 SHUM2PRP -.53125 SHUM2PRH .43758 SHUM2POH .52942 * r = 0.4458
UM3 (N=284)	
Accuracy 87.68% Canonical correlation 0.55 UM3MD .43180 UM3BLMES .51380 UM3LPOS1 .40914 UM3LPRE1 -.24319 UM3LPREH .24499 UM3AN_LC -.32131 * r = 0.6518	Accuracy: 71.83% Canonical correlation 0.35 SHUM3PRP -.47889 SHUM3POM .65295 SHUM3PRH .53012 UM3AN_BC .40073 * r = 0.2004

Table 3.9. Continued

Raw variables	Shape variables
LM1 (N=253)	
Accuracy: 86.96% Canonical correlation 0.63 LM1MD .48795 LM1BLDIS .40068 ILM1L_MC -.23111 LM1LPMET -.24061 LM1POS_M -.22487 LM1AN_HY .30673 LM1AN_CR -.32216 * r = 0.4816	Accuracy: 81.03% Canonical correlation 0.53 SHLM1BLD .62919 SHLM1LMC -.48726 SHLM1LPE .40858 LM1POS_D .29104 LM1AN_HY .52165 LM1AN_CR -.63665 * r = 0.1101
LM2 (N=283)	
Accuracy: 91.87% Canonical correlation 0.71 LM2BLMES .57314 LM2BLDIS .47827 ILM2L_CI -.19669 LM2LPOST -.31578 LM2LPREH -.18292 LM2LPOME -.20170 LM2LPOEN .19864 LM2AN_LC -.16043 LM2AN_HY .22948 LM2AN_CR -.35807 * r = 0.4121	Accuracy: 83.75% Canonical correlation 0.58 SHLM2BLM -.98950 SHLM2LMC .43379 SHLM2LPO .38685 SHLM2LP4 .60877 LM2AN_HY -.43772 LM2AN_CR .61065 * r = -0.1235
LM3 (N=256)	
Accuracy: 94.14% Canonical correlation 0.70 LM3MD .49480 LM3BLMES .58175 ILM3L_MC -.18964 LM3LPOME -.31599 LM3LPOEN .25737 LM3AN_CR -.32608 * r = 0.7211	Accuracy: 79.30% Canonical correlation 0.49 SHLM3DFO -.39550 SHLM3BLM -.88381 SHLM3LMC .49723 SHLM3LPO .34950 SHLM3LP4 .62705 SHLM3LP5 -.32230 LM3AN_CR .68090 * r = -0.3478
Average accuracy 91.40% Average canonical correlation 0.70	Average accuracy 78.59% Average canonical correlation 0.48

Table 3.10 Mean dental dimensions in two chimpanzee species. 'M' Male, 'F' Female.

	P. troglodytes			*P. paniscus*			% Difference
Variable	F Mean	M Mean	Total Mean	F Mean	M Mean	Total Mean	(P.t total-P.p total)/P.p total * 100
UI1MD	11.74	11.82	11.78	10.21	10.61	10.36	14%
UI1BL	9.25	9.41	9.33	7.46	7.92	7.64	22%
UI1 Average	**10.50**	**10.62**	**10.56**	**8.84**	**9.27**	**9.00**	**17%**
UI2MD	8.74	8.82	8.77	7.42	7.81	7.57	16%
UI2BL	8.51	8.6	8.55	6.96	7.34	7.11	20%
UI2 Average	**8.63**	**8.71**	**8.66**	**7.19**	**7.58**	**7.34**	**18%**
UCMD	11.42	14.44	12.88	9.1	11.16	9.9	30%
UCBL	9.34	11.36	10.32	7.02	8.71	7.68	34%
UC Average	**10.38**	**12.90**	**11.60**	**8.06**	**9.94**	**8.79**	**32%**
UP3MD	8.07	8.15	8.11	7.39	7.51	7.44	9%
UP3BL	10.31	10.56	10.43	9.19	9.43	9.28	12%
UP3 Average	**9.19**	**9.36**	**9.27**	**8.29**	**8.47**	**8.36**	**11%**
UP4MD	7.37	7.48	7.42	6.3	6.44	6.35	17%
UP4BL	10.03	10.19	10.11	8.61	8.83	8.7	16%
UP4 Average	**8.70**	**8.84**	**8.77**	**7.46**	**7.64**	**7.53**	**16%**
UM1MD	10.25	10.49	10.36	8.72	8.86	8.78	18%
UM1BLMES	10.6	10.71	10.65	9.35	9.51	9.42	13%
UM1BLDIS	10.33	10.53	10.43	9.23	9.36	9.28	12%
UM1 Average	**10.39**	**10.58**	**10.48**	**9.10**	**9.24**	**9.16**	**14%**
UM2MD	10.08	10.28	10.17	8.83	9.13	8.94	14%
UM2BLMES	10.79	11.03	10.9	9.52	9.63	9.56	14%
UM2BLDIS	10.02	10.22	10.12	8.72	9.14	8.87	14%
UM2 Average	**10.30**	**10.51**	**10.40**	**9.02**	**9.30**	**9.12**	**14%**
UM3MD	9.15	9.52	9.33	8.16	8.27	8.21	14%
UM3BLMES	10.19	10.51	10.34	9.13	9.22	9.17	13%
UM3BLDIS	8.77	9.06	8.91	7.67	7.85	7.74	15%
UM3 Average	**9.37**	**9.70**	**9.53**	**8.32**	**8.45**	**8.37**	**14%**
LI1MD	7.73	7.7	7.72	7.09	7.36	7.2	7%
LI1BL	8.6	8.76	8.67	6.72	7.22	6.92	25%
LI1 Average	**8.17**	**8.23**	**8.20**	**6.91**	**7.29**	**7.06**	**16%**
LI2MD	8.24	8.6	8.4	7.4	7.57	7.47	12%
LI2BL	8.97	9.21	9.08	6.88	7.12	6.98	30%
LI2 Average	**8.61**	**8.91**	**8.74**	**7.14**	**7.35**	**7.23**	**21%**
LCMD	10.98	13.16	12.03	8.48	9.92	9.02	33%
LCBL	9.75	11.39	10.54	7.28	8.51	7.74	36%
LC Averae	**10.37**	**12.28**	**11.29**	**7.88**	**9.22**	**8.38**	**35%**
LP3MD	10.75	11	10.87	8.97	9.13	9.03	20%
LP3BL	8.49	8.76	8.61	7.42	7.42	7.42	16%

Table 3.10 continued

LP3 Average	**9.62**	**9.88**	**9.74**	**8.20**	**8.28**	**8.23**	**18%**
LP4MD	7.69	7.89	7.78	6.78	7.15	6.92	12%
LP4BL	8.8	9.11	8.94	7.74	7.75	7.74	16%
LP4 Average	**8.25**	**8.50**	**8.36**	**7.26**	**7.45**	**7.33**	**14%**
LM1MD	10.78	11	10.88	9.86	9.83	9.85	10%
LM1BLMES	9.23	9.43	9.32	8.58	8.53	8.56	9%
LM1BLDIS	9.57	9.74	9.65	8.72	8.55	8.65	12%
LM1 Average	**9.86**	**10.06**	**9.95**	**9.05**	**8.97**	**9.02**	**10%**
LM2MD	11.16	11.39	11.26	10.01	10.37	10.16	11%
LM2BLMES	9.92	10.2	10.05	8.78	8.98	8.86	13%
LM2BLDIS	9.97	10.14	10.05	8.68	8.87	8.76	15%
LM2 Average	**10.35**	**10.58**	**10.45**	**9.16**	**9.41**	**9.26**	**13%**
LM3MD	10.57	10.81	10.68	9.12	9.23	9.16	17%
LM3BLMES	9.46	9.81	9.63	8.21	8.1	8.17	18%
LM3BLDIS	9.26	9.45	9.35	7.95	8.11	8.01	17%
LM3 Average	**9.76**	**10.02**	**9.89**	**8.43**	**8.48**	**8.45**	**17%**
AVERAGE DIFFERENCE							**18%**

Overall size, however, does not account for all of the dental differences. It is noteworthy, in particular, that the discriminant scores for the DF 1 of LM1 and LM2 are not highly correlated with size (r = 0.4816 and 0.4121, respectively p = 0.0001, Table 3.9.). And, when the effect of overall size is explicitly reduced in the analyses using shape variables, the classification accuracy is still fairly high (79% on average), although the accountable variance is now, predictably, much lower, only about 50% (Table 3.9.). The size-related and non size-related variables that have a high loading on the DF and are therefore responsible for group separation are summarized in Table 3.11.

In addition to the metric data, qualitative, nonmetric data were examined in order to find out what morphological traits differentiate the two species. Chi-square statistics with associated p-values of less than 0.001 were used to identify the variables differentiating the two. The traits that showed significant correlation with sex were not included in this analysis. Because *P. troglodytes*, in particular, is characterized by a high range of within-species variation the differences between the species were not of an absolute nature. Rather, the differences are in the frequency of occurrence of dental traits. To rule out the possibility that these differences were caused by the markedly different sample sizes, several random samples of *P. troglodytes* were drawn so as to match the sample size of *P. paniscus*. The differences between the two species using the total sample size still prevailed in randomly drawn samples.

Based on these statistical analyses, the differences between the two species

in overall size, shape, and qualitative characters are summarized in Table 3.11. Some of the nonmetric dental differences, for example, the position of the anterior transverse crest, the position of the hypoconulid, and the absence of the tuberculum sextum (or the sixth cusp) in P. paniscus have been recognized previously (Johanson, 1974; Kinzey, 1984). Differences in morphological characters on the anterior dentition are reported here for the first time. These are of particular importance in evaluating functional and dietary differences between the two species (see discussion below). Johanson (1974) and Kinzey (1984) also reported other age and wear related differences in the anterior dentition that could not be evaluated in this study because of the selective sampling of relatively unworn adult teeth.

Within-group variation

The final hypothesis to be tested is that chimpanzees are characterized by high within-population variation. I calculated ranges of variation for populations, subspecies and species and compared intra- population variation with intra-subspecific and intra-specific variation. I selected only the linear (length and breadth) dimensions of all teeth, and using descriptive statistics such as the maximum, minimum, mean and standard deviation I calculated the coefficient of variation (CV) and range as a percentage of mean (R%) for these 38 variables. Small sample sizes are likely to result in exceptionally high CVs and low R% values (Cope, 1989; Cope & Lacy, 1992), implying, in this case, that if I were to use all 16 populations for calculating CVs and R%, there would be a high

Table 3.11 Differences between *P. paniscus* and *P. troglodytes* based on chi-square and discriminant analyses (both with p statistics of less than 0.001). Frequency of occurrence of non-metric characters in parenthesis.

Pan paniscus	*Pan troglodytes*
Mean mesiodistal and buccolingual dimensions of teeth shorter	Mean mesiodistal and buccolingual dimensions of teeth longer
Mesial notch on lingual side of incisors often absent (70% of UI1, 94% UI2, 100% LI1, 100% LI2)	Mesial notch on lingual side of incisors more often present (60% UI1, 35% UI2, 36% LI1, 50% LI2)
Median lingual pillar often absent on UI1 (100%), UI2 (94%), LI1 (63%) and LI2 (57%)	Median lingual pillar often present on UI1 (53%), UI2 (26%), LI1 (70%), and LI2 (80%)
Cingulum on UI2 more often continuous ledge along cervical margin (55%)	Cingulum on UI2 more often swelling at base tapering towards apex (68%)
Mesiobuccal, distobuccal and distolingual tubercles on UP3 often present (98%, 94%, 74%)	Mesiobuccal, distobuccal and distolingual tubercles on UP3 not that common (70%, 70%, 41%)
UM1 anterior transverse crest more often meets protocone (53%)	UM1 anterior transverse crest more often meets preprotocrista (56%),
The distal cusps of UM1 more closely spaced	The distal cusps of UM1 more widely spaced
UM2 anterior transverse crest often absent (57%)	UM2 anterior transverse crest often present (80%), often meeting preprotocrista (60%)
The postmetacrista of the UM3 is shorter	The postmetacrista of the UM3 is longer
The hypoconulid more lingually placed on all three lower molars	The hypoconulid is more buccally placed on all three lower molars.
The cristid obliqua more buccally placed making a wider angle when connected with the distal cusps	The cristid obliqua more lingually placed making a narrower angle when connected with the distal cusps.
Mesiobuccal development groove on LM1 and LM2 often present as wide notch (89% and 86%)	Mesiobuccal development groove on LM1 and LM2 not as often present as wide notch (53% and 55%)
Tuberculum sextum on LM2 and LM3 often absent (98% and 85%)	Tuberculum sextum on LM2 and LM3 more often present (35% and 46%)
Lingual developmental groove on LM3 often absent (49%)	Lingual developmental groove on LM3 infrequently absent (11%)

probability of incorrectly supporting the null hypothesis (high variation within populations) with the CV (a type I error) or falsely rejecting it with the R% (a type II error). I therefore selected from each of the four subgroups a single population that had a sample size of greater than 30 individuals – population 1 from *P. t. verus*, population 6 from *P. t. troglodytes*, populations 10, 11 and 12 combined from *P. t. schweinfurthii* (intergroup centroid distances show these populations to be closely affiliated), and population 15 from *P. paniscus*. I randomly drew 30 individuals from these populations. Thirty individuals were also randomly drawn from the three subspecies of *P. troglodytes* and the two species of *Pan* – these, of course, were represented by much larger sample sizes. I thus drew an equal sample from the population, subspecies and species, which helped control for the effect of sample size in causing false estimates of variation. Bootstrapping methods were used and 1000 random samples of 30 were drawn with replication from each of the populations, subspecies and species. These were then used in calculating average CV and R% for the 38 variables.

Appendix 1 lists the CV and R% for the 38 variables in the four populations, the three subspecies and the two species of chimpanzees. Tables 3.12 to 3.15 are summary tables comparing CV and R% within and between population, subspecies and species. Table 3.12 compares the CV and R% within each of the four subgroups – the three subspecies of *P. troglodytes* and *P. paniscus*. Variation within the population is compared with the more inclusive subspecies and species.

The table provides a frequency count of the number of variables, out of 38, where the maximum CV values were recorded in the population, subspecies or species. In *P. t. verus*, for example, only in the case of 5 variables were the maximum CV values seen at the level of the population (population 1, in this case). Three variables reported maximum values at the level of the subspecies, and the remaining 30 variables had highest CVs at the level of the species. This would suggest that at least in the case of *P. t. verus*, the species is more variable than the subspecies and population. This, however, is not true for the other subspecies of *P. troglodytes*: in *P. t. troglodytes* the maximum CV was recorded in the species in the case of only 15 variables, and in *P. t. schweinfurthii* in only 18 variables. In *P. t. schweinfurthii*, in addition, only in 9 cases is the highest CV recorded at the level of the subspecies, whereas 11 variables have the highest CV values at the level of the population. The R% shows a similar trend – in *P. t. verus* the maximum variation is often seen at the level of the species (28 out of 38 variables), whereas in *P. t. troglodytes* the highest R% value is seen in the species in only 9 out of 38 variables, and in *P. t. schweinfurthii* in 19 out of 38 variables.

Table 3.13 shows the number of variables that follow the expected increase in variation from population to species. In *P. t. troglodytes* only 8 out of 38 variables show the sequential increase in CV values. In *P. t. verus* and *P. t. schweinfurthii*, respectively, 12 and 15 variables show the sequential progression, but in *P. paniscus*, which is not divided into subspecies, 25 variables have higher CVs within the species compared to the population.

Table 3.12 Comparison of CV and R% between population, subspecies and species. Number of times highest CVs or R% recorded in population, subspecies or species. Total number of variables: 38.

	CV			R%		
	Pop	Subsp	Species	Pop	Subsp	Species
P. t. verus	5	3	30	6	4	28
P. t. troglodytes	5	18	15	10	19	9
P. t. schweinfurthii	11	9	18	13	6	19
P. paniscus	13	25		21	17	

Table 3.13 Number of variables out of 38 showing sequential progression of variation from population to species

	CV	R%
P. t. verus	12	5
P. t. troglodytes	8	3
P. t. schweinfurthii	15	7
P. paniscus	25	17

Table 3.14 Intersubspecies comparison. Number of variables out of 38 for which highest CV and R% recorded in each subspecies.

	CV	R%
P. t. v	5	6
P. t. t.	18	20
P. t. s	15	12

Table 3.15 Interspecies comparison. Number of variables for which highest CV and R% recorded in each species

	CV	R%
P. troglodytes	26	24
P. paniscus	12	14

When subspecies of *P. troglodytes* are compared by tabulating the frequencies of maximum CV and R% recorded in each (Table 3.14) it is seen that maximum values are recorded less frequently within *P. t. verus* compared to the other two subspecies. Highest CVs are encountered for only 5 out of 38 variables in *P. t. verus*, but 18 and 15 variables recorded maximum CVs in *P. t. troglodytes* and *P. t. schweinfurthii*, respectively. When the two species are compared in a similar manner (Table 3.15), it is seen that *P. troglodytes* has a higher frequency of maximum variance than *P. paniscus*.

These simple comparisons help highlight the following conclusions:

1. *P. t. verus* is characterized by low intrasubspecific variation when compared with the other two subspecies of *P. troglodytes*. This is clear when variation within the subspecies is compared to the species (Table 3.12), and when the three subspecies are compared with one another (Table 3.14). In mtDNA sequences the west African chimpanzees were likewise found to be less diverse compared to other populations of *P. troglodytes* (Gonder, 2000).
2. Variation within *P. paniscus* is lower than *P.troglodytes*. Comparing CV and R% between the two species it is seen that CVs are higher in *P. troglodytes* in 26 out of 38 variables and R% is higher in 24 variables (Table 3.15).
3. On the whole, variation does not increase substantially in chimpanzees in a hierarchical fashion. Table 3.13 shows that only in *P. paniscus* does variation increase when proceeding from population to species. In the subspecies of *P. troglodytes* this progression is not seen. *P. t. troglodytes*, in particular, shows

higher levels of diversity in CV and R% values at the level of the subspecies (Table 3.12). In Table 3.16 the means and standard deviations of the 38 linear dimensions are compared for the average population, subspecies and species. It reveals that means and standard deviations are similar between populations, subspecies and species of chimpanzee. Figure 3.7 shows the comparison of CV within population, subspecies and species in the LM1 and LM2, the least variable teeth in chimpanzees. Although there is a progressive increase in CV in these six variables the increase is not large.

A similar pattern of variation is seen with the nonmetric data. In table 3.17 discrete dental characters whose chi-square statistics show significant differences ($p<0.01$) between the species were chosen and frequencies were calculated within each population, subspecies and species. It shows that within each of the species qualitative characters are found at similar frequencies in the population, subspecies and species.

This patterning of chimpanzee variation, where most of the variation within the species is observable at the level of the population has not been reported previously. Shea and Coolidge (1988) found craniometric distances between traditional subspecies of *P. troglodytes* to be much less than that noted for the subspecies of *G. gorilla*. Morin *et al.* (1994) found high diversity within the Gombe population – 15 different mtDNA haplotypes were recorded from 19 individuals sampled. Morin *et al.* (1994), Goldberg & Ruvolo (1997) and Gagneux *et al.* (1999) also found identical mtDNA haplotypes in populations separated by

hundreds of kilometers. Morin *et al*. (1994) have suggested that this pattern of variation could be explained by the social structure of chimpanzees. The implications of this for dental data and chimpanzee systematics will be discussed in the next section.

Discussion

This study has demonstrated that dental traits are effective in recognizing *P. troglodytes* and *P. paniscus* as distinct species. When partitioned into populations, all populations of *P. paniscus* are readily distinguished from populations of *P. troglodytes* using raw dental measurements, size-corrected dental measurements, and non-metric dental characters. Significant differences were noted in most tooth positions. However, the differences were of degree rather than kind, suggesting that were they to be encountered as fossils, with sufficiently large sample sizes, paleontologists would readily discriminate the chimpanzees as distinct species. Several previous dental, postcranial and craniometric studies have conclusively demonstrated this distinction (Johanson, 1974; Jungers & Susman, 1984; Kinzey, 1984; Groves, 1986; Shea & Groves, 1987; Shea & Coolidge, 1988; Groves *et al.*, 1992; Shea *et al.*, 1993; Uchida, 1996).

The difference between the two species has often been explained as a size-related difference; *P. paniscus* is smaller, overall, than *P. troglodytes* (Schwartz, 1929; Coolidge, 1933; Hill, 1969). McHenry & Corruccini (1981); Shea (1983b, 1983c, 1984); and Jungers & Susman (1984) have been able to qualify this size-related difference by demonstrating the role of biomechanical and ontogenetic

Table 3.16 Average means, standard deviations and CV of linear dimensions of four populations, four subspecies and two species.

	Population			Subspecies			Species		
Variable	Mean	Std Dev	CV	Mean	Std Dev	CV	Mean	Std Dev	CV
UI1MD	11.43	0.78	6.87	11.44	0.81	7.09	11.07	0.84	7.59
UI1BL	8.95	0.51	5.70	8.91	0.52	5.87	8.48	0.54	6.33
UI2MD	8.49	0.73	8.64	8.51	0.72	8.55	8.17	0.74	9.07
UI2BL	8.21	0.60	7.29	8.23	0.58	7.05	7.83	0.56	7.13
UCMD	11.97	1.66	13.71	12.12	1.65	13.46	11.39	1.52	13.18
UCBL	9.57	1.39	14.49	9.65	1.35	13.99	9.00	1.24	13.79
UP3MD	7.92	0.64	8.10	7.95	0.66	8.25	7.77	0.66	8.49
UP3BL	10.11	0.71	7.01	10.15	0.70	6.84	9.85	0.64	6.44
UP4MD	7.19	0.66	9.32	7.20	0.71	9.97	6.89	0.72	10.49
UP4BL	9.75	0.55	5.65	9.76	0.62	6.33	9.40	0.57	6.03
UM1MD	10.06	0.48	4.82	10.03	0.51	5.13	9.57	0.53	5.51
UM1BLMES	10.42	0.55	5.27	10.40	0.58	5.57	10.03	0.60	6.01
UM1BLDIS	10.22	0.52	5.07	10.19	0.55	5.36	9.85	0.53	5.29
UM2MD	9.89	0.58	5.82	9.88	0.59	5.96	9.56	0.56	5.77
UM2BLMES	10.57	0.60	5.61	10.59	0.62	5.83	10.23	0.58	5.66
UM2BLDIS	9.80	0.71	7.29	9.81	0.72	7.36	9.49	0.70	7.35
UM3MD	9.08	0.70	7.72	9.05	0.71	7.84	8.76	0.66	7.47
UM3BLMES	10.02	0.70	6.97	10.04	0.73	7.21	9.75	0.68	6.90
UM3BLDIS	8.57	0.79	9.18	8.59	0.80	9.30	8.32	0.76	9.06
LI1MD	7.63	0.52	6.81	7.63	0.54	7.07	7.46	0.57	7.69
LI1BL	8.24	0.51	6.21	8.23	0.51	6.26	7.79	0.50	6.47
LI2MD	8.15	0.65	7.95	8.20	0.69	8.49	7.94	0.71	8.99
LI2BL	8.54	0.48	5.57	8.56	0.50	5.81	8.03	0.49	6.10
LCMD	11.23	1.32	11.62	11.30	1.31	11.47	10.52	1.15	10.81
LCBL	9.73	1.12	11.49	9.79	1.14	11.61	9.14	1.06	11.56
LP3MD	10.41	0.67	6.41	10.41	0.71	6.75	9.95	0.64	6.36
LP3BL	8.28	0.57	6.89	8.33	0.63	7.56	8.02	0.59	7.31
LP4MD	7.60	0.60	7.93	7.60	0.62	8.13	7.35	0.62	8.50
LP4BL	8.67	0.68	7.83	8.71	0.70	8.06	8.34	0.71	8.50
LM1MD	10.73	0.53	4.90	10.67	0.54	5.10	10.36	0.56	5.41
LM1BLMES	9.21	0.50	5.45	9.18	0.51	5.55	8.94	0.51	5.68
LM1BLDIS	9.52	0.51	5.36	9.46	0.53	5.59	9.15	0.54	5.93
LM2MD	11.00	0.61	5.57	10.99	0.65	5.92	10.71	0.66	6.14
LM2BLMES	9.84	0.56	5.67	9.83	0.60	6.13	9.45	0.60	6.39
LM2BLDIS	9.74	0.54	5.52	9.75	0.56	5.71	9.40	0.55	5.83
LM3MD	10.29	0.62	5.98	10.30	0.65	6.31	9.91	0.62	6.16
LM3BLMES	9.29	0.59	6.34	9.29	0.62	6.66	8.90	0.62	6.93
LM3BLDIS	9.03	0.59	6.50	9.01	0.63	6.96	8.67	0.60	6.91

Figure 3.7 Comparison of mean CV in populations, subspecies and species

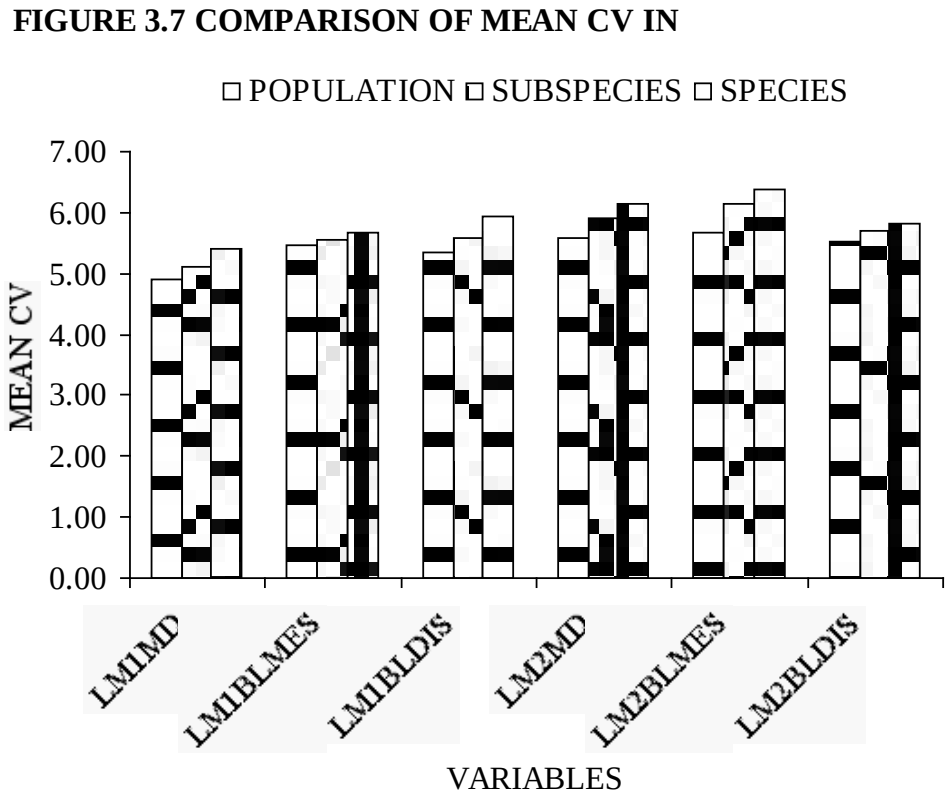


Table 3.17 Frequencies of discrete dental characters in population, subspecies and species

Variable	Pop 1	P. t. v	P. t	Pop 6	P. t. t	P. t.	Pop 10, 11, 12	P. t. s	P. t	Pop 15	P. p
UI1 median lingual pillar	63%	60%	53%	49%	49%	53%	53%	54%	53%	0%	0%
LI1 median lingual pillar	80%	79%	72%	65%	68%	72%	71%	70%	72%	41%	37%
LI2 median lingual pillar	84%	85%	82%	81%	83%	82%	72%	76%	82%	50%	43%
LI1 mesial notch	45%	44%	36%	38%	41%	36%	22%	21%	36%	0%	0%
LI2 mesial notch	59%	57%	47%	37%	47%	47%	35%	37%	47%	0%	0%
UP3 distolingual tubercle	32%	34%	41%	45%	43%	41%	46%	47%	41%	72%	74%
UP4 transverse ridge	82%	80%	80%	77%	81%	80%	73%	76%	80%	54%	54%
UM2 anterior transverse crest	75%	74%	84%	93%	92%	84%	85%	84%	84%	37%	43%
UM2 sulcus obliquus	99%	99%	98%	95%	98%	98%	96%	96%	98%	75%	74%
LM1 wide mesiobuccal dev groove	59%	55%	53%	75%	57%	53%	44%	45%	53%	89%	89%
LM2 tuberculum sextum	39%	39%	35%	38%	37%	35%	24%	26%	35%	3%	2%

scaling in causing the differences. The difference between the species in most cranial and postcranial proportions can be explained by ontogenetic scaling – adult *P. paniscus* culminates growth at a point resembling subadult *P. troglodytes*. However, this relationship of ontogenetic allometry is not seen in all body parts, hindlimb dimensions being a notable exception. In hindlimb dimensions *P. paniscus* shows negative allometry so that hindlimbs are relatively longer than *P. troglodytes*. Jungers & Susman (1984) found in addition that female *P. t. schweinfurthiii* and *P. paniscus* are similar in body size and limb proportions, thus pointing out that this is a relationship of pattern rather than allometry.

The size-related difference between the two species is corroborated by the dental data in this study, and most of the differences in dental dimensions can be explained by isometric scaling – the Geometric Mean, which serves as a proxy for overall tooth size correlates strongly with the scores for the discriminant function when untransformed variables are used in discriminant analysis, and when size-corrected variables are used, classification accuracy is reduced. However, this scaling relationship is not equivalent for all tooth types: the discriminant scores for LM1 and LM2 do not show a strong correlation with the Geometric Mean (Table 3.9) and the difference between the two species in mean linear dimensions of UP3 and LM1 are less compared to the other teeth (Table 3.10). Moreover, canine size in *P. paniscus* is much smaller (30% smaller) compared to the other teeth (only about 18% smaller), but canine size dimorphism (ratio of male/female canine size) is similar in both species (male canines are 21% larger than female, Table 3.10).

This would suggest that the canines, UP3, LM1 and LM2 exhibit negative allometry so that UP3, LM1 and LM2 are larger but canines are smaller in *P. paniscus* relative to the other teeth. The reason for this difference in *pattern* (cf. Jungers & Susman, 1984) is unclear but is presumably related to differential dietary strategies (in the case of the molars) and sociosexual behavior (for the canines).

Differences between the two species are also seen in non-metric, non size-related dental traits. The most prominent difference is in the morphology of the anterior dentition: on the lingual side of the incisor the cingulum is often a continuous ledge, the mesial notch is often absent, and the median lingual pillar is absent in *P. paniscus*. In addition, the anterior transverse crest of the upper molars often meets the protocone, and on lower molars the hypoconulid is more lingually placed, the cristid obliqua is more buccally placed and the mesiobuccal development groove is often a wide notch. Kinzey (1984) proposed that characters such as the distally oriented anterior transverse crest in the upper molars, along with the wide mesiobuccal development groove in the lower molars of *P. paniscus* are part of a functional complex designed to provide a better shearing blade for processing the higher proportion of herbaceous vegetation in the bonobo diet. Aspects of incisor morphology, such as narrower upper central incisors with greater wear are said to be part of this folivorous strategy (Kinzey, 1984). Kinzey's dietary hypothesis is related to reports that the bonobo diet relies heavily on terrestrial herbaceous foods (Badrian & Malenky, 1984), and was popularized by Wrangham (1986), who suggested that herbaceous foods, which are absent from the diet of

P. troglodytes because of competition from sympatric gorillas, constitutes the major difference between the two species and explains the larger group size in bonobos. Subsequent reports have indicated, however, that bonobos do not rely heavily on herbaceous vegetation (Malenky & Stiles, 1991).

In dental metric and non-metric characters, *P. t. verus* is clearly separated from the other subspecies of *P. troglodytes*. Many of the non-metric characters differentiating this subspecies from the other subspecies are similar to those differentiating *P. paniscus* from *P. troglodytes*. In particular, frequencies for ridge-like cingulum on the UI1s, buccally oriented anterior transverse crest on upper molars, and wide mesiobuccal development groove on the lower molars are very similar to that in *P. paniscus* (Table 3.8). These are the characters used by Kinzey (1984) to suggest a functional adaptation related to folivory in *P. paniscus*. The occurrence of similar characters at similar frequencies suggests that such an explanation will have to be made for *P. t. verus* as well. However, there is no information indicating a dietary preference for tough herbaceous vegetation in the West African chimpanzees. Chimpanzees from the Taï forest in the Ivory Coast are known to crack nuts and obtain a large portion of their dietary intake from this food source (Boesch & Boesch, 2000), but nut-cracking behavior is localized and not observed in other West African populations where the same nut trees are abundant (Boesch *et al.*, 1994). It is possible that the West African chimpanzees have a component of tough herbaceous vegetation in their diet, particularly since they are not restrained by competition from gorillas, as proposed by Wrangham (1986), but

so far no such reports are available. Therefore, the dietary hypothesis, which explains the difference between the two species does not explain the presence of similar dental features in *P. t. verus*. In order to evaluate the proposal that the dentition of *P. paniscus* is functionally adapted to a folivorous diet, better data will be needed on the dietary strategies of West African chimpanzees, which bear dental similarities with *P. paniscus.*

It is in characters of the anterior dentition, such as the absence of median lingual pillar and mesial notch on the incisors, that *P. paniscus* differs consistently from all the subspecies of *P. troglodytes* (Table 3.8). The functional implication of these characters is unclear at this time. In humans, characters such as shovelled incisors confer no particular selective advantage and cannot be correlated with particular dietary habits (Dahlberg, 1949; Hrdlicka, 1920). In the absence of known functions for such characters, or of dietary strategies that characterize only *P. paniscus* to the exclusion of all the subspecies of *P. troglodytes*, it is assumed that these characters have no known selective advantage and their high frequencies in *P. paniscus* are a result of genetic drift.

Nonselective genetic drift can presumably also explain the higher frequencies for discrete dental characters in a population of *P. t. verus* compared to the species. Several discrete dental characters, including the presence of the median lingual pillar, mesial notch, sulcus obliquus on the UM2, wide mesiobuccal development groove on the LM1 and tuberculum sextum on the LM2 (Table 3.17) are recorded at higher frequencies within the population than the species. This

pattern was also observed by Eckhardt (1987), who recorded nasal region morphology at a higher frequency within a population of *P. t. verus* from Central Liberia (from the Senckenberg Museum, not included in this study) than the species. Such a phenomenon suggests a population bottleneck in this subspecies. In both raw and shape variable analyses Mahalanobis distances are greater between this subspecies and the others than between the other two (Table 3.9). This separation is accompanied by a reduction in levels of diversity. Low variation within this subspecies compared to the others is seen in the CV and R% values (Table 3.14). Higher frequencies for discrete characters within the population and subspecies relative to the species would signify a trend towards fixation for such characters through reduction in the gene pool of the subspecies due to increasing isolation. Hartl (1988) has used several mathematical models to demonstrate that fluctuating frequencies and reduced diversity are common correlates of nonselective, genetic drift.

While *P. t. verus* is clearly distinguishable and distinctive as a subspecies of *P. troglodytes*, the other two traditionally recognized subspecies, *P. t. troglodytes* and *P. t. schweinfurthii* are remarkably indistinguishable. The difficulty in classifying individuals belonging to these subspecies (Table 3.4), the low Mahalanobis distances between the two (Table 3.5) and the paucity of dental characters that define and differentiate the two (Tables 3.7 and 3.8) indicate that they share genetic material. This may either be due to a more recent evolutionary history, or the ineffectiveness of the River Ubangi in separating them. On the other

hand, the distinctiveness of a population from Eastern Nigeria indicates that the River Sanaga exerts a greater influence in preventing gene flow than the Ubangi. Despite variable levels of distinction and diagnosability, however, all three groups (*P. t. verus, P. t. troglodytes, P. t. schweinfurthii*), and perhaps even *P. t. vellerosus*, are considered to be valid subspecies of *P. troglodytes*, more closely related to each other than they are to *P. paniscus*. The variable criteria used in defining subspecies in the extant context calls into question the reliability of this taxonomic category, and the likelihood of diagnosing subspecies in the paleontological context. An understanding of the evolutionary and phylogeographic history of the genus *Pan* could possibly help in interpreting the patterns of variation and population differentiation within this group. The characteristics of extant taxa that arise from their unique evolutionary history, and the utility of such taxa as models for discriminating fossil species will be evaluated in a subsequent chapter (Chapter Five).

Conclusions

(1) Dental data support the conclusion that *P. troglodytes* and *P. paniscus* are distinct species. The differences between them can be explained by size, negative allometry and genetic drift. It is possible that selection for dietary differences are present but these will need to be reevaluated in light of the dental similarity between *P. paniscus* and *P. t. verus*.

(2) *P. t. verus* is well separated from the other subspecies of *P. troglodytes* in dental metric and non-metric characters. In linear dimensions this subspecies

has reduced variation compared to the other two subspecies. There is also greater fluctuation in the frequency of discrete dental traits. This pattern of variation is consistent with this subspecies having been subject to a population bottleneck followed by genetic drift.

(3) *P. t. troglodytes* and *P. t. schweinfurthii* are very close in odontometric distance and share great similarity in discrete dental characters. This could be due to greater gene flow between the two subspecies or a more recent ancestry. The pattern of population substructure reveals that the River Ubangi does not exert a strong influence in separating the gene pools of these two subspecies. Nevertheless, it does exert a certain amount of influence.

(4) This study does not support the conclusion that chimpanzees from both sides of the Niger River are closely related. Chimpanzees from the west of the Niger are, on average, more closely associated with a population on the south of the Sanaga River. Chimpanzees from the east of the Niger and north of the Sanaga form distinct populations well separated from the west African, *P. t. verus* and the central African, *P. t. troglodytes* and *P. t. schweinfurthii*. In other words, this study supports the status of *P. t. vellerosus*, but demarcates this subspecies by the River Niger on the west and the River Sanaga on the east. It does not, however, support the proposal that *P. t. vellerosus* is most closely associated with *P. t. verus*. The closest affiliate for this subspecies was found to be *P. t. troglodytes* on the south of the Sanaga.

(5) In chimpanzees the range of dental variation does not increase markedly when proceeding up the nested hierarchy from population to species. Much of the variation within the species is visible in the population. The chimpanzee social structure of female dispersal and high levels of gene flow can explain this pattern.

(6) Populations on the east of the River Ubangi, south of the River Kasai and east of the River Lomani appear to be distinct from other populations around them. This conclusion will need to be substantiated with larger samples.

CHAPTER FOUR
Gorilla

Introduction

Gorilla, like *Pan* is endemic to equatorial Africa. Unlike *Pan* it has, at least until recently, been considered to be a genus with a single species. It is the largest of the living primates, is characterized by a high degree of sexual dimorphism and is the sister taxon to the *Pan-Homo* clade. The large size and degree of dimorphism make gorillas useful for studying possible ranges of inter-sexual and intra-specific variation in fossil primates, particularly in the large-bodied Miocene hominoids. Because of the phylogenetic affinity to chimpanzees and humans, gorilla models are also useful for examining patterns of variation in extinct hominids.

The population structure of gorillas has been studied thoroughly. Groves (1967, 1970b) sampled gorilla crania from their entire geographic range in Africa and demonstrated, using craniometric measurements, that gorilla populations can be divided into three major clades: one in west Africa and two in east Africa. He designated these as subspecies of *Gorilla gorilla*: *G. g. gorilla* in lowland West Africa, *G. g. graueri* in lowland East Africa, and *G. g. beringei* in highland East Africa. The presence of these three taxonomic groups has been validated using several different types of data, both morphological and molecular. Molecular studies, however, have led to the proposal that West and East African gorillas should be classified as two species: *G. gorilla* and *G. beringei*, with *graueri* as a subspecies of *G. beringei*. More recent studies have focused on other aspects of

Gorilla systematics, such as the affinities of isolated populations, the range of variation within and between populations, and the nature and degree of genetic contact between populations.

The purpose of this chapter is to examine the population systematics of *Gorilla* using dental data. Two independent sets of data, dental metrics and discrete dental characters will be used to: (1) identify the major population divisions in gorillas, (2) ascertain the dental affinities of isolated *Gorilla* populations, and (3) study the nature of intra- and inter-population variation in gorillas. These objectives ultimately relate to the overarching questions addressed in this thesis namely, how useful are dental data for distinguishing between the commonly recognized species, subspecies and populations of modern African apes, and can paleontological systematics be considered to be comparable to neontological systematics?

Background

Distribution and taxonomy

Gorillas are distributed in the West and East of equatorial Africa: in the West from the Cross River area at the Nigeria-Cameroon border, through the western part of the Central African Republic and southward to Angola; in the East from the eastern part of the Democratic Republic of Congo to southwestern Uganda and northwestern Rwanda in East Africa (Figure 4.1). A distance of about a 1000km along the Congo River from about 16^0 E to 26^0 E is devoid of gorillas (Wolfheim, 1983). Even within the two main centers of distribution, gorilla

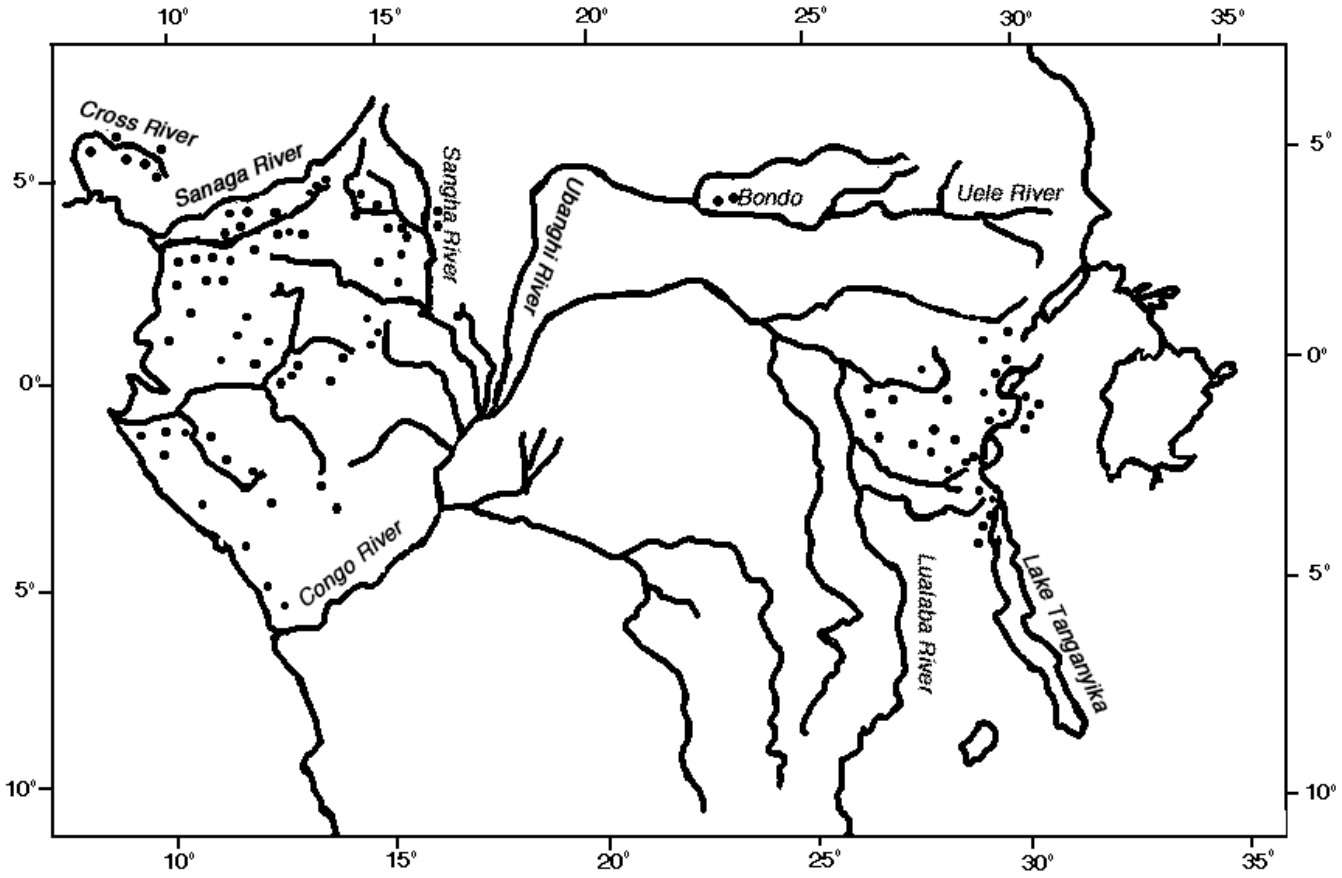


Figure 4.1 Solid circles show distribution of gorillas in equatorial Africa (adapted from Dixon, 1981)

populations are patchily distributed and several populations are isolated. Population densities for the entire genus are declining and some populations have become extinct in historical times. The genus is classified as endangered by the IUCN and there is an urgent need for conservation (Oates, 1996). Most of the isolated populations when first introduced to western science were designated as new species or subspecies (reviewed in Jenkins, 1990). Although these were later subsumed under the nomen *G. gorilla* (Coolidge, 1929), the names are available and many have recently been resurrected so as to meet the criteria for providing protected status (Sarmiento *et al.*, 1996; Stumpf *et al.*, 1998; Sarmiento & Oates, 2000; Groves 2001).

The population in southern Nigeria along the Cross River is a small population once thought to be extinct (Dixson, 1981). Its presence has since been reaffirmed (Harcourt *et al.*, 1989). Following the recognition of the Sanaga River as a biogeographic barrier (Grubb, 1990; Gonder *et al.*, 1997) the affinities of the Cross River gorillas was reexamined (Stumpf *et al.*, 1998; Sarmiento & Oates, 2000; Groves 2001). This population is now recognized to be morphologically distinct from populations on the south of the Sanaga River and from the East African gorillas. Subspecies status has been accorded to them reinstating a previously assigned name, *G. g. diehli* Matschie, 1904 (Stumpf *et al.*, 1998; Sarmiento & Oates, 2000; Groves 2001).

The populations from the south of the Sanaga River, covering the area from there to the mouth of the Congo River in the south and past the Sangha River in the east (Figure 4.1) are included within the subspecies *G. g. gorilla*. The population densities for this subspecies are higher than elsewhere (Wolfheim, 1983). Variability in mtDNA is also higher than in the eastern subspecies (Garner & Ryder, 1996) indicating that there could be further substructure within this region than hitherto recognized.

Another isolated population from the locality of Djabbir near Bondo on the Uele River in the northeastern part of the Democratic Republic of Congo (Figure 4.1) is known only from museum specimens. Based on cranial measurements Groves (1970b) included it within *G. g. gorilla*, but recently Sarmiento (records of the Royal Museum, Tervuren) placed the few known specimens in a distinct subspecies, *G. g. uellensis* Schouteden, 1927.

The gorillas from east Africa are found at variable altitudes. In the Virunga region of Rwanda a secluded population inhabits a high altitude montane forest (3900 m). This population is morphologically distinct from eastern and western lowland gorillas (Coolidge, 1929; Schaller, 1963; Groves, 1970a; 1970b), and is recognized as a distinct subspecies, *G. g. beringei*. Another small population from the Bwindi Impenetrable Forest in Uganda about 35 km from Virunga bears genetic similarity to the Virunga mountain gorillas (Garner & Ryder, 1996; Jensen-Seaman & Kidd, 2001) and is often allocated to that subspecies. Sarmiento *et al.* (1996),

however, noted a few morphological and behavioral differences between this population and the Virunga gorillas and suggested that they do not belong to the same subspecies. They did not provide an alternative name.

Around the Itombwe Massif west of Lake Tanganyika (Figure 4.1), and the Utu and Mwenga-Fizi region along the eastern border of the Democratic Republic of Congo gorillas are found in lowland forests at altitudes of about 1000 to 1500 m (Omari *et al.*, 1999). Groves (1967, 1970b) found that in cranial morphology these gorillas fall midway between the mountain gorillas and western lowland gorillas. He placed them in the subspecies *G. g. graueri* thus demonstrating that gorillas in equatorial Africa have a clinal pattern of segregation, with western lowland gorillas at one end, eastern lowland gorillas in the middle and eastern highland gorillas at the other end of the continuum.

Gorilla populations from Kahuzi-Biega and Tshiaberimu mountains in Eastern Zaire, which are found at an altitude of up to 3300m (Hall *et al.*, 1998), between the eastern lowland and highland regions, have disputed allocation. Groves & Stott (1979), after reviewing their morphological affinities, concluded that both populations are intermediate in morphology between *G. g. graueri* and *G. g. beringei* but provisionally placed them in *G. g. graueri*. Gorillas from the Kahuzi-Biega region inhabit both lowland and montane regions. Saltonstall *et al.* (1998) reported a few differences in mtDNA D-loop haplotypes between individuals from the lowland and montane region, but concluded that the two populations are genetically linked. Jensen-Seaman & Kidd (2001) found that

gorillas from the lowland and higher altitude regions are more similar to each other than either is to the Virunga gorillas. They also found similarities in the D-loop haplotypes of Tshiaberimu and Kahuzi-Biega gorillas. Sarmiento & Butynski (1996) suggested reviving the nomen *G. g. rex-pygmaeorum* Schwarz, 1927 for the Tshiaberimu gorillas, and if revived Jensen-Seaman & Kidd (2001) suggest allocating the Kahuzi-Biega gorillas to this subspecies.

In conclusion, driven by the need for conservation the taxonomy of gorillas is currently undergoing considerable revision. Molecular data have only recently been called to bear on the question of gorilla systematics. With the intention of resolving the phylogenetic position of humans within the great ape clade, Ruvolo *et al.* (1994) studied variability in mtDNA in the great apes and found that in COII sequences there are greater differences between western gorillas (*G. g. gorilla*) and eastern gorillas (*G. g. graueri* and *G. g. beringei*) than between the two species of *Pan*. Garner & Ryder (1996), Saltonstall *et al.* (1998), and Jensen-Seaman & Kidd (2001) were able to substantiate this conclusion by drawing samples from a wider area and studying mtDNA variability in both the COII and D-loop region. Garner and Ryder (1996) studied variability in the mtDNA D-loop region within and between gorilla populations and also found that: (1) the two eastern clades, lowland gorillas (*G. g. graueri)* and mountain gorillas (*G. g. beringei*) are distinct, but closely related, (2) variability in mtDNA within both these groups, as calculated by comparing transition and transversion numbers is low, whereas within the western lowland gorillas (*G. g. gorilla*) variability is three to four times higher, and (3) the

Bwindi gorillas are mitochondrially nearly identical to the Virunga gorillas.

Jensen-Seaman & Kidd (2001) sequenced mtDNA from four East African gorilla populations: Tshiaberimu, Virunga, Bwindi and Kahuzi-Biega. They found several D-loop haplotypes that linked Virunga and Bwindi gorillas, and Kahuzi-Biega and Tshiaberimu gorillas. Both clades had low levels of genetic diversity and showed evidence of a recent population bottleneck, which they believe coincided with the last glacial maximum at about 18,000 years ago (Livingstone, 1967, 1975).

Over the years gorillas have thus gone from being recognized as one genus which included 11 species and 15 subspecies (reviewed in Coolidge, 1929), to one species with two subspecies (Coolidge, 1929), one species with three subspecies (Groves, 1967) and finally as one genus with two species (Ruvolo *et al.*, 1994; Ruvolo, 1996; Groves, 2001; Jensen-Seaman & Kidd, 2001) and possibly seven subspecies at the present time.

Adaptive patterns

The fluctuating state of gorilla taxonomy is reflective of the underlying diversity in the adaptive pattern of gorillas. Throughout their distribution gorillas show remarkable variability in morphology, habitat, diet, locomotor pattern and group size. Until recently, most information about gorilla behavior came from the Virunga region in Rwanda where mountain gorillas have been studied consistently for the last 35 years (Fossey, 1974; Harcourt, 1979; Watts, 1996). This study helped foster the notion that gorillas are obligate folivores with a predominantly terrestrial mode of locomotion, large group size, small daily range, and low inter-

group aggression (Fossey, 1974; Harcourt, 1979; Watts, 1996). Virunga gorillas, however, are a relict population which originated from a recent population bottleneck (Jensen-Seaman & Kidd, 2001) and exhibit low ranges of diversity.

Western and eastern lowland gorillas have proved to be relatively more difficult to study (Remis, 1997). Long term studies have only recently been initiated. Data emerging at present show that in contrast with their highland congeners, lowland gorillas have greater flexibility and variability in adaptive strategies.

Mountain gorillas are mostly folivorous and consume high quality terrestrial herbs that are abundant year-round (Watts, 1984; 1996; Fossey & Harcourt, 1977; Doran & McNeilage, 1998). Western lowland gorillas, on the other hand, commonly supplement their herbivorous diet with a component of fruit, herbs, shrubs, bark and insects (Williamson *et al.*, 1990; Kuroda *et al.*, 1996; Tutin *et al.*, 1991; Remis, 1997). They also exhibit seasonality in diet consuming a large proportion of fleshy fruit when in season, but switching to fibrous herbs when fruits are scarce. The degree of frugivory in eastern lowland gorillas is intermediate between the western lowland and eastern mountain gorillas and is correlated with the diversity of fruit available (Yamagiwa *et al.*, 1994). Eastern lowland gorillas at higher altitudes are more like mountain gorillas and have a larger herbaceous component to their diet (Casimir, 1975; Watts, 1996).

The dietary preference of gorillas influences group size, within and between-group competition and arboreality. Mountain gorillas, because the protein-

rich herbaceous foods they prefer are plentiful year-round generally do not have inter-group conflicts over food patches (Watts, 1996). Their groups are most commonly composed of a single dominant silverback male, 2-3 females and 4-5 offspring. However, group sizes can be as large as 34 individuals and might include up to four subordinate males (Robbins, 1995). These gorillas are largely terrestrial and their daily range is only about 500m/day (Watts, 1996).

For western lowland gorillas, Remis (1997) has suggested that their characteristic preference for fruits governs their greater arboreality, smaller foraging units and more aggressive inter-group encounters. The overall group structure is the same as mountain gorillas with one or two silverback males and two to four females (Remis, 1997). Average group size is smaller than mountain gorillas (Olejniczak, 1996) and splitting and sub-grouping is fairly common (Remis, 1997).

Behavioral information for eastern lowland gorillas is scarce. Available evidence suggests that at high altitudes eastern lowland gorillas have day ranges either the same or slightly greater than mountain gorillas. Day ranges are observed to fluctuate seasonally depending on the availability of food resources (Casimir, 1975; Goodall, 1977).

The dispersal patterns of lowland gorillas are not well documented. In mountain gorillas both sexes emigrate from their natal group. Male dispersal is not as common as female dispersal and some males may reside in their natal group as subordinate males. Females commonly transfer out of their natal group and may

emigrate more than once during their reproductive life (Watts, 1996). However, females do not travel long distances to mate (Harcourt, 1978).

These differences in behavior and habitat are accompanied by differences in morphology. Many of the morphological features that differentiate gorilla subgroups are considered to be adaptive responses to feeding and behavioral strategies. Thus, a harem-forming social structure and a largely folivorous diet are said to explain the large body size and heightened sexual dimorphism in gorillas (Watts, 1984). Predictably then, because the eastern gorillas show a greater commitment to folivory and have a social group with a single dominant male, body size is larger and sexual dimorphism is greater than the western gorillas.

The morphological differences between the three commonly recognized subspecies are summarized in Table 4.1. As can be seen the main contrast lies between the eastern highland and western lowland gorillas and many of the differences are adaptive in nature. The smaller anterior teeth, larger molars, and wider mandibular corpora of the mountain gorilla are adaptations for folivory (Groves, 1970a; Uchida, 1998). The adducted great toe and presence of the peroneus tertius muscle are adaptations for terrestriality (Sarmiento, 1992). In the western lowland gorilla the relatively wider incisors and divergent great toe signify adaptations for greater frugivory and arboreality (Sarmiento, 1994; Uchida, 1998).

G. g. diehli, the newly reinstated subspecies is differentiated from *G. g. gorilla*, the other western lowland subspecies in having a smaller skull size, wider biorbital breadth, significantly less cheek tooth occlusal surface area, and narrower incisor chord and palate width (Sarmiento & Oates, 2000; Groves, 2001).

Table 4.1 Morphological differences between three gorilla subspecies (summarized from Shultz, 1934; Vogel, 1961; Groves, 1970a, 1970b; Shea, 1984; Sarmiento, 1992, 1994; Uchida, 1998; Taylor, 2002).
? indicates subspecies not included in comparison.

Character	***G. g. gorilla***	***G. g. graueri***	***G. g. beringei***
Teeth	Small compared to mountain gorilla of same size	Largest of all three subspecies	Large compared to lowland gorilla of same size
Anterior teeth	Wide compared to molars	Narrow compared to molars	Narrow compared to molars
Lower P3	Sectorial	Sectorial	Rounded, non-sectorial
Talonid of lower P4	Large	Small	Large
Sexual dimorphism in dental dimensions	Not high	High	High
Additional cusps on M3s	Not common	Not common	Common
Palate	Short	Long	Long
Mandibular corpus and symphysis	Narrow	Narrow	Wide
Area for masseter	Small	?	Large
Mandibular ramus	Low	High	Higher
Position of mental foramen	Posteriorly placed, often under LP4	Anteriorly placed under LP3	Anteriorly placed above LP3
Number of mental foramina	Single	Often multiple	Often multiple
Projection above nasal septum	Present	Absent	Absent
Vertebral border of scapula	Straight	Straight	Sinuous
Clavicle	Relatively short	Relatively short	Relatively long
Great toe	Short, divergent	Short, divergent	Long, parallel to other toes
Peroneus tertius muscle	Not frequent	Not frequent	Frequent
Silverback	Extends to thighs	Restricted to back	Restricted to back

This Study

Based on the review of previous studies the following hypotheses regarding gorilla systematics can be formulated for testing using dental data:

(1) The main separation in gorilla populations is between western gorillas on one hand and eastern gorillas on the other.

(2) Within the eastern region the lowland gorillas and mountain gorillas form distinct groups.

(3) Within the western clade the Cross River gorillas are distinguished from the other western gorillas.

(4) Gorillas from the Uele River region are similar to the western lowland gorillas.

(5) The Bwindi (or Kayonza) gorillas are most similar to the Virunga gorillas.

(6) The Utu and Mwenga-Fizi gorillas resemble each other and so do the Kahuzi and Tshiaberimu gorillas.

(7) The Kahuzi and Tshiaberimu gorillas are intermediate between the Utu, Mwenga Fizi and the Virunga gorillas.

(8) Within-group variation in the Cross River gorillas, eastern lowland gorillas and eastern highland gorillas is low, but variation within western lowland gorillas is high.

(9) Average within population variation in gorillas is low and between population variation is high.

My study sample included 299 dental specimens and was drawn from all known populations in equatorial Africa (Table 4.2). The localities included within

each of the populations are described in Chapter 2, and shown on a map (Figure 2.2). A large proportion of the study material (about 69%) came from West Africa, and as can be seen in Table 4.2, males form a sizeable portion of the sample. This reflects an underlying bias in museum collections and affects all museum-based studies (*e.g.*, Groves, 1970b). The imbalance in sex ratios did not affect this study too strongly because the sexes were treated separately in most analyses. When molar dimensions were converted into shape variables the two sexes were combined since molar shape variables do not display a significant correlation with sex.

The sample size for populations 12, 13 and 14 is small. These are individuals from the Bwindi forest, Mt. Kahuzi and the Uele River region, respectively. Due to their small sample sizes they were not included in the discriminant procedures but their affinities were examined in a post-hoc manner using the discriminant scores from the larger samples to classify them.

The remaining populations, populations 1 to 11, have fairly large sample sizes (Table 4.2). When segregated by sex the sample sizes are reduced, more drastically for females than males because of the original imbalance in sex ratios. Since all the populations with smaller samples originate from East Africa, and their inter-population affinities are being contested, they were not recombined with other populations but left as distinct groups. Results based on these smaller samples should therefore be evaluated with caution.

Table 4.2 Gorilla study sample

Pop.	Region	N	Male %, Female %
Gorilla		**299**	**62, 38**
Gorilla gorilla diehli		**29**	**69, 31**
1	Cross River	29	69, 31
Gorilla gorilla gorilla		**177**	**63,37**
2	Coastal Cameroon	21	81, 19
3	Coastal Gabon	28	54, 46
4	Southern Gabon & Cabinda	40	85, 15
5	Sangha River	15	60, 40
6	Batouri	24	38,,62
7	Inland Cameroon	49	61, 39
Gorilla gorilla graueri		**40**	**67, 33**
8	Utu	30	63, 37
9	Mweng-Fizi	10	70, 30
Gorilla gorilla rex-pygmaeorum		**21**	**67, 33**
10	Tshiaberimu	17	35, 65
13	Kahuzi	4	100, 0
Gorilla gorilla beringei		**30**	**52, 48**
11	Virunga	28	54, 46
12	Kayonza (Bwindi)	2	50, 50
Gorilla gorilla uellensis		**2**	**50, 50**
14	Uele River	2	50, 50

Populations

Sexual dimorphism

Gorilla males have larger dental dimensions than females (Swindler, 1976; Greene, 1973). However, sexual dimorphism is not significant in all dental dimensions and it is not uniformly seen in all gorilla populations. I used a one-way Anova with a $p<0.05$ to identify dental variables that have a significant correlation with sex within each population. I found that in all populations the following dental dimensions differ significantly by sex: the buccolingual width of the incisors, the length, breadth and height of the canines, and the height of the labial cusps of the

premolars. In other dental dimensions sexual dimorphism is greater in the gorillas from East Africa, in particular, populations 8 (Utu) and 11 (Virunga) than in the West African gorillas, as also shown by Uchida (1998). When dental dimensions are expressed as shape variables, thus correcting for size, most premolar and molar dimensions do not differ significantly between the sexes, but all canine dimensions still do (Uchida, 1998). This indicates that within a group male and female postcanine teeth are similar in shape although they differ in size.

Discrete dental traits, on the whole, do not exhibit a significant association with sex (chi-square $p<0.01$), except for the following traits: UC lingual cingulum, UC mesial groove, UC lingual groove, LC cingulum, LC lingual groove, LC distal groove. In the qualitative analyses the sexes were combined excluding from the list the above sex-specific traits.

Population structure

To examine how variation is partitioned between gorilla populations I used discriminant analysis to classify populations sorted by tooth type and sex. Separate analyses were conducted for the size-corrected and non size-corrected variables. A total of 24 analyses were performed: 6 for each type of molars, repeated for each sex using size and shape variables. A step-wise procedure was used so as to identify variables that are most effective at separating groups. The canonical scores for the discriminant functions were then used to calculate squared generalized distances between all population pairs. This procedure is similar to that used by Groves (1970b) in his craniometric study.

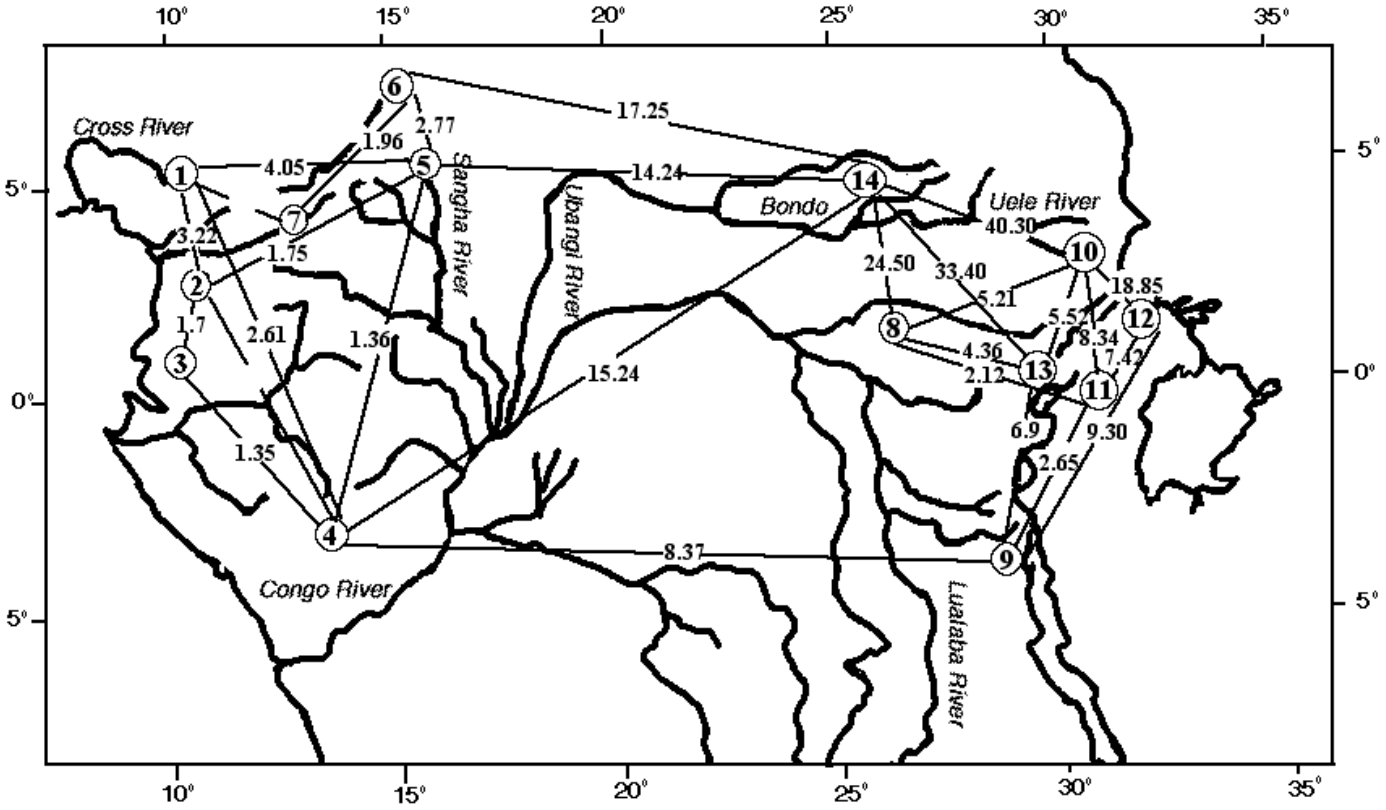


Figure 4.2 Squared generialized distances between gorilla populations (after Groves, 1970)

Tables 4.3 and 4.4 show the squared generalized distances between population pairs for males and females for the raw variables. The distances were calculated by averaging the distances between all tooth types. Figure 4.2 shows the distances on a map of Africa. Figure 4.3 shows a scatter plot for the first two discriminant functions for all populations. These two functions account for about 68% of the observable variance. The scores were averaged for all the teeth and for the sexes to derive the scatter plot. The main observations that emerge from the distance matrices, which can also be viewed graphically in the scatter plot in Figure 4.3, are as follows:

(1) Gorilla populations fall into two main clusters: populations 1 to 7 belong in one cluster, while populations 8 to 13 fall in the second cluster. For both males and females, inter-group distances within the cluster are lower than inter-group distances between clusters. The two clusters correspond with the two main geographical divisions of gorillas in West and East Africa.

(2) Population 14 is most closely affiliated with populations 1 to 7 from West Africa. This is the population from the Uele River region.

(3) Within the West African cluster of populations 1 to 7, population 1, from the Cross River region is more distinct from populations 2 to 7 than those populations are from each other.

(4) Within the cluster of populations 8 to 13 from East Africa, gorillas from population 10, Tshiaberimu, are removed from the other east African populations.

(5) Population 13, the Mwenga-Fizi gorillas, for which only males were studied, is similar to Utu and the Tshiaberimu gorillas.

(6) Population 12 from the Kayonza region shares the greatest similarity with the Virunga population.

(7) Population 11 and population 8, from the Virunga highlands and the Utu lowlands respectively, display very low interdemic distances and are more closely related to each other than either is to the other East African populations.

The first 6 conclusions support the hypotheses outlined above – clear separation of East and West African gorillas, the West African affiliation of the Uele gorillas, the distinctiveness of the Cross River gorillas, the resemblance between the Kayonza and Virunga gorillas, the resemblance between the Utu and Kahuzi gorillas, and the closeness of the Mwenga-Fizi, Tshiaberimu and Kahuzi gorillas to the Utu gorillas. One observation that is contrary to expectation is the close similarity between gorillas from the highland Virunga region and the Utu lowlands.

As can be seen from Tables 4.3 and 4.4, interdemic distances between the Utu (population 8) and Virunga gorillas (population 11) are lower on the whole than the distances between other East African populations. This observation does not change when raw variables are transformed into shape variables (Tables 4.5 and 4.6).

POP	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	0.00	3.22	4.63	2.61	4.05	4.82	3.64	9.57	9.72	20.63	7.85	12.71	17.13	15.07
2	3.22	0.00	1.70	**0.74**	1.75	2.03	**1.20**	7.04	7.91	18.67	5.55	11.06	15.23	16.44
3	4.63	1.70	0.00	1.35	2.96	2.50	2.19	6.65	7.99	19.48	4.73	9.91	13.87	14.62
4	**2.61**	**0.74**	**1.35**	0.00	**1.36**	2.46	1.23	6.85	8.37	19.13	5.23	9.60	15.12	15.24
5	4.05	1.75	2.96	1.36	0.00	2.77	1.60	7.76	9.09	18.33	5.86	9.22	16.28	**14.14**
6	4.82	2.03	2.50	2.46	2.77	0.00	1.96	7.03	6.94	17.81	5.23	12.22	14.56	17.26
7	3.64	1.20	2.19	1.23	1.60	**1.96**	0.00	5.24	6.29	15.24	4.09	9.44	12.47	14.36
8	9.57	7.04	6.65	6.85	7.76	7.03	5.24	0.00	2.96	**5.21**	**2.12**	9.47	**4.36**	24.50
9	9.72	7.91	7.99	8.37	9.09	6.94	6.29	2.96	0.00	7.17	2.65	9.30	6.90	28.20
10	20.63	18.67	19.48	19.13	18.33	17.81	15.24	5.21	7.17	0.00	8.34	18.85	5.52	40.30
11	7.85	5.55	4.73	5.23	5.86	5.23	4.09	**2.12**	**2.65**	8.34	0.00	**7.42**	7.05	22.50
12	12.71	11.06	9.91	9.60	9.22	12.22	9.44	9.47	9.30	18.85	7.42	0.00	13.07	0.00
13	17.13	15.23	13.87	15.12	16.28	14.56	12.47	4.36	6.90	5.52	7.05	13.07	0.00	33.40
14	15.07	16.44	14.62	15.24	14.14	17.26	14.36	24.50	28.20	40.30	22.50	0.00	33.40	0.00

Table 4.3 Mahalanobis distances between gorilla populations using raw variables. Average for all tooth types for males. Lowest distance between population pairs shown in bold.

POP	1	2	3	4	5	6	7	8	9	10	11	12	14
1	0.00	7.00	9.62	6.10	8.37	7.82	5.42	9.82	15.88	14.86	9.14	13.41	7.94
2	7.00	0.00	8.33	3.44	4.45	4.62	2.77	13.88	19.80	19.38	10.30	14.41	5.21
3	9.62	8.33	0.00	6.58	4.43	3.14	4.10	7.26	10.90	11.00	3.24	11.62	7.08
4	**6.10**	3.44	6.58	0.00	**2.64**	3.35	2.59	11.40	17.02	16.84	7.51	13.23	**4.22**
5	8.37	4.45	4.43	2.64	0.00	4.01	3.11	10.04	16.14	16.12	5.48	10.93	5.28
6	7.82	4.62	**3.14**	3.35	4.01	0.00	**1.79**	9.78	12.57	12.81	6.56	13.66	4.31
7	5.42	**2.77**	4.10	**2.59**	3.11	**1.79**	0.00	7.66	12.32	12.42	4.96	10.19	4.91
8	9.82	13.88	7.26	11.40	10.04	9.78	7.66	0.00	**5.35**	**2.20**	**2.83**	**5.39**	10.55
9	15.88	19.80	10.90	17.02	16.14	12.57	12.32	5.35	0.00	5.70	7.34	11.56	17.91
10	14.86	19.38	11.00	16.84	16.12	12.81	12.42	**2.20**	5.70	0.00	6.91	9.51	13.83
11	9.14	10.30	3.24	7.51	5.48	6.56	4.96	2.83	7.34	6.91	0.00	6.62	7.95
12	13.41	14.41	11.62	13.23	10.93	13.66	10.19	5.39	11.56	9.51	6.62	0.00	18.31
14	7.94	5.21	7.08	4.22	5.28	4.31	4.91	10.55	17.91	13.83	7.95	18.31	0.00

Table 4.4 Mahalanobis distances between gorilla populations using raw variables. Average for all tooth types for females. Lowest distance between population pairs shown in bold. No females examined from population 13.

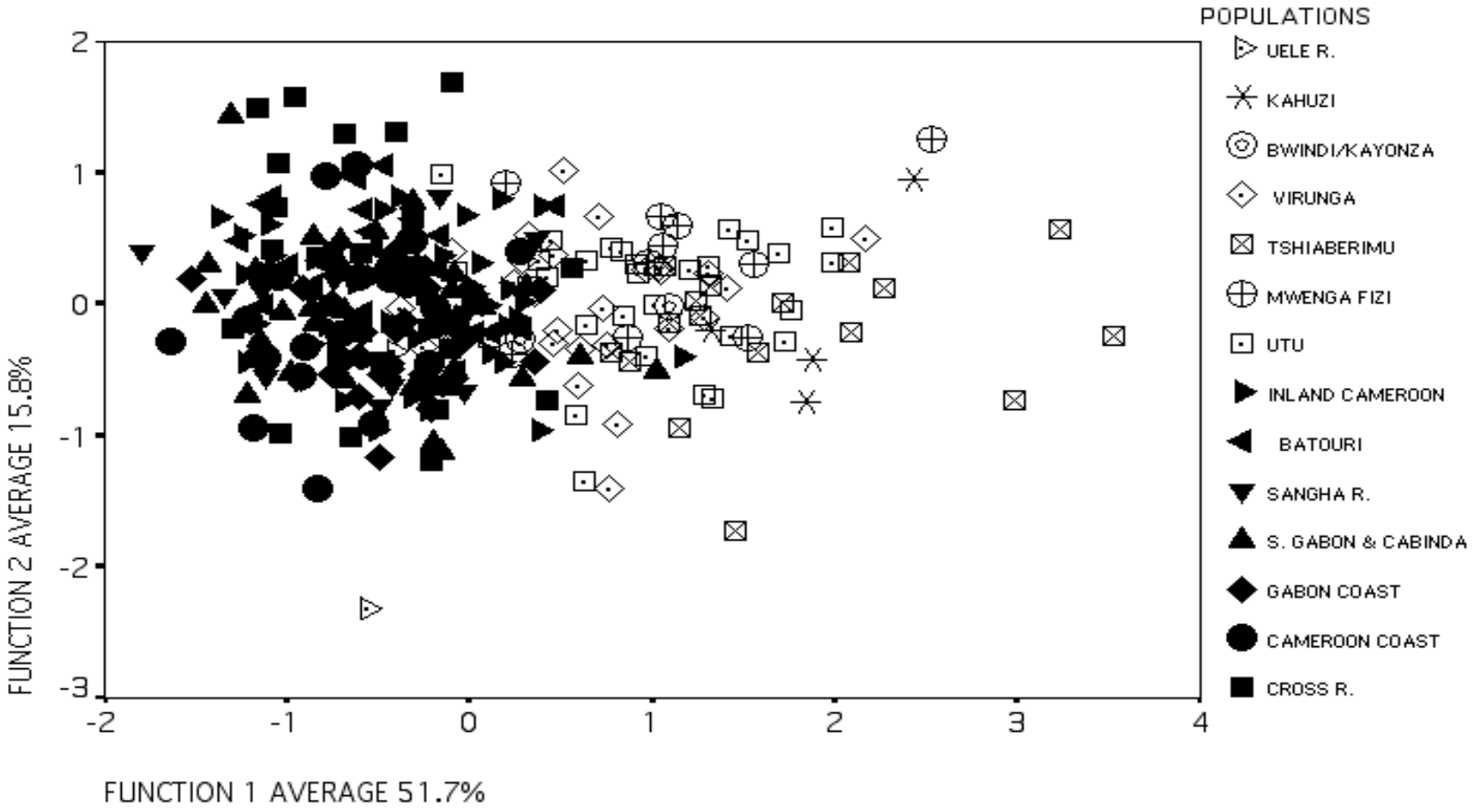


Figure 4.3 Scatter plot of discriminant function1 by discriminant function 2 for gorilla populations. Average discriminant scores for upper and lower molars using raw variables, males and females combined.

The distance matrix based on the raw variables (Tables 4.3 and 4.4) and the associated scatter plot (Figure 4.3) also reveals that the Virunga gorillas occupy an intermediate position between the western lowland and the Utu groups. This is unlike Groves' (1970b) craniometric placement of the Virunga gorillas as well separated from the western lowland gorillas, with the eastern lowland gorillas at an intermediate position.

It is possible that the raw variable distance matrix and the scatter plot display an effect of size, and that the intermediate placement of the Virunga gorillas reflects the intermediate dental size of this group compared to the eastern lowland and western lowland gorillas. Uchida (1998) has demonstrated that in dental size, as measured using linear dimensions and cusp base area measurements, the Virunga gorillas lie between the western lowland and eastern lowland gorillas. To test for the role of size in explaining the variance in this study I calculated Pearson's Correlation coefficients between the scores for the first two discriminant functions (DF) and the Geometric Mean (GM). Only the values for males are reported because the sample size for this group is larger. The first DF for the raw variables, which accounts for 51.7 % of the variance shows a significant correlation ($p<0.001$) with GM, but the correlation is not strong: 0.5931 for LM1, 0.6073 for LM2, 0.4984 for LM3, 0.3604 for UM1, 0.2840 for UM2, and 0.3257 for UM3. The second DF accounts for 15.8 % of the variance and has a non-significant ($p>0.01$) and weak correlation with the lower molars (-0.0127, 0.1145 and 0.0343 for LM1, LM2 and LM3) and UM3 (-0.1408), but a significant although weak

correlation with the UM1 and UM2: 0.3422 for the UM1, and 0.4605 for the UM2. This suggests that in the case of the UM1 and UM2, a component of size is responsible for causing variance in both functions. All in all, size does play a role in differentiating gorilla populations, but the role is not strong.

When the analysis is conducted using shape variables, the Utu gorillas are placed much closer to the western lowland gorillas, with the Virunga gorillas differentiated along the second axis (Figure 4.4). In the distance matrix generated from the shape variables (Tables 4.5 and 4.6), inter-demic distances between the Virunga and other western lowland populations are still low, but the distance between the Utu and the western lowland populations is reduced compared to the raw variable matrix. Another population whose position changes when the effect of size is corrected is the Cross River gorillas. Comparing Figure 4.3 and 4.4 it is seen that this population is placed closer to the eastern populations when raw variables are transformed into shape variables. The effect of allometry (the size-related information that is preserved after taking into account overall size) seems to be negligible in causing this variance. This is seen in the correlation coefficients of the logged GM with the scores for the discriminant functions. For the first two functions, which together account for about 66% of the variance, correlation coefficients are not significant ($p>0.1$) for the UM1, UM2, LM1 and LM3, and although significant for the LM2 and UM3, the correlations are low (0.1660 for the first DF and -0.1961 for the second DF for the LM2, and -0.2868 for the first and 0.2072 for the second for the UM3). By comparing the explainable variance and the

POP	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	0.00	3.38	4.51	2.33	3.31	4.26	2.42	4.69	4.80	7.51	4.47	10.59	7.00	17.67
2	3.38	0.00	1.65	0.97	2.48	2.13	1.38	5.46	6.01	11.14	4.46	12.19	9.94	16.86
3	4.51	1.65	0.00	1.60	3.02	1.99	2.01	4.66	5.65	11.18	3.56	10.49	7.94	16.78
4	**2.33**	**0.97**	**1.60**	0.00	**1.58**	2.19	**0.85**	3.97	5.22	9.43	3.32	**8.38**	7.61	16.88
5	3.31	2.48	3.02	1.58	0.00	2.92	1.86	6.49	7.06	11.00	5.33	9.90	10.94	15.14
6	4.26	2.13	1.99	2.19	2.92	0.00	1.92	5.65	5.58	10.92	4.57	12.97	9.82	19.70
7	2.42	1.38	2.01	**0.85**	1.86	**1.92**	0.00	4.21	4.76	9.07	3.62	10.73	8.19	**13.68**
8	4.69	5.46	4.66	3.97	6.49	5.65	4.21	0.00	2.72	**3.27**	**2.30**	10.51	**4.29**	16.73
9	4.80	6.01	5.65	5.22	7.06	5.58	4.76	2.72	0.00	4.48	2.43	11.34	6.18	19.76
10	7.51	11.14	11.18	9.43	11.00	10.92	9.07	3.27	4.48	0.00	5.62	16.69	6.51	20.80
11	4.47	4.46	3.56	3.32	5.33	4.57	3.62	**2.30**	**2.43**	5.62	0.00	9.34	5.55	19.65
12	10.59	12.19	10.49	8.38	9.90	12.97	10.73	10.51	11.34	16.69	9.34	0.00	10.98	0.00
13	7.00	9.94	7.94	7.61	10.94	9.82	8.19	4.29	6.18	6.51	5.55	10.98	0.00	25.83
14	17.67	16.86	16.78	16.88	15.14	19.70	13.68	16.73	19.76	20.80	19.65	0.00	25.83	0.00

Table 4.5 Mahalanobis distances between gorilla populations using shape variables. Average for all tooth types for males. Lowest distance between population pairs shown in bold.

POP	1	2	3	4	5	6	7	8	9	10	11	12	14
1	0.00	12.14	18.99	11.27	13.79	12.92	10.09	14.75	18.40	14.15	16.84	17.00	11.62
2	12.14	0.00	7.86	3.93	3.86	4.58	2.60	10.55	14.11	10.48	9.08	9.27	4.82
3	18.99	7.86	0.00	6.29	3.48	4.06	4.37	6.51	9.64	6.03	4.17	8.92	5.48
4	**11.27**	3.93	6.29	0.00	4.16	3.96	2.78	7.43	11.70	7.99	6.69	9.06	**2.52**
5	13.79	3.86	**3.48**	4.16	0.00	3.06	**2.23**	6.20	8.94	6.04	4.05	6.47	5.21
6	12.92	4.58	4.06	3.96	3.06	0.00	2.50	9.07	12.06	7.71	7.01	10.57	5.80
7	10.09	**2.60**	4.37	**2.78**	**2.23**	**2.50**	0.00	6.22	9.16	6.26	4.23	8.16	4.30
8	14.75	10.55	6.51	7.43	6.20	9.07	6.22	0.00	5.71	**1.99**	**2.43**	7.77	7.71
9	18.40	14.11	9.64	11.70	8.94	12.06	9.16	5.71	0.00	5.04	6.08	12.36	15.41
10	14.15	10.48	6.03	7.99	6.04	7.71	6.26	**1.99**	**5.04**	0.00	3.51	8.94	7.50
11	16.84	9.08	4.17	6.69	4.05	7.01	4.23	2.43	6.08	3.51	0.00	**6.29**	7.00
12	17.00	9.27	8.92	9.06	6.47	10.57	8.16	7.77	12.36	8.94	6.29	0.00	13.82
14	11.62	4.82	5.48	2.52	5.21	5.80	4.30	7.71	15.41	7.50	7.00	13.82	0.00

Table 4.6 Mahalanobis distances between gorilla populations using shape variables. Average for all tooth types for females. Lowest distance between population pairs shown in bold.

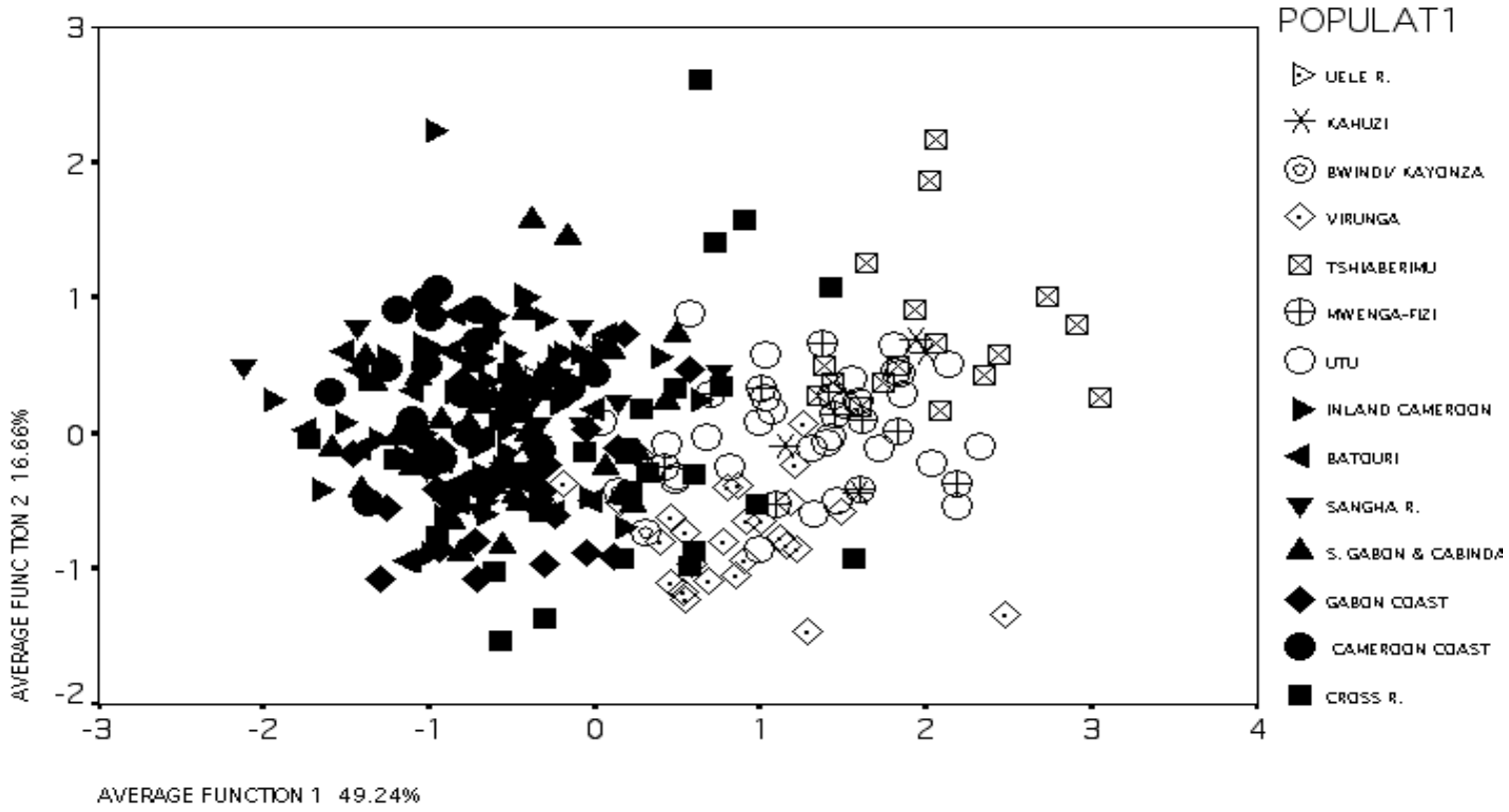


Figure 4.4 Scatter plot of discriminant function1 by discriminant function 2 for shape variables in gorilla populations. Average discriminant scores for upper and lower molars using shape variable, males and females combined.

accuracy of membership assignment using raw and shape variables it is possible to determine the contribution of size in the total variance: when raw variables are used 67.5% of the variance is explained by the first two functions and the membership accuracy is 36.78%. When the analysis is performed using shape variables the explainable variance is reduced by merely two percentage points to 65.9% and classification accuracy drops to 33.16%. This suggests that size does not contribute greatly to group separation in gorillas. Since the role of allometric relationships in explaining this variance is also small, the bulk of the evidence suggests that shape (but not size-related shape) is most important in separating gorilla populations.

The raw and shape variables responsible for causing group separation are shown in Tables 4.7 and 4.8. A comparison of the two tables reveals that most of the discriminating variables are the same. The length and breadth dimensions have the highest correlation coefficients with the disciminant functions. In the East African populations these dimensions are longer. In particular, the breadth of the molars at the distal end is longer. The molars in the eastern populations are elongated and broader than in the western populations. This was also demonstrated by Booth (1971). The variables differentiating the subgroups within each of these two groups and the functional significance will be elaborated in the following sections.

Another observation from the discriminant analysis and the Mahalanobis distance matrix (Tables 4.3 to 4.6) concerns the nature of population structure within the West African and East African clusters. Population 1 (Cross River) is

divergent from populations 2 to 7. Population 3 (Gabon coast) and population 6 (Batouri) also have slightly higher interdemic distances, which suggests that they deviate from the rest in dental metrics. On the whole, however, inter-group distances between the West African populations are relatively low. In contrast the distances between the East African populations are high. For example, distances from populations 8, 9 and 11 to 10 and 12 (Mt.Tshiaberimu and Bwindi/Kayonza, respectively) are fairly high, from 5.21 to 9.47 in the raw variable analysis (Table 4.3). Even the distances between the eastern populations that are closely related, for example, Utu (population 8) and Mwenga-Fizi (population 9) are higher than comparable distances in West Africa – 2.96, whereas 2.96 is the highest distance between any two populations in West African cluster (Table 4.3). While it is possible that greater Mahalanobis distances between East African populations are artifacts of a small sample size and therefore overestimated, these findings agree with recent mtDNA studies which indicate that isolated populations in East Africa are distinct from one another (Jensen-Seaman & Kidd, 2001). The molecular studies also suggest that these populations exhibit low levels of within group genetic diversity, presumably due to reduced gene flow between them (Garner & Ryder, 1996).

UM1	Func 1	Func 2	UM2	Func 1	Func 2	UM3	Func 1	Func 2
Males	**56.83%**	**15.28%**		**73.79%**	**13.15%**		**49.00%**	**18.42%**
UM1BLDIS	1.00894		UM2MD	1.03763		UM3MD	.99242	
UM1AN_BC	.58706	.75119	IUM2A_ME	-.59488	.43455	UM3LPOPR	-.48210	-.46257
UM1AN_LC		.63528	UM2LPOPR	-.57086	.89744	IUM3A_ME	-.44961	
IUM1L_MC		-.61663	UM2POS_M	.49373		UM3POS_D		.70192
UM1LPOS2		.55570	UM2BLMES		.70931	UM3LPOST		-.55010
UM1LPOPR	-.40956	.52237						
Females	**59.34%**	**16.91%**		**65.25%**	**15.78%**		**59.21%**	**15.20%**
UM1BLDIS	1.12192		UM2MD	-.61456	1.16667	UM3BLMES	.58231	
UM1LPOS2	-.66914		UM2BLDIS	-.53884	-1.17014	IUM3A_DI	-.48950	.82034
UM1MD		.66081	UM2LPOPR	.62489		UM3LPRE1	.44764	
UM1LPOST		-.71082	IUM2L_CI	.40799				
UM1LPRE1		.48963	IUM2L_DC		-.45565			
UM1LPOPR		.44412						
IUM1L_CI		.43698						

LM1	Func 1	Func 2	LM2	Func 1	Func 2	LM3	Func 1	Func 2
Males	**60.35%**	**13.96%**		**82.82%**	**12.24%**		**51.27%**	**12.89%**
LM1MD	.61787		LM2MD	.81631		LM3MD	.92247	
ILM1A_ME	-.58167		LM2LPMET	.45016		LM3LPREH	-.40701	
LM1LPENT	-.47364	-.48112	LM2POS_D		.89362	LM3LPOME		-.59337
LM1BLDIS	.42322					LM3AN_CR		.53756
ILM1L_DC		.92364				ILM3A_ME		.51784
						LM3LPOHY		-.42887
Females	**56.20%**	**29.10%**		**51.41%**	**24.25%**		**51.95%**	**25.32%**
LM1BLMES	.99476		LM2BLDIS	-.85984		LM3MD	.78375	.40329
LM1LPENT	-.77678		LM2LPOEN	.59866		ILM3L_MC	.46311	.78205
ILM1L_DC		.71080	ILM2L_DC		-.52736	LM3BLDIS	.43303	
LM1LPOS1		.62625	LM2POS_M		.57152	LM3LPOS1		-.90490
			LM2AN_CR		.51524			

Table 4.7 Standardized canonical discriminant function coefficients for raw variables for first two functions. Percent of variance explained by each function shown. Only coefficients above 0.40 shown.

UM1	Func 1	Func 2	UM2	Func 1	Func 2	UM3	Func 1	Func 2
Males	**62.20%**	**14.79%**	**Males**	**69.98%**	**17.78%**	**Males**	**49.95**	**17.82**
SHUM1BLD	-.89581	-.73353	SHUM2MD	1.17339	1.20901	SHUM3MD	.51946	
SHUM1PO1	.79017		SHUM2PO1	-1.08233		SHUM3BLD	.45047	
SHUM1POH	.40589		UM2POS_M	.81678		UM3AN_LC	-.41902	.51824
SHUM1LDC		.98804	SHUM2MFO	-.73660	.65568	SHUM3PO1	-.41156	-.54384
SHUM1LCO		.44763	SHUM2BLD		-1.17662	UM3POS_D		.80375
Females	**54.74%**	**19.96%**	**Females**	**49.52%**	**20.77%**	**Females**	**60.39%**	**21.25%**
SHUM1BLD	1.63585		SHUM2BLD	1.06514	.93797	SHUM3BLD	.59415	
SHUM1MD	-.98688	1.12014	SHUM2PO1	-.95806	.42367	SHUM3PR1	.51782	.61216
UM1AN_BC	.55313		SHUM2MD		-1.75847	UM3AN_LC	-.43158	.40601
UM1POS_D	.41025		SHUM2LDC		.83379	SHUM3DFO		.75293
SHUM1LCI	.40134	1.23260						

LM1	Func 1	Func 2	LM2	Func 1	Func 2	LM3	Func 1	Func 2
Males	**44.51%**	**23.75%**	**Males**	**56.27%**	**21.37%**	**Males**	**40.33%**	**18.36%**
SHLM1BLD	.61930	-.94753	SHLM2LPM	.84864		SHLM3MD	.88986	
LM1AN_BC	.52039		LM2AN_HY	.44850		SHLM3LPM	.77991	
SHLM1LPE	-.50068		LM2POS_D		-.59222	SHLM3LCI	.75715	.58977
LM1POS_M	-.49884		LM2AN_CR		-.41798	SHLM3LP3	.48950	
SHLM1LDC		1.16653				LM3AN_CR	-.47284	
						SHLM3MFO		-.83125
Females	**57.76**	**22.50**	**Females**	**30.10%**	**27.72%**	**Females**	**51.49%**	**24.93%**
SHLM1BLM	1.02347		SHLM2LDC	.63723	.77546	SHLM3POH	.84465	-.64859
LM1POS_D	.91856	.45496	LM2POS_M	-.43378		LM3AN_HY	.81347	
SHLM1MFO	-.65796		SHLM2BLD		-.85061	SHLM3LMC		.99327
SHLM1LPO	-.46932		SHLM2LP5		.75862			
SHLM1LPE		.91285	SHLM2LP1		-.47295			
SHLM1LMC		-.44131						

Table 4.8 Standardized canonical discriminant function coefficients for shape variables for first two functions. Percent of variance explained by each function highlighted. Only coefficients above 0.40 shown.

Discrete dental traits were used to further explore the nature of variation in gorilla populations. These data provide independent assessment of the population structure in gorillas. For each of the dental traits I calculated group means, or an average character state (methodology explained in Chapter Two) and used these in a hierarchical clustering procedure. The nearest neighbor algorithm was used. The results are presented in the form of a dendrogram (Figure 4.5) so as to provide a graphical representation of the separation between groups.

Most of the conclusions of the metric analysis are repeated in this dendrogram. As can be seen, the West African populations (1 to 7) are closely placed, with population 1 from the Cross River slightly separated from the rest. The East African populations (8 to 11) do not form a clear cluster. Populations 12, 13 and 14 are isolated from the rest of the populations but this is most likely due to the small sample sizes.

When the dendrogram is constructed excluding populations 12, 13 and 14 (Figure 4.6), once again the West African populations cluster together - population 1, and to some extent 3 and 6 are separated from the western populations; population 11 is the next most closely related to this cluster; and populations 8, 9 and 10 are equally separated from population 11 and do not form a single cluster.

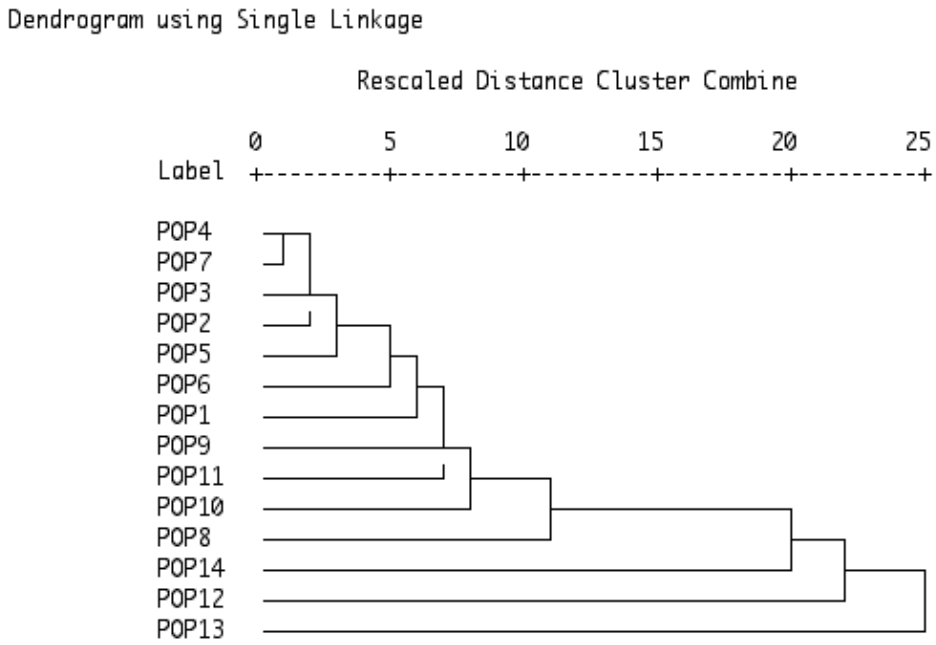


Figure 4.5 Dendrogram showing hierarchical cluster solution for discrete dental characters.

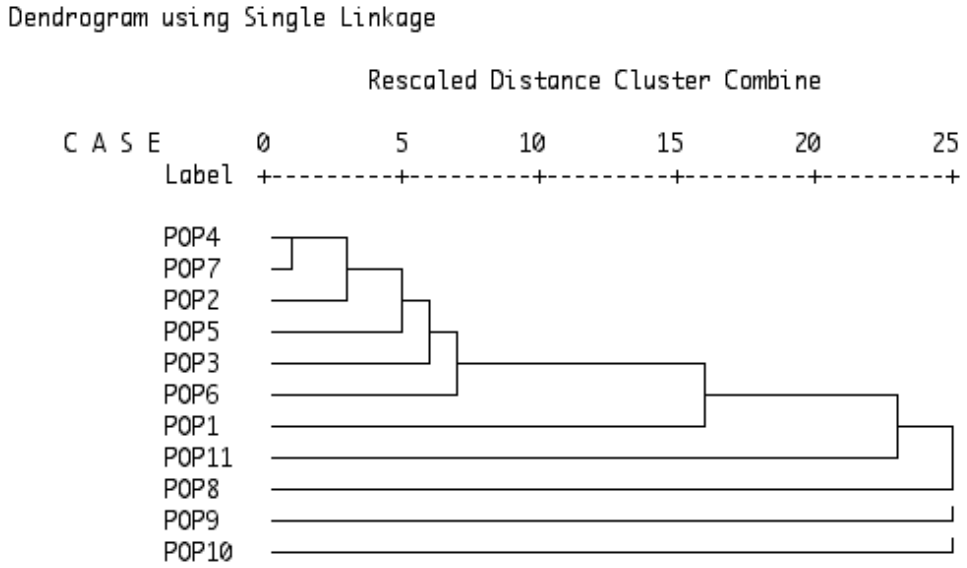


Figure 4.6 Dendrogram showing hierarchical cluster solution for discrete dental characters. Populations with small sample sizes excluded.

Following the hierarchical clustering analysis I used a chi-square statistic with a $p<0.05$ to identify dental traits that significantly differ between gorilla populations. Of about 150 traits studied, 60 were found to occur at significantly different frequencies in the populations (Table 4.9). Only populations with a sample of 10 individuals or greater are shown. This tabulation of frequencies confirms that there is high level of variability among gorilla populations. The frequencies that are markedly different from the others are highlighted. This helps to make evident the populations that are strikingly different in dental frequencies. To draw broad generalizations, in about 40 out of 60 traits one or more populations from East Africa exhibit significantly different frequencies from the West African populations. In at least 12 of the 40 traits all available East African populations show similarities in frequencies that consistently differ from the West African populations. Populations 3 and 6 from West Africa also deviate from the others in several traits. Population 1, for lack of adequate samples could not be used in all comparisons. For the traits studied this population shows affinity with the other West African populations, and also a few distinctive features. It is possible that some of the differences in frequencies, especially those between the western and eastern clades are related to dietary adaptations. However, the role of other evolutionary forces such as drift also needs to be considered.

Table 4.9 Frequencies of dental traits showing significant differences (chi-square p<0.05) among gorilla populations. Frequencies markedly different from the rest are highlighted.

POP	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**
N	**22**	**17**	**29**	**30**	**13**	**27**	**38**	**21**	**10**	**13**	**23**
Cingulum UI1 discontinuous		0	0	0		0	**7**	**8**			0
Cingulum UI1continuous		15	4	6		4	4	**23**			11
Cingulum UI1bulge tapering towards apex		85	96	94		96	89	**69**			**78**
Cingulum UI1continuous and bulge		0	0	0		0	0	0			**11**
Lingual pillar median-UI1		23	17	25		11	26	23			**72**
Mesial marginal ridge-UI1		31	35	25		31	50	**75**			**83**
Distal marginal ridge-UI1		38	40	21		37	32	**82**			**89**
Mesial fovea- UI1		38	39	23		54	61	33			**94**
Cingulum UI2 discontinuous		43	**7**	50		37	59	**7**		**14**	**24**
Cingulum UI2continuous		29	43	38		19	19	**86**		**86**	**60**
Cingulum UI2bulge tapering towards apex		29	**50**	12		**44**	19	7		0	12
Cingulum UI2continuous and bulge		0	0	**12**		0	3	0		0	4
Mesial marginal ridge-UI2		29	33	15		18	15	**50**		**57**	**64**
Distal marginal ridge-UI2		29	48	19		22	24	**61**		**57**	**80**
Distal fovea- UI2		43	44	**29**		52	58	**20**	**11**	**0**	**20**
Mesiolingual tubercle-UP3	9	5	3	8	0	0	15	**34**	10	6	23
Mesial cingulum - UP3	94	85	94	92	**61**	100	90	89	90	**71**	**61**
Distal cingulum - UP3	82	85	97	95	71	100	96	97	90	88	**42**
Buccal cingulum - UP3	9	9	3	3	0	9	2	**41**	**30**	**59**	0
Mesiolingual tubercle-UP4	13	10	19	13	0	22	8	**32**	**50**	0	**38**

Table 4.9 Frequencies of dental traits showing significant differences (chi-square p<0.05) among gorilla populations (contd.)

POP	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**
N	**22**	**17**	**29**	**30**	**13**	**27**	**38**	**21**	**10**	**13**	**23**
Distobuccal tubercle-UP4	83	76	89	84	79	94	94	83	90	**35**	77
Distal cingulum - UP4	**52**	81	97	87	71	97	80	97	100	94	78
Buccal cingulum - UP4	4	9	0	0	7	16	4	**45**	**30**	**35**	7
Pericone on UM1	30	0	34	35	**54**	7	24	**65**		**55**	8
Mesostyle on UM1	0	5	3	3	0	3	10	**74**	**33**	**64**	8
Paraconule on UM2	21	38	23	44	40	**87**	**65**	59	50	29	28
Distoconule on UM2	46	14	54	29	13	22	20	**70**	**90**	**82**	38
Pericone on UM2	29	0	33	36	27	**3**	18	34	**10**	35	**7**
Mesostyle on UM2	0	0	0	3	0	3	4	**27**	10	6	0
Crista obliqua on UM3	**50**	10	21	0	8	3	11	24		14	8
Paraconule on UM3	12	30	15	22	15	**59**	**34**	**42**		25	17
Distoconule on UM3	59	25	62	46	31	31	44	**89**		**85**	**71**
Cingulum LI1 discontinuous		21	**8**			24	38	**7**		**0**	**0**
Cingulum LI1continuous		**43**	84			**60**	**50**	93		100	87
Cingulum LI1bulge tapering towards apex		**36**	8			16	12	0		0	13
Mesial marginal ridge-LI1		0	52	20		12	12	61		**90**	**93**
Distal marginal ridge-LI1		0	60	22		16	14	**82**		**90**	**93**
LI1-distal fovea		20	35	6		12	29	**54**		10	13
Cingulum LI2 discontinuous		29	0	19		12	24	6		0	18
Cingulum LI2continuous		43	**89**	59		68	61	**78**		**86**	41

Table 4.9 Frequencies of dental traits showing significant differences (chi-square p<0.05) among gorilla populations (contd.)

POP	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**
Average N	**22**	**17**	**29**	**30**	**13**	**27**	**38**	**21**	**10**	**13**	**23**
Cingulum LI2bulge tapering towards apex		29	12	11		20	16	17		14	**41**
Cingulum LI2continuous and bulge		0	0	**11**		0	0	0		0	0
Lingual pillar median-LI2		21	12	33		36	39	56	**89**	50	9
Mesial marginal ridge-LI2		7	40	18		28	24	50	44	**86**	41
Distal marginal ridge-LI2		89	62	**40**		**40**	**51**	83		93	73
LP3-Distolingual tubercle		90	100	92	**77**	100	98	92	100	**79**	**79**
LP4-Distolingual tubercle		100	100	94	100	97	95	96	100	**73**	100
Trigonid crest-LM1continuous		16	0	33	17	23	19	**50**	12	**60**	29
Trigonid crest-LM1interrupted		21	17	24	0	5	8	27	22	**40**	25
Trigonid crest-LM1twinned continuous		47	56	27	**75**	36	46	5	44	0	17
Trigonid crest-LM1twinned interrupted		16	27	16	8	36	27	18	22	**0**	29
Distobuccal dev. gr-LM1thin		35	**97**	58	67	**4**	33	**82**	33	60	72
Distobuccal dev. gr-LM1wide notch		60	**3**	39	33	**96**	67	14	67	30	28
Tuberculum intermed-LM1		30	47	21	25	50	30	23	11	60	**0**
Distobuccal dev. gr.-LM2 thin		40	**94**	49	67	7	41	**88**	**89**	**80**	63
Distobuccal dev. gr.-LM2 wide notch		60	**6**	46	33	93	59	**8**	**11**	**13**	37
Ling. dev. gr.-LM3		55	70	78	**100**	41	62	**100**		**86**	**87**
Distobuccal dev. gr.-LM3 thin		40	90	51	69	**11**	39	71		75	64
Distobuccal dev. gr.-LM3 wide notch		50	**7**	46	31	89	61	29		25	36
Tuberculum sex-LM3		30	50	49	54	**11**	29	61		**100**	**91**

In all essential respects the results of the qualitative analyses are congruent with the findings of the quantitative analyses. The reiteration of the position of the Virunga gorillas (Figures 4.3 and 4.4) as intermediate between the western and Utu gorillas raises questions about the correspondence between the results of Groves' (1970b) craniometric study and this odontometric study. Groves (1970a) suggested that the main difference between the mountain and other gorillas was of a dietary nature and mentioned characters of the dentition, such as larger teeth with higher crowns, as being the predominantly distinguishing characters. Behavioral studies have confirmed the dietary distinction of the mountain gorilla (Watts, 1996). Yet, this study with its primary focus on dental data does not support Groves' suggestion of dental distinction. It is possible that features of the jaw and palate distinguish the mountain gorilla from the eastern lowland gorilla, but in features of the dentition the two are more similar. This is confirmed by Uchida's (1992) dental and craniometric study. The dental plots in her study (Figures 4.4. to 4.8, Uchida, 1996) place *G. g. beringei* between *G. g. gorilla* and *G. g. graueri*. In her craniometric study, on the other hand, *G. g. beringei* is markedly distinct from the other two subspecies, and she is able to identify many more cranial, especially mandibular, characters that differentiate *G. g. beringei* from *G. g. graueri*.

In the next section the populations will be combined into the known subspecies so as to highlight the dental differences between them, and the role of function and non-functional forces in causing the differences will be evaluated.

Subspecies

Having studied the pattern of dental variation in gorilla populations, it is now possible to study the nature of dental differences between the major subgroups of gorillas. Based on the results of the population level analysis and the consensus opinion from other morphological, molecular and behavioral studies I divided the gorillas into four subspecies - the Cross River gorillas, the western lowland gorillas, the eastern lowland gorillas and the eastern highland gorillas (*G. g. diehli, G. g. gorilla, G. g. graueri* and *G. g. beringei*, respectively). Population 1 was the sole representative of *G. g. diehli*, populations 2 to 7 and population 14 were placed in *G. g. gorilla*, populations 8 to 10 and 13 were included in *G. g. graueri*, and populations 11and 12 formed *G. g. beringei*.

A step-wise discriminant analysis was performed using sex-segregated raw and shape variables. The average classification accuracy and the variables with high loading on the discriminant functions were found to be the same for both analyses. As demonstrated above shape variables are most effective in differentiating gorillas and therefore the results of only the shape analyses are reported here. Since sexual dimorphism is reduced when molar dimensions are converted into shape variables (Uchida, 1998, reconfirmed in this study) the sexes were combined thus bolstering sample sizes. The average classification accuracy for the four subspecies is 76% (Table 4.10). Once the variables with high loading factors on the discriminant functions were identified, a one-way Anova was applied to these variables – F-statistics with a probability of 0.05 show which group means

differed significantly and how the groups differed from one another. These variables and their role in differentiating the subspecies are summarized in Table 4.11.

Table 4.10 Average classification accuracy of gorilla subspecies based on step-wise discrimininant analysis of shape variables.

	N	*G. g. diehli*	*G. g. gorilla*	*G. g. graueri*	*G. g. beringei*
G. g. diehli	14	11	2	0	1
		78.57%	14.28%	0%	7.14%
G. g. gorilla	152	19	115	8	10
		12.5%	**75.66%**	5.26%	6.58%
G. g. graueri	50	4	3	39	4
		8.00%	6.00%	**78.00%**	8.00%
G. g. beringei	26	2	2	3	19
		7.69%	7.69%	11.54%	**73.08%**
Total	**242**	**Average classification accuracy: 76.33%**			

Chi-square statistics were used to identify the subspecies that differed significantly in the frequencies of non-metric dental traits. These differences are also shown in Table 4.11. Discrete dental traits on the canines were not used in the comparison because they were found to have a significant correlation with sex. Table 4.12 displays the mean of the raw linear dimensions for each of the sexes in all four subspecies so as to provide a comparison with the shape variables.

Based on these analyses, the following dental features can be used to differentiate the four subspecies (see also Tables 4.11 and 4.12):

G. g. diehli: Smallest of the four subspecies in most linear (length and breadth) dental dimensions. On the premolars the mesiobuccal tubercle and mesial and distal

cingulum observed at a high frequency on the UP3, and distal and lingual cingulum on the UP4. Otherwise tubercles and cingulum not common on premolars. Even when corrected for overall tooth size upper molar length and width fairly short compared to other subspecies, but UM3 relatively long and wide at distal end. Higher incidence of anterior transverse crest meeting protocone. Buccal cusps not mesially placed compared to lingual cusps, crista obliqua on UM3 more common than on other subspecies, postparacrista, postprotocrista and posthypocrista fairly short, but posthypocrista on UM3 relatively longer than on other subspecies. Accessory tubercles on upper molars not frequent except for distoconule on UM2 and UM3. Protocone fairly tall, also metacone on UM3 but paracone shortest of all subspecies. Lower molar length and width relatively short but mesial and distal cusps widely spaced on LM2. Cristid obliqua more lingually placed than other subspecies, cusps with fairly long crests, except for premetaconid cristid on LM3 and preentocristid on LM1. Lower molar cusps also relatively tall.

G. g. gorilla: In raw linear dimensions upper central incisors widest of all subspecies; in females upper and lower canines tallest, in males lower but not upper canines tallest of all subspecies; all other linear dimensions smaller than two eastern subspecies. Upper incisors commonly have lingual bulge. Compared to eastern subspecies low incidence of median lingual pillar, mesial and distal marginal ridges and mesial and distal foveae on lingual side of incisors. On the LI2 the distal fovea frequently seen. On premolars additional tubercles not common, but mesial and distal cingulum on the UP3 and distal cingulum on the UP4

frequently observed. When corrected for absolute tooth size length and breadth dimensions of upper molars less than other subspecies and distal cusps relatively closely spaced. Anterior transverse crest commonly meets preprotocrista. Buccal cusps more mesially placed than lingual cusps but not as mesial as on the eastern subspecies. Postparacrista shortest, but postprotocrista and posthypocrista longest of all subspecies. Crista obliqua on UM3 often missing. Paraconule often seen on UM1 and UM2; distoconule on UM2 and UM3 also common, but not as common as in *G. g. graueri*. Paracone, metacone and hypocone relatively tall but protocone relatively shorter. Lower molar length, width and distance between cusps relatively short. Trigonid crest often twinned on LM1 and LM2; on LM3 single but often interrupted. Lingual development groove on LM3 often missing; distobuccal development groove more commonly a wide notch on all lower molars; cristid obliqua on all three lower molars more buccally placed than in *G. g. diehli* and *G. g. graueri*; preentoconid on LM1 and postentoconid on LM2 relatively longer than *G. g. graueri*, hypoconulid tall on LM2 and LM3, metaconid tall on LM1 and LM2; tuberculum intermedium on LM1 at nearly same frequency as *G. g. graueri*, but tuberculum sextum less frequent than eastern subspecies.

G. g. graueri: In linear dimension of molars largest of the four subspecies. Mean linear dimensions of most antemolar teeth less than *G. g. beringei*, with following exceptions: UCBL in males, LI1MD and LI2MD in males, UCHT and LCMD in females, and UP3BL in both sexes - these dimensions highest in *G. g. graueri*. On the incisors thin ridge of cingulum commonly found skirting the cervical margin,

although on the UI1 a lingual bulge also commonly seen. Median lingual pillar and mesial and distal marginal ridges commonly encountered on the lingual side of incisors; mesial fovea on UI1 fairly common, but rare on LI2; distal fovea not frequent on UI2, but frequently seen on LI2. On premolars higher incidence of cingulum than other subspecies, additional tubercles also quite frequent but less than *G. g. beringei*. In length, and mesial and distal width of molars even after correcting for overall size this subspecies longest. Molar cusps fairly widely spaced. On upper molars anterior transverse crest commonly meets preprotocrista; buccal cusps placed relatively more mesially than other subspecies; postparacrista, postprotocrista and posthypocrista all relatively long. Crista obliqua on UM3 more commonly encountered than on *G. g. gorilla* and *G. g. beringei*; upper molar cusps relatively short. On lower molars trigonid crest mostly single (not twinned); lingual development groove on LM3 routinely observed; distobuccal development groove mostly a thin groove; cristid obliqua relatively lingually placed; molar crests relatively long except, preentoconid cristid on LM1 and postentoconid cristid on LM2; molar cusps not tall except hypoconulid on LM2 which is relatively tall. A high frequency of accessory tubercles on all molars and premolars.

G. g. beringei: Linear dimensions of most antemolar teeth longest of four subspecies, highest degree of sexual dimorphism (index of male to female dental dimensions) especially in canine and P3MD dimensions; linear dimensions of molars less than *G. g. graueri* but more than western subspecies. Incisor morphology similar to *G. g. graueri*: UI1 with high frequency of lingual bulge,

other incisors with cingulum skirting cervical margin. Morphology of LI2 different: lingual bulge more common, median lingual pillar, continuous cingulum and distal fovea less common than on *G. g. graueri*. On premolars cingulum less commonly observed but mesiolingual tubercle on LP4 more frequently observed. When size corrected length of upper molars and mesial and distal width still relatively long, second only to *G. g. graueri*. However, UM3 length and distal width narrower than *G. g. diehli*. Anterior transverse crest more often meets preprotocrista; on UM1 and UM3 buccal cusps more mesial than lingual cusps; on UM2 the buccolingual orientation of mesial cusps not as oblique. Postprotocrista shortest of all subspecies, and postparacrista longest; posthypocrista fairly short. Crista obliqua on UM3 not frequent. Accessory tubercles on upper molars less frequent than on *G. g. graueri*. Upper molar cusps relatively tall. Lower molar length and width relatively long, but LM2 distal width narrowest of all subspecies with distal cusps placed relatively more closely placed than other subspecies. Trigonid crest on lower molars with about equal frequencies of single, interrupted, twinned and twinned interrupted appearances. Cristid obliqua on lower molars the most buccally placed of all subspecies. Lingual development groove on LM3 most often present, and distobuccal development groove more commonly a thin groove on all lower molars. Crests on lower molars not long on the whole except for premetaconid cristid on LM3 and preentoconid cristid on LM1. Tuberculum sextum on the LM2 and LM3 routinely observed but the tuberculum intermedium and sextum on the LM1 quite rare. Lower molars cusps relatively tall: protoconid and hypoconid

tallest on LM1 and LM2 of all four subspecies, but metaconid quite short; on LM2 hypoconid tallest, but hypoconulid and metaconid shortest.

This tabulation of differences helps to assess the nature of variation within and between gorilla subspecies. It is seen that the two eastern subspecies, *G. g. graueri* and *G. g. beringei* share the greatest affinity, and in turn the greatest distinction from the West African subspecies in features relating to dental size. Indeed, in the discriminant analysis of the upper and lower molars the highest loading on the discriminant functions was achieved by the relative length and breadth of molars and the distance between cusps (Tables 4.7 and 4.8). The two eastern subspecies are similar in several non-size related discrete dental traits as well. For example, they both have relatively narrow upper central incisors with a higher prevalence of lingual bulge, mesial and distal marginal ridges and mesial foveae; upper molars with mesially placed buccal cusps and relatively long postparacrista; lower molars with a narrow distobuccal development groove and a high frequency of the tuberculum sextum on the LM2 and LM3. These differences are likely to be of a functional nature related to different dietary strategies of the eastern and western groups. However, the relationship between dental morphololgy and diet as discussed below, is a complex one confounded by aspects of phylogenetic inertia and drift and no simple correlation can be established between the two. The dietary differences between the subspecies and the corresponding dental traits will be addressed in greater detail in the discussion section.

The major conclusions of previous dental studies in gorillas are supported

by this study. Groves (1970a) observed that mountain gorillas have cheek teeth with higher crowns and greater likelihood of extra cusps on the distal molars. This seemingly anecdotal observation is substantiated here. *Gorilla gorilla graueri*, however, was found to have an even higher frequency of additional cusps on the molars. Uchida (1998) studied subspecies differences in cusp base areas. Although her results are not directly comparable, this study concurs with her on the relative importance of molar cusps in differentiating the subspecies. Molar cusps she identified as being relatively larger were found in this study to be also taller, and vicé versa (*contra* Swindler, 1976). For example, the paracone on UM2 and metaconid on LM1 is relatively taller in *G. g. gorilla* than *G. g. graueri* but the hypoconid on the LM1 is shorter. In *G. g. beringei*, the metacone is taller on UM1 but shorter on UM3 and hypoconid is taller on LM2 than the other subspecies. In contrast with her study, however, cusps such as the protocones on the UM2 and the mesial cusps on the LM3 were found not to differ significantly between subspecies.

Subspecies differences in qualitative dental traits have not been studied in gorillas previously and therefore these results cannot be evaluated in a comparative manner. In chapter 5 dental traits in gorillas will be compared with chimpanzees to test if the differences can be interpreted from a dietary and ecological perspective.

Table 4.11 Dental variables differentiating *Gorilla* subspecies based on chi-square and correlation coefficients of discriminant functions ($p < 0.05$ for chi-square and one-way Anova). If sample size less than 10 frequencies not shown. 1, 2, 3, 4: progression of trait from least to greatest.

Variable	Tooth type	*G. g. diehli*	*G. g. gorilla*	*G. g. graueri*	*G. g. beringei*
Incisors					
cingulum continuous along cervical margin	UI1		**5%**	33%	11%
	UI2		**30%**	90%	62%
	LI1		**64%**	94%	88%
	LI2		65%	84%	**42%**
bulge on lingual side tapering towards apex	UI1		93%	**53%**	78%
	UI2		**30%**	3%	12%
	LI2		16%	11%	**42%**
median lingual pillar	UI1		**19%**	50%	72%
	LI2		30%	61%	**13%**
mesial marginal ridge	UI1		**36%**	86%	83%
	UI2		**21%**	49%	62%
	LI1		**21%**	68%	82%
	LI2		**25%**	59%	38%
distal marginal ridge	UI1		**33%**	93%	89%
	UI2		**28%**	57%	80%
	LI1		**25%**	80%	88%
	LI2		**45%**	91%	71%
mesial fovea	UI1		**46%**	59%	94%
	LI2		**22%**	7%	0%
distal fovea	UI2		**45%**	10%	19%
	LI2		86%	91%	**67%**
Premolars					
mesiobuccal tubercle	UP3	71%	**45%**	72%	68%
mesiolingual tubercle	UP3	**9%**	**6%**	21%	22%
	UP4	**13%**	**13%**	26%	37%
	LP4		25%	25%	**48%**
mesial cingulum	UP3	91%	90%	83%	**63%**
distal cingulum	UP3	82%	93%	97%	**44%**
	UP4	**52%**	86%	97%	79%
lingual cingulum	UP3	**30%**	13%	14%	7%
	UP4	48%	39%	52%	**21%**
buccal cingulum	UP3	9%	5%	**46%**	0%
	UP4	4%	6%	**40%**	7%
Molars upper					
length	UM2	1	2	4	3
	UM3	3	1	4	2

Table 4.11 continued

mesial width	UM3	2	1	4	3
distal width	UM1	1	2	4	3
	UM2	2	1	4	3
	UM3	3	1	4	2
distance between distal cusps	UM1	2	1	3	4
	UM2	3	1	4	2
cta meets preprotocrista	UMI	**39%**	75%	76%	63%
	UM3	56%	68%	42%	**23%**
cta meets protocone	UMI	**30%**	15%	7%	4%
buccal cusps placed more mesial than lingual cusps	UM1	1	2	3	4
	UM2	3	2	4	1
	UM3	1	2	4	3
postparacrista length	UM1	2	1	3	4
	UM2	2	1	3	4
postprotocrista length	UM1	2	4	3	1
	UM2	2	4	3	1
posthypocrista length	UM1	1	4	2	3
	UM2	1	4	3	2
	UM3	4	1	3	2
crista obliqua	UM3	**50%**	9%	22%	8%
paraconule	UM1	**22%**	52%	62%	**28%**
	UM2	**21%**	52%	48%	**27%**
distoconule	UM2	46%	27%	**78%**	41%
	UM3	59%	42%	**86%**	68%
pericone	UM1	30%	24%	**56%**	8%
mesostyle	UM1	0%	6%	**63%**	8%
	UM2	0%	2%	**17%**	0%
paracone height	UM1	1	3	2	4
	UM2	1	4	2	3
metacone height	UM1	1	3	2	4
	UM3	3	4	2	1
protocone height	UM1	3	2	1	4
	UM3	3	2	1	4
hypocone height	UM2	2	4	1	3
Molars lower					
length	LM3	1	2	4	3
mesial width	LM1	2	1	4	3

Table 4.11 continued

distal width	LM1	2	1	4	3
	LM2	3	2	4	1
distance between mesial cusps	LM2	4	1	3	2
distance between distal cusps	LM2	4	2	3	1
trigonid crest single and continuous	LM1		18%	**47%**	27%
	LM2		11%	**30%**	18%
	LM3		20%	**54%**	33%
trigonid crest single but interrupted	LM1		**14%**	29%	27%
	LM3		50%	**36%**	52%
trigonid crest twinned continuous	LM1		**45%**	11%	19%
trigonid crest twinned interrupted	LM1		23%	**13%**	27%
	LM2		37%	**13%**	21%
ling dev groove	LM3		**66%**	96%	88%
distobuccal dev gr thin	LM3		**49%**	77%	63%
distobuccal dev gr wide	LM1		**50%**	27%	30%
	LM2		**50%**	9%	34%
	LM3		**49%**	23%	37%
cristid obliqua buccally placed	LM1	1	3	2	4
	LM2	1	3	2	4
	LM3	2	3	1	4
posthypoconid cristid length	LM2	4	2	3	1
prehypoconulid cristid length	LM3	3	2	4	1
posthypconulid cristid length	LM2	4	1	3	2
premetaconid cristid length	LM2	3	1	4	2
	LM3	1	2	4	3
preentoconid cristid length	LM1	1	3	2	4
postentoconid cristid length	LM2	4	3	2	1
tuberculum intermed	LM1		34%	36%	**7%**
tuberculum sextum	LM1		6%	**18%**	0%
	LM2		**32%**	73%	79%
	LM3		**36%**	79%	92%
protoconid height	LM1	3	2	1	4
hypoconid height	LM1	3	2	1	4
	LM2	2	3	1	4
hypoconulid height	LM2	2	4	3	1
	LM3	2	4	1	3
metaconid height	LM1	3	4	1	2
	LM2	3	4	2	1

Table 4.12 Mean linear dimensions in *Gorilla* subspecies.

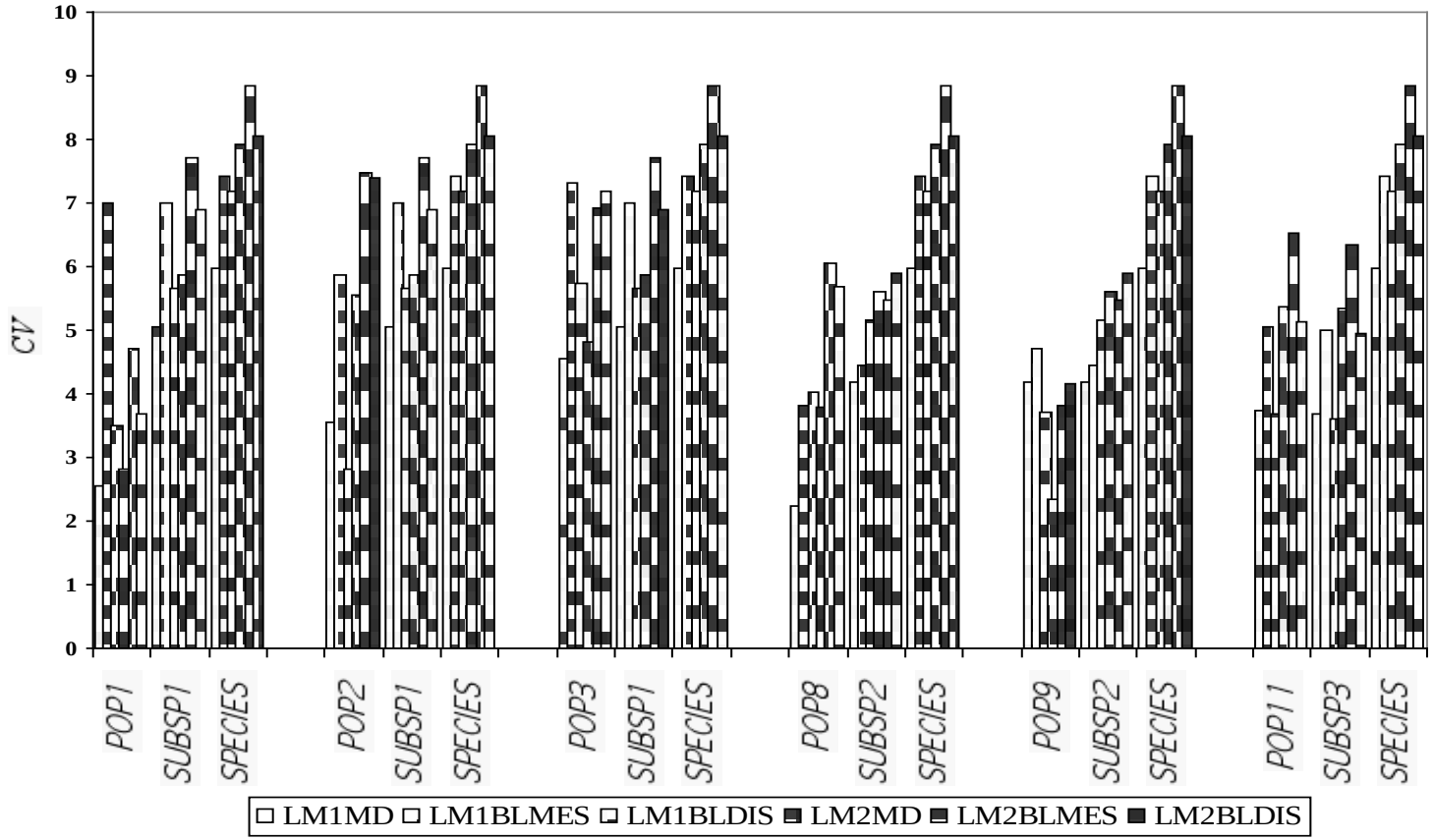
	G. g. diehli		*G. g. gorilla*		*G. g. graueri*		*G. g. beringei*	
	M	F	M	F	M	F	M	F
N	**8**	**3**	**92**	**52**	**28**	**19**	**13**	**11**
UI1MD	13.1	11.3	13.9	13.2	13.2	12.6	13.0	12.9
UI1BL	10.7	8.5	10.8	10.1	11.2	10.4	11.9	11.0
UI1HT	12.9	8.8	13.1	11.8	13.4	12.1	14.2	12.2
UI2MD	9.2	8.0	9.7	8.9	9.9	9.1	10.1	9.7
UI2BL	9.3	7.2	10.0	8.8	11.0	10.1	11.9	10.6
UI2HT	12.7	8.2	11.7	10.5	11.6	10.0	12.6	10.7
UCMD	20.2	13.0	21.1	14.8	21.3	14.8	22.9	14.6
UCBL	14.9	11.2	15.8	11.8	16.7	12.5	17.8	12.3
UCHT	29.3	15.1	30.6	17.7	31.6	16.2	28.4	14.1
UP3MD	11.6	11.0	11.9	11.1	12.5	11.8	13.1	11.7
UP3BL	15.2	13.6	15.7	14.8	17.5	16.5	16.8	15.9
UP4MD	10.7	10.3	11.1	10.7	11.9	11.5	12.3	11.6
UP4BL	14.4	13.4	15.2	14.3	17.1	15.9	16.1	15.6
UM1MD	14.5	13.9	14.9	14.3	16.0	15.2	15.7	14.6
UM1BLMES	13.6	12.7	14.3	13.3	15.4	14.6	14.8	13.9
UM1BLDIS	13.4	12.9	13.9	13.1	15.9	15.0	15.3	14.3
UM2MD	14.9	14.4	15.9	15.3	18.0	16.8	17.2	15.7
UM2BLMES	13.9	13.7	15.1	14.3	16.7	15.5	16.7	14.9
UM2BLDIS	13.8	13.2	14.5	13.6	16.2	15.2	16.3	14.7
UM3MD	14.7	13.4	15.0	13.7	16.8	15.5	15.9	14.3
UM3BLMES	13.5	12.4	14.6	13.3	15.8	15.1	15.3	14.0
UM3BLDIS	12.9	11.4	12.7	11.5	14.6	13.5	13.7	12.4
LI1MD	7.8		7.8	7.5	8.2	7.7	8.0	7.4
LI1BL	8.3		9.2	8.3	9.9	9.2	10.3	9.2
LI1HT	10.0		10.8	10.0	11.4	10.9	11.6	11.2
LI2MD	9.0		9.1	8.3	9.1	8.5	9.0	8.5
LI2BL	10.3		10.6	9.3	11.3	10.3	11.8	10.8
LI2HT	12.3		12.9	11.8	13.5	11.9	13.8	12.0
LCMD	17.3		17.7	13.1	18.1	13.3	18.9	13.2
LCBL	14.0		14.5	11.0	15.0	11.5	15.6	10.8
LCHT	24.0		27.2	17.1	25.7	15.4	23.3	14.5
LP3MD	16.6	13.4	17.4	15.1	17.7	15.4	18.3	15.4
LP3BL	13.3	11.2	14.0	12.5	14.5	12.5	14.8	12.8
LP4MD	12.3	11.8	12.2	13.2	10.3	11.2	11.7	12.3
LP4BL	13.2	13.3	14.7	14.5	10.9	12.5	13.6	13.5
LM1MD	14.9	14.8	15.9	15.3	17.2	16.0	16.9	15.6
LM1BLMES	12.3	11.5	12.9	12.1	14.2	13.4	13.4	12.7
LM1BLDIS	12.5	12.0	12.9	12.3	14.4	13.5	14.1	13.1

Table 4.12 Mean linear dimensions in *Gorilla* subspecies (continued)								
	G. g. diehli		*G. g. gorilla*		*G. g. graueri*		*G. g. beringei*	
	M	F	M	F	M	F	M	F
N	**8**	**3**	**92**	**52**	**28**	**19**	**13**	**11**
LM2MD	16.8	16.2	17.4	16.8	19.8	18.4	18.7	17.1
LM2BLMES	13.6	12.8	14.5	13.6	16.3	15.0	15.8	14.3
LM2BLDIS	13.9	13.2	14.4	13.7	16.1	15.2	15.2	14.4
LM3MD	16.8	16.7	17.4	16.2	19.9	18.6	19.2	17.5
LM3BLMES	13.7	13.5	14.0	12.9	15.1	14.0	14.9	13.7
LM3BLDIS	13.2	12.0	13.1	12.2	14.5	13.6	14.2	13.2

Within-group variation

To check if the high levels of between-group dental variability I encountered are accompanied by low levels of within-group dental variability, I compared ranges of variation within populations and along the taxonomic hierarchy from population to subspecies to species. Using the coefficient of variation (CV) and range as a percentage of mean (R%) I calculated the ranges of variation for the linear dimensions of molars (mesiodistal length and buccolingual breadth at the mesial and distal cusps) for sex-segregated populations. I then combined the populations into the traditionally recognized subspecies (*G. g. gorilla*, *G. g. graueri* and *G. g. beringei*) and then into a single species and calculated the same statistics for these higher order taxonomic categories. The results of this analysis, as shown in Tables 4.13 and 4.14 and exemplified in Figure 4.7, can be summarized as follows: (1) although there are exceptions, CV and R% values are low in all populations but increase progressively in the subspecies and species, (2) in most dimensions the eastern populations (8, 9, and 11), and to some extent the Cross

Figure 4.7 Comparison of CV across populations, subspecies and species



	Populations									Subspecies			Species
	1	2	3	4	6	7	8	9	11	*G. g. gor*	*G. g. gra*	*G. g. ber*	*G. gorilla*
Average N	**10**	**16**	**14**	**27**	**9**	**26**	**15**	**6**	**13**	**108**	**30**	**14**	**152**
UM1MD	3.52	4.81	5.77	5.38	2.94	6.08	3.76	4.85	4.58	5.33	5.61	4.58	6.22
UM1BLMES	5.61	4.16	7.83	8.05	9.47	6.75	5.18	6.55	7.59	7.05	5.51	7.59	7.54
UM1BLDIS	4.94	5.05	7.29	7.40	4.21	6.86	5.11	4.63	4.25	6.57	5.96	4.25	8.57
UM2MD	3.77	6.01	5.57	5.11	7.23	7.41	5.46	5.37	5.97	6.47	6.23	5.97	8.41
UM2BLMES	5.19	5.23	9.27	7.28	8.54	6.54	4.33	6.90	7.44	7.27	5.56	7.44	8.48
UM2BLDIS	6.75	6.41	8.61	6.81	9.25	7.69	11.36	4.11	4.83	7.62	9.15	4.83	9.40
UM3MD	5.09	6.79	7.87	7.49	8.54	7.50	6.98	10.11	9.02	7.17	8.15	9.02	9.03
UM3BLMES	4.35	7.81	9.66	7.75	13.71	8.06	5.36	4.72	7.51	8.60	6.33	7.51	8.75
UM3BLDIS	5.52	8.23	9.93	9.71	9.39	9.54	8.43	6.84	10.84	8.96	8.93	10.84	10.63
LM1MD	2.54	3.54	4.56	5.01	3.81	5.39	2.24	4.18	3.73	5.06	4.18	3.67	5.98
LM1BLMES	7.01	5.86	7.32	6.30	6.68	6.81	3.81	4.71	5.06	7.00	4.45	5.00	7.43
LM1BLDIS	3.51	2.82	5.75	6.37	6.09	6.22	4.03	3.71	3.68	5.66	5.15	3.61	7.20
LM2MD	2.80	5.57	4.82	6.00	5.39	6.12	3.79	2.35	5.36	5.86	5.59	5.34	7.93
LM2BLMES	4.70	7.48	6.92	7.14	8.19	7.88	6.06	3.82	6.53	7.70	5.47	6.33	8.84
LM2BLDIS	3.67	7.39	7.19	6.42	6.64	6.53	5.67	4.16	5.14	6.90	5.90	4.94	8.05
LM3MD	6.53	7.76	6.91	6.95	10.23	6.56	7.56	2.50	8.89	7.25	7.28	8.58	9.47
LM3BLMES	7.94	9.95	7.85	8.36	10.01	8.56	8.42	5.84	5.71	8.58	7.15	5.51	8.61
LM3BLDIS	8.71	7.69	8.89	8.74	11.50	7.01	9.00	9.22	6.83	8.47	9.14	6.62	9.56

Table 4.13 Comparison of CV in gorilla populations, subspecies and species. Only males.

	Populations									Subspecies			Species
	1	2	3	4	6	7	8	9	11	*G. g. gor*	*G. g. gra*	*G. g. ber*	*G. gorilla*
Average N	**10**	**16**	**14**	**27**	**9**	**26**	**15**	**6**	**13**	**108**	**30**	**14**	**152**
UM1MD	13.86	16.38	19.95	24.25	9.94	20.83	14.09	11.68	14.44	25.17	23.88	14.44	36.66
UM1BLMES	22.07	13.27	24.45	29.92	27.21	24.04	18.85	19.19	23.98	33.22	24.35	23.98	34.39
UM1BLDIS	16.60	13.57	26.14	27.50	12.32	25.12	17.04	12.39	13.13	30.45	24.22	13.13	40.28
UM2MD	15.80	20.46	16.82	20.51	22.26	31.32	21.97	14.71	17.97	33.48	30.79	17.97	41.87
UM2BLMES	16.35	16.38	32.66	34.28	28.13	27.45	16.55	17.72	25.21	38.56	24.64	25.21	40.54
UM2BLDIS	21.42	19.08	30.49	27.24	25.46	28.27	42.21	9.39	14.50	33.40	41.37	14.50	44.90
UM3MD	16.90	22.35	26.73	33.60	33.83	31.39	29.84	30.52	29.13	40.86	36.92	29.13	49.97
UM3BLMES	15.72	21.47	29.47	31.39	48.61	35.14	17.18	13.47	25.65	49.28	23.50	25.65	48.22
UM3BLDIS	17.72	26.44	35.59	46.99	32.63	35.57	34.30	17.82	33.41	47.13	39.52	33.41	59.91
LM1MD	6.56	12.90	15.13	20.70	13.30	17.22	7.59	11.23	13.36	26.17	17.82	13.39	32.29
LM1BLMES	16.63	18.29	22.44	23.21	20.51	23.41	12.71	11.63	18.01	32.50	16.03	18.07	31.69
LM1BLDIS	8.85	9.00	17.39	19.58	19.57	23.37	11.66	8.70	14.36	25.97	16.76	14.37	32.76
LM2MD	5.85	18.03	16.43	28.65	16.34	20.94	16.48	5.46	17.65	28.26	30.75	17.58	44.81
LM2BLMES	11.38	25.55	26.42	25.91	22.44	28.64	25.91	10.59	21.62	32.45	25.75	21.58	38.85
LM2BLDIS	9.08	27.36	23.11	25.55	19.29	26.38	21.93	11.99	16.48	30.94	30.54	16.48	46.52
LM3MD	16.85	30.17	24.33	24.16	30.74	28.27	28.93	6.21	31.88	34.31	32.51	31.88	50.91
LM3BLMES	20.77	36.67	28.73	35.69	31.81	33.59	30.62	15.80	17.94	38.53	29.87	17.94	37.72
LM3BLDIS	23.33	31.21	27.20	40.29	42.30	31.62	31.10	21.63	24.00	44.24	34.16	24.00	48.22

Table 4.14 Comparison of R% in gorilla populations, subspecies and species. Only males.

River population (1) exhibit lower CV and R% values than West African populations (2, 3, 4, 6, 7), and (3) CV and R% within the eastern subspecies, *G, g, graueri* and *G. g. beringei* are lower than within *G. g. gorilla*. These univariate statistics support the findings of molecular studies regarding greater levels of diversity in West African populations and comparatively lower levels in the East African populations. Mean linear dental dimensions for these successive taxonomic groups are also shown in Appendix 2.

The comparison of CV and R% values across taxonomic categories makes it clear that on the whole ranges of variation are low in gorilla populations. This helps highlight an important feature of the nature of variation in gorillas, namely, that populations in gorillas are maintained as distinct entities with low levels of diversity and clear separation between them. This finding has important implications for understanding the problems in gorilla taxonomy and for drawing out the contrasts between patterns of variation in gorillas and chimpanzees. The implications of this will be discussed below. It is worth bearing in mind when considering the final conclusion above, that the population and the subspecies for *G. g. beringei* do not constitute increasingly larger geographical entities, but are practically identical especially in terms of the samples utilized in this study.

Discussion

This study with its use of quantitative and qualitative dental variables upholds the conclusion of previous molecular and morphological studies in suggesting that the main split in gorillas lies between the West African and the East

African gorillas. Gorilla populations from the western region (west of about 16^0 E in the Central African Republic) are distributed over a large geographical area, but they are similar to each other in dental morphology and distinct from the East African populations. Gorilla populations east of about 26^0 E in the Democratic Republic of Congo are much more patchily distributed, found at variable altitudes and do not share such close dental affinity, yet they are all clearly separable from the West African populations. Gorilla skulls, supposedly from the Uele River region about 400 miles east of the western gorilla distribution, are closest in dental features to western gorillas.

Prior to 1970 a two-way division of gorillas was the consensus opinion (Schaller, 1963). However, it was thought that the eastern gorillas were mainly highland forms and the western gorillas a lowland group. At present although there is a greater appreciation of the variability in the habitat and altitudinal distribution of gorillas, especially in the eastern part of its range, most of the known morphological features and adaptive strategies contrast the eastern and western groups (Table 4.1). One such morphological feature is size. The general opinion has been that the eastern gorillas are larger. Comparative data shows that although this is true for maxillary and mandibular measurements, and tooth size (Groves, 1970a; Uchida, 1998), on the whole body size differences between the eastern and western gorillas are not significant (Jungers & Susman, 1984). In this study, linear dimensions of most teeth were found to be larger in the eastern gorillas (Table 4.12). Despite the longer dimensions, however, I found that overall tooth size does

not serve to differentiate the molars. The first two discriminant functions, which account for the greatest variance in the discriminant analysis, and effectively separate the eastern from the western gorillas, show only a weak correlation with size as represented the Geometric Mean. When the effect of size is removed, by indexing every variable against the Geometric Mean and converting them into shape variables, the accuracy of classification is the same, but Pearson's correlation with the Geometric Mean is diminished. Clearly, a combination of dental characters serve to distinguish and differentiate gorillas and not all the characters have a positive correlation with size. In Figure 4.8 dental traits that have the highest loadings on the first two discriminant functions for the UM2 are used to illustrate the combination of shape characters that differentiate gorilla subspecies. The UM2 of *G. g. beringei*, for example, has relatively long mesiodistal and buccolingual dimensions, but crest lengths are relatively short. Thus, a simple explanation of molar size difference does not serve to differentiate the eastern African gorillas from those in western Africa.

Gorillas are also characterized by a high degree of sexual dimorphism. Male gorilla body weight is typically more than double that of females (Jungers & Susman, 1984). Male upper canines are about double the height of female upper canines and lower canines in males are about 60% taller (Table 4.12). And yet sexual dimorphism is not so obvious in premolars and molars. In *G. g. beringei* and *G. g. graueri* female molars are significantly smaller than male molars. When converted to shape variables, however, the difference in size is no longer

significant. These examples help to show that differences in gorilla molars both between sexes and between subspecies are maintained by isometric scaling. That molar size is maintained isometrically between the sexes was also demonstrated by Uchida (1998).

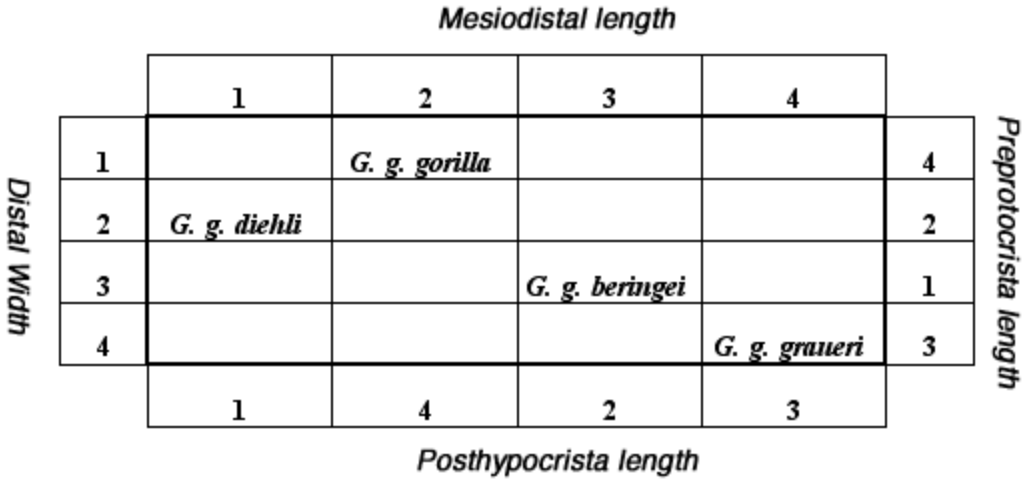


Figure 4.8 Combination of UM2 shape characters used to differentiate gorilla subspecies. 1, 2, 3, 4 represents progression of character from least to greatest.

Differences in dietary strategies constitute the most convincing difference between the eastern and western gorillas. Several years of observational data have confirmed that the diet of mountain gorillas is a specialized folivory, composed of tough and bulky herbs, stems, shoots and pith (Schaller, 1963; Watts, 1996). The

western lowland gorilla diet, on the other hand, while still relying on leaves, vines and bark (Williamson *et al.,* 1990; Tutin *et al.,* 1997) is characterized by a seasonal dependence on fruits (Remis, 1997). It is expected that these contrasting dietary strategies will display adaptive correlates in the masticatory complex. This is indeed true of mandibular morphology. Compared to western lowland gorillas, mountain gorilla mandibles have significantly wider corpora and symphyses, a larger area for the massetter muscle and higher mandibular rami and condyles relative to the occlusal plane of the mandible (Taylor, 2002).

Kay (1975; 1977), Hylander (1975a, 1975b) and Kay & Hylander (1978) have outlined several dental characters that differentiate folivorous from frugivorous anthropoids. Based on these descriptions and the known dietary differences, one would expect that compared to their lowland congeners mountain gorillas have (1) narrower incisors relative to size of molars (2) taller molar crowns (3) sharper shearing crests on molars, and (4) wider grooves between molar cusps.

Uchida (1998) has demonstrated that relative to molar row length UIs are widest in *G. g. gorilla* and increasingly narrower in *G. g. graueri* and *G. g. beringei* thus supporting the claim of an adaptive response to dietary preference. Groves (1970a) pointed out that molar crowns are taller in *G. g. beringei*, but he presented no comparative data. My study with its comprehensive set of dental measurements shows that, contrary to expectations, not all of the above folivory-related characters have their most extreme manifestation in *G. g. beringei*. The dental traits outlined in Table 4.11 reveal that (1) relative to overall size, molar crowns are tall in *G. g.*

beringei but they are also tall in *G. g. gorilla* (2) on the whole, crests connecting tips of cusps are longer in *G. g. graueri* than *G. g. beringei*, and (3) although wide grooves are observed in *G. g. beringei,* for example, the distobuccal development groove on the lower molars is wide, frequencies for this trait are higher in *G. g. gorilla*.

The observed dental morphology of *G. g. beringei* does not display the distinctive features of a greater commitment to folivory that are seen in the mandible. In fact, in dental morphology *G. g. graueri* is the most divergent from the others. *G. g. graueri* differs from *G. g. beringei* and *G. g. gorilla* not only in having relatively larger teeth, but also in the relatively long molar crests and shorter cusps, and the frequency of accessory tubercles.

The mountain gorilla and the western lowland gorilla share several similarities in dental features: the UI1 more commonly has a lingual bulge, accessory tubercles on the premolars are not frequent, the trigonid crest on the lower molars is single or twinned but interrupted, the cristid obliqua is buccally placed and molar cusps are tall. The elucidation of these characters fits with the observation that populations of *G. g. graueri* were more displaced from the other populations in the scatter plots in Figures 4.3 and 4.4, and justifies the intermediate position of the mountain gorilla relative to the eastern and western lowland gorilla in all matrices.

Several reasons can be proposed to explain why the morphology of the molars did not display the distinctive features seen in the mandible of the mountain

gorilla. The most basic reason could be a methodological one. It is possible that the two-dimensional method of measuring is not accurate because it does not capture features like the angle between the cusp tip and occlusal basin, which presumably is sharper in folivorous taxa. Another explanation could be that most of the folivory-related dental traits outlined above are based on theoretical predictions. The mastication of tougher foods such as those consumed by the mountain gorilla could require a different loading regime than that used in shearing leaves, and correspondingly different dental features are likely to be emphasized. A primarily folivorous dietary strategy, after all, characterizes the entire genus and therefore it is not surprising to find dental traits related to folivory in the other subspecies as well. It has been shown often that correlations between morphology and diet do not follow expected predictions (Shea 1983a, 1983b; Taylor, 2002). As pointed out by Taylor (2002) in order to evaluate these correlations in a serious manner controlled studies are required that analyze the structural properties of the tougher foods and the biomechanical loading patterns in the breakdown of the food. In addition dental traits shared by all subspecies because of their common evolutionary history need to be contrasted with the traits shared by the two eastern subspecies because of their more recent evolutionary history. To conclude, the association between dental morphology and diet is complex, especially at the infraspecific level and needs to be evaluated taking into account aspects of drift and phylogenetic inertia.

Conclusions

(1) In dental morphology gorilla populations in the western and eastern parts of Africa fall into two distinct clusters.

(2) The Cross River gorillas are well separated from the rest of the West African populations in dental traits, and the populations from coastal Gabon and Batouri are separated to a lesser degree.

(3) In the eastern part of gorilla distribution the Virunga population is not very different from the Utu population in dental features.

(4) The eastern populations are all clearly separated from each other in dental traits.

(5) Ranges of variation in dental metrics are lower in the eastern populations than in the West African population.

(6) Size is not a useful criterion for explaining the difference between molars in gorilla subspecies.

(7) The correlation between diet and dental morphology cannot be easily established for gorilla subspecies.

CHAPTER FIVE

Comparison and Interpretation

Introduction

Pan and *Gorilla* are large-bodied primates, included, along with *Homo*, in the family Hominidae. As members of the same family they are closely related, yet the two lineages diverged several million years ago (Ruvolo *et al.,* 1991), and *Pan* shares a closer evolutionary relationship with *Homo* (they are sister taxa). In their present distribution both African ape genera are limited principally to the tropical forest region of equatorial Africa, and they display several adaptations that are suited for this habitat. It is conceivable, therefore, that their patterns of dental diversity are influenced to some extent by their shared evolutionary history, to some extent by the history of the African forests they inhabit, and to some extent by their unique evolutionary trajectories, in particular, their ecological and social adaptive strategies.

In this chapter, patterns of dental variation in *Pan* and *Gorilla* are compared. I use the comparison to revisit the questions initially posed by this study. These questions are: (1) how do patterns of variation revealed using dental data compare with those based on other kinds of data. Or, how useful are dental characters for differentiating between populations, subspecies and species of African apes? (2) How influential are factors of size and scaling, diet, and the random forces of genetic drift for understanding patterns of dental variation in the

African apes? (3) How useful is the evolutionary and biogeographic history of these apes for understanding present patterns of dental diversity?

Through these questions I examine the feasibility of congruence between paleontological and neontological systematics. Because of the scant and fragmentary nature of fossil data, the degree and patterns of variation in neontological species are commonly used for delimiting fossil species. In order to do that, however, the appropriateness of neontological species as models must be evaluated. Therefore, the final question to be asked is: how appropriate are extant taxa as models for understanding patterns of variation in fossil taxa? These questions are addressed in this chapter by bringing together the results of my analyses, and attempting to understand dental patterns of chimpanzees and gorillas from the perspective of their shared and unique evolutionary history. In the latter half of the chapter, dental patterns in the African apes are applied to evaluate patterns of dental variation in fossil taxa.

Partitioning of variation in *Pan* and *Gorilla*

Results of this study

Figure 5.1 shows the putative barriers between chimpanzee populations as determined by this study. The main separation lies between populations on the north and south of the Congo River. In dental distances, three populations from the south of the Congo are equally well separated from all populations on the north of the river. The populations from West Africa, west of the Niger are the next most distinctive. When differences in dental size are controlled, these populations are

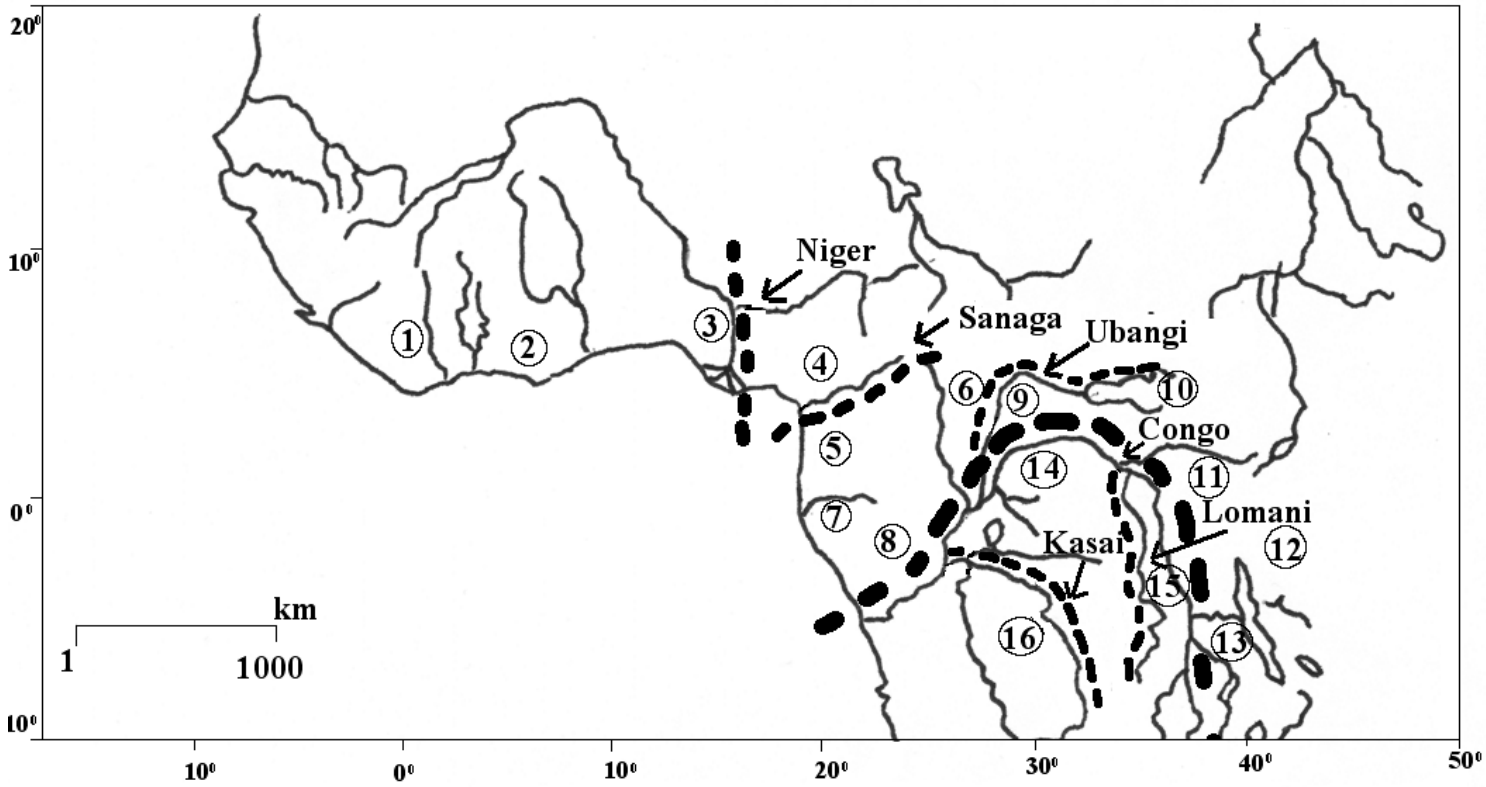


Figure 5.1 Partitioning of dental variation among chimpanzee populations. Strength of segmented line indicates level of difference between populations.

strongly divergent, even more than populations from the south of the Congo. The population between the Niger and Sanaga follows the west African populations in distinction of diagnosis. This is a single population, represented by a relatively small sampling of individuals in this study. With added samples this conclusion could change. The populations from Sanaga to Ubangi and Ubangi to Tanzania are fairly close in dental distances. Several populations, with large samples, are present on either side of the Ubangi, and all of these show remarkable affinity. However, populations from the west and east of the Ubangi, although in close geographical proximity show closer affiliation with populations to their west and east, respectively. This leads to the speculation that the Ubangi exerts a moderate influence as a geographical barrier, but it is less effective than the Congo, the Niger, and perhaps, even the Sanaga. Populations from the south of the Congo, separated by the rivers Kasai and Lomani have high inter-demic distances between them, and this could indicate further subdivisioning within these populations. However, this conclusion will remain preliminary until augmented by larger samples.

Among gorillas, the primary separation lies between the eastern and western gorillas. Figure 5.2 shows this separation on a map of equatorial Africa. Other divisions among gorilla populations are not as distinctive as the east-west divide. In West Africa, the Cross River population is easily separated from all the West African populations, and by logical extension, all populations from East Africa. All other West African populations from Cameroon to Central African Republic and

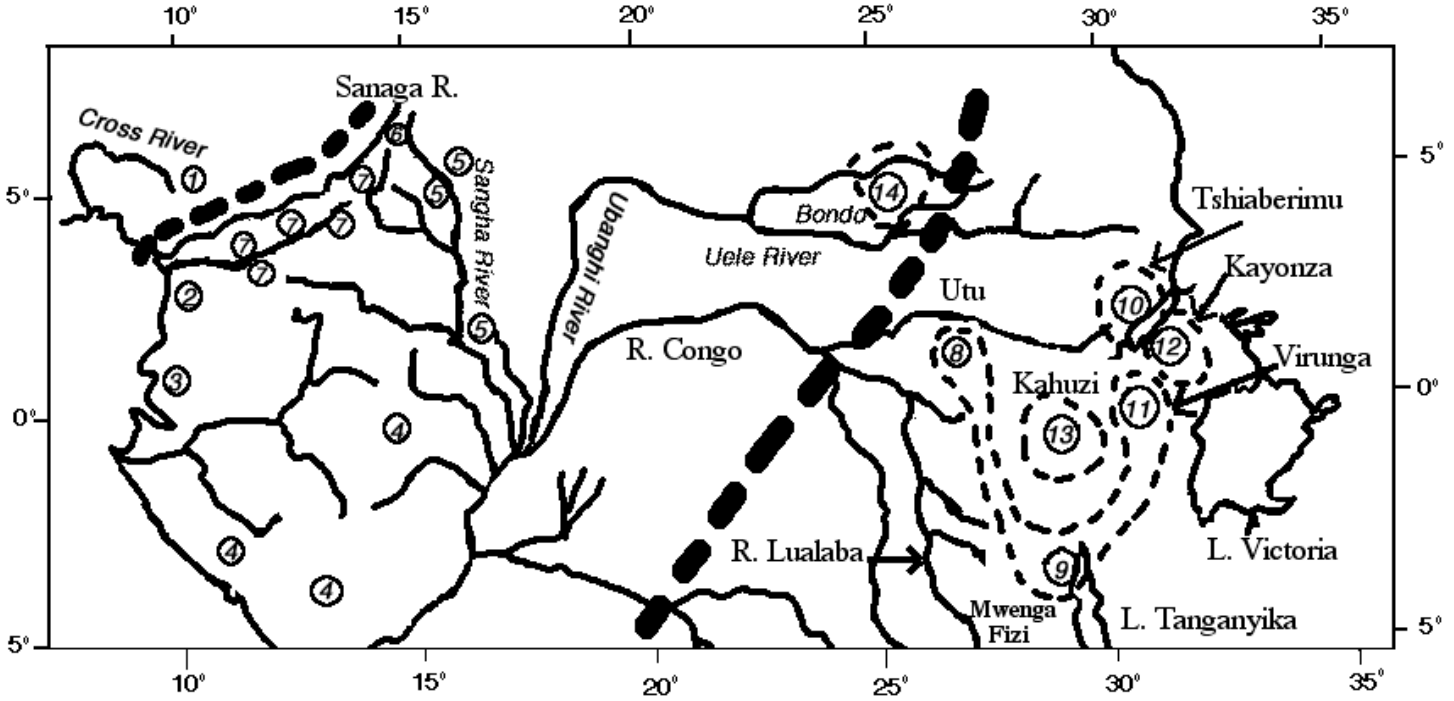


Figure 5.2 Partitioning of dental variation among gorilla populations. Strength of segmented line indicates level of difference between adjoining populations.

south of there to Angola form a single cluster. In East Africa, the only recognizable cluster is between the lowland populations from Utu and Mwenga-Fizi. However, the Virunga population, a highland population with similar inter-demic distances also falls within this cluster. The populations from Tshiaberimu, Kahuzi and Kayonza have high inter-demic distances and are distinct from one another, although Kahuzi and Tshiaberimu are slightly closer to each other. It is notable that, unlike chimpanzees, the separation between gorilla populations does not coincide with geographical barriers, such as rivers. The East and West African populations, which are the best differentiated of gorilla populations, are marked by a gap in distribution. In West Africa it is possible that the River Sanaga plays a role in separating the Cross River population from the other West African populations, but its role can be inferred only because it is known to separate several other vertebrate taxa (Grubb, 1982). In East Africa it is commonly thought that altitude differences are important for differentiating gorillas, yet, on the one hand, populations at similar altitudes are distinct from one another (Virunga and Kayonza); and on the other populations from low and high altitudes (Utu and Virunga) are similar in dental morphology.

Comparison with extablished taxonomy

The traditional view of chimpanzee taxonomy (Hill, 1967; 1969) recognizes populations on either side of the Congo River as distinct species, with the populations on the north of the Congo, subdivided by the rivers Niger and Ubangi, recognized as subspecies (Hill, 1967; 1969). The patterning of dental diversity in

this study provides only partial support for this traditional view. The main point of departure is that variable levels on intragroup variation characterize the traditionally recognized subspecies of *P. troglodytes,* and thus, as a taxonomic category the subspecies are not equivalent. Previous craniometric studies have not shown these results (Shea & Coolidge, 1988; Shea & Groves, 1987; & Shea *et al.*, 1993). In this study the West African *P. t. verus*, in particular, is characterized by low levels of diversity and is well diverged from the others, and *P. t. troglodytes* and *P. t. schweinfurthii* have higher levels of diversity and are closely related. The distinct status of *P. t. verus* has been alluded to by several studies (Uchida, 1992; Braga, 1995; Morin *et al.,* 1994; Gonder, 2000; Groves, 2001), most strongly by the mtDNA studies (Morin *et al.,* 1994; Gonder, 2000). The affinity between *P. t. schweinfurthii* and *P. t. troglodytes* has been recorded, only recently, by a mtDNA study (Gonder, 2000). Thus, the results of this study agree with several previous studies, but not so well with craniometric studies.

The widely accepted view of gorilla taxonomy recognizes one species and three subspecies: one in West Africa, one in the lowland region of East Africa and one in the highlands of East Africa (Groves, 1970b). The eastern lowland subspecies (*Gorilla gorilla graueri*) is considered to be intermediate between the other two. The results of my study do not support this taxonomy, which was based on a craniometric study. The highland subspecies, *G. g. beringei* cannot be differentiated dentally from the lowland subspecies, *G. g. graueri*. More importantly, only two major lineages of gorillas are recognized in this study, with

the Great Divide of the Congo River separating the two: those from west Africa and those from east Africa. Several mtDNA studies have suggested that the eastern and western gorillas are distinct enough to be designated separate species (Ruvolo *et al.*, 1994; Saltonstall *et al.*, 1998; Jensen-Seaman & Kidd, 2001). A recently revised taxonomy reflects this view (Groves, 2001). My study also recognized the Nigerian gorillas from the Cross River area as distinct from other West African gorillas (see also, Stumpf *et al.*, 1998; Sarmiento & Oates, 2000). Once again, the patterns of dental study revealed by my study are supported by several studies, particularly by mtDNA analyses. However, my odontometric results do not agree with the results of craniometric studies.

The results of my study indicate that, on the whole, dental morphology is capable of revealing patterns of population diversification in the African apes. Levels of dental similarity show excellent correspondence with known levels of population differentiation in these apes. This finding has implications for the use of dental morphology for studying historical processes such as phylogeny reconstruction at the supraspecific level. The role of dental morphology in phylogeny reconstruction is discussed below.

Biogeography

Chimpanzees and gorillas dwell principally in the tropical forests of equatorial Africa. Within these forests they are found clustered with several other mammalian taxa in areas described as biozones or Centers of Species Richness (Grubb, 1982). It is believed that these biozones are refugia (Haffer, 1977; 1982) –

centers with self-sustained and stable environments that were able to withstand the vicissitudes of the Pleistocene climate in Africa, and thus offer protection to the biotic community clustered within. Refugia theory (Haffer, 1982), as well as the closely related Habitat theory (Vrba, 1992), suggests that all living forms have a close relationship with their habitat and respond to climatic fluctuations that cause a disruption in their habitat by vicariance (redistributing themselves within the fragmented habitat) or dispersal into refugia. When the climatic "crunch" is over migration and dispersal takes place again. The level of species richness in an area helps to identify past refugia. It is possible that present-day distribution patterns of chimpanzees and gorillas are closely related to past climate and a history of their tropical habitat. The patterns of dental diversity in these apes can be explained by examining their biogeographic history.

In support of the Refugia theory there are several lines of evidence to suggest that after about 2.8 million years the climate in Africa became dependent on the glacial and interglacial cycles of the northern hemisphere (deMenocal, 1995; deMenocal & Rind, 1993; Partridge, *et al*., 1995; Maley, 1996). In response to the advancing and retreating of ice sheets in the upper latitudes, local climate in Africa went through cooler and arid, and warmer and wetter periods, respectively (Livingstone, 1975; 1993; Hamilton, 1992; Bonnefille, Roeland & Guiot, 1990; deMenocal, 1995; Maley, 1991; 1996; Nichol, 1999). Evidence for this comes from aeolian dust deposits (deMenocal, 1995; Maley, 1996), lake sediments (Talbot *et al*., 1984), ancient sand dunes (Nichols, 1999), deep-sea cores (Hamilton, 1992;

Livingstone, 1993), and fossil pollen (Maley, 1996). The last glacial maximum, at about 18,000 years ago, is thought to have been the most severe (Livingstone, 1993; deMenocal, 1995; Maley, 1996). Haffer (1977; 1982) and others have suggested that the adverse climatic conditions of the glacial periods led to the formation of refugia. The existence of these refugia cannot be confirmed directly but Kingdon (1971) has suggested that the large faunal areas in present-day Africa mark the presence of past refugia.

Based on the distribution of forest mammals in Africa today, Grubb (1982; 1990) identified five large faunal regions as Centers of Species Endemism (also called biozones or Centers of Species Richness). They correspond with the large forest blocks in Africa: West Africa, West-Central Africa, East-Central Africa, East Africa, and South Central Africa (Figure 5.3). The West African Center includes upper Guinean forests and the Liberian and the Gold Coast center. The West-Central Center is situated west of the Congo River and includes all the West-Central forests including Bamenda Highlands, Rio Muni and the Oogue area. The East-Central Center includes the forests north and east of the great bend the Congo River and includes the Kivu and Ubangi-Uele region. The Eastern Center includes forests east of the Rift Valley, and the South-Central Center includes the forests south of the Congo River.

Not all African mammals can be assigned to these Centers, however. Several endemic taxa are found outside the major centers. Grubb (1982) suggested that in addition to the major centers there are other minor centers that are linked to

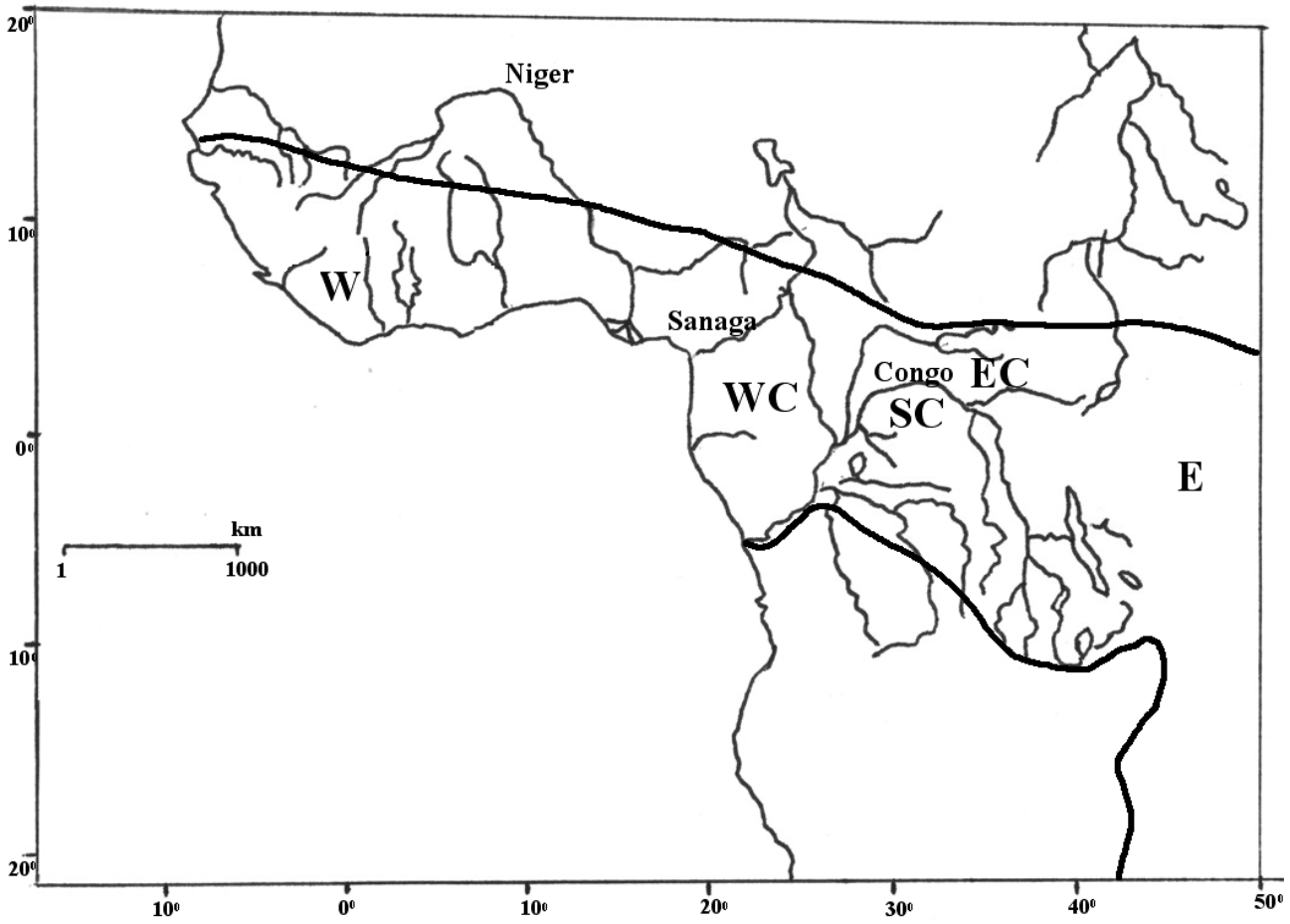


Figure 5.3 Distribution of Centers of Species Endemism in tropical Africa: Western (W), West-Central (WC), East-Central (EC), South-Central (SC) and Eastern (E). Adapted from Grubb, 1982; 1990.

the major ones, and there is an understanding that these were peripheral Pleistocene refugia. The composition of some centers is more complex than what is suggested by Grubb's (1982) distribution. The East-Central Center, for example, seems to have had several interconnected centers that followed the tributaries of the Congo River, rather than one large core area (Colyn, Gautier-Hion & Verheyen, 1991).

The understanding that the present faunal centers are remnants of Pleistocene refugia is further complicated by the fact that several geographical barriers, such as rivers influence the present-day distribution of African mammals. In addition, other influences such as the vagility of mammals, interspecific competition, and vegetational zones can affect distribution patterns (Oates, 1988). In conclusion, although geological and climatic history can be used to explain patterns of diversity and dispersal, other factors related to the species evolutionary and adaptive history are also influential.

The pattern of diversity displayed by chimpanzees in this study can be understood partly by the Plio-Pleistocene refuge theory. The lower levels of diversity seen in the West African chimpanzee, *P. t. verus*, for example, can be explained as a bottleneck event and a history of past isolation. The divergent status of this group is shared by several other taxa from the Western Center of Endemism. A listing of endemic taxa in this region (Grubb, 1982) shows that a high number of endemics and isolated subspecies are found here. The percentage of the fauna that is discretely within this center is higher than the other centers (except the Eastern center). The River Niger, however, does not serve as a major faunal barrier. The

number of taxa limited by this river (that are not found on the other side) are not as high as that limited by the Sanaga. The distinct status of West African chimpanzee in this study suggests that even if not the Niger, a barrier of some sort promoted its isolation in West Africa and limited its dispersal.

The role of the Sanaga as a dispersal barrier is remarkable. Although it is not as large as the Niger, it serves to separate at least 12 or 13 primate taxa along its main body (Grubb, 1990). The apportionment of dental diversity in this study suggests that it probably had a causative role in isolating populations of *P. t. vellerosus* from populations in southern Cameroon.

The distribution of bonobos along the south of the Congo River appears to be influenced partly by its Plio-Pleistocene history and partly by the barrier provided by the river. According to Grubb (1990), in terms of the number of primate taxa that are confined to one bank and not seen on the other, the Congo River exerts the greatest overall impact on the distribution of African primates. Bonobos are confined to the swampy inner basin of the river, but several other dominant and versatile taxa have used the river system to spread out (Kingdon, 1989). Kingdon (1989) believes that levées and sump-lands in the inner Congo basin helped bonobos to survive several arid periods within this habitat, but it probably had a more diverse habitat in the past.

The results of this study indicate that without the influence of strong extrinsic barriers such as rivers to limit their distribution, chimpanzee dispersal continues unchecked. The dental affinity between West and Central African

chimpanzees suggests the absence of a strong barrier. In a study measuring levels of genetic diversity in chimpanzee populations from Eastern Africa, Goldberg (1998) found that, contrary to expectation, populations located within Plio-Pleistocene forest refugia do not exhibit higher genetic diversity than those of other populations. This finding suggests that chimpanzees lived both in and out of refugia during periods when tropical forests were confined to refugia (Goldberg, 1998). Goldberg suggests that the extreme vagility of the species makes them capable of maintaining gene flow across varied habitats.

The gorilla distribution patterns is as complex as chimpanzees, and cannot easily be explained merely by the Plio-Pleistocene refuge theory. In West Africa gorilla populations are found within the Western Center of Endemism. Given the role of the Sanaga River as a major faunal barrier, populations separated by the Sanaga are predictably distinct from the other western populations. All the other western populations, however, form a fairly cohesive cluster, especially if one compares these populations with gorilla populations from East Africa. In East Africa gorillas are found widely separated from the western populations. Populations are found in isolated pockets at variable altitudes and they are dentally distinct from one another. To understand this pattern of diversity it is important to take into account the local phenomenon of rifting that affected this region.

Along with climatic fluctuations related to global warming and cooling, the tectonic activity in the African Rift caused fragmentation of African forests. As volcanic mountains rose, lowland riverine forest was replaced by montane forest

(Coetzee, 1964; van Zinderen Bakker & Coetzee, 1972). This would cause vicariance or dispersal of lowland adapted taxa (Colyn *et al*., 1991).

Paleoenvironmental evidence also suggests that the last glacial maximum caused a drop in temperatures in East Africa, ranging between 8^0C to 2^0C (Coetzee, 1964; van Zinderen Bakker & Coetzee, 1972; Bonnefille *et al.*, 1990). This additionally would have led to a lowering of montane forest at the expense of riverine forest (Colyn *et al*., 1991). Although it is not clear how taxa such as gorillas adapted to such severe changes in climate and habitat, Colyn *et al*. (1991) suggest that the presence of minor refuges in the East Central region reflect the fact that taxa did not conglomerate in major refugia but dispersed into several nuclei around the main river system. Kingdon (1989) suggests that the highlands provided an important retreat for the gorillas because gorillas were able to exploit the vast quantities of low-level herbage available within the changed highland habitat. Jensen-Seaman & Kidd (2001) place the split between lowland and mountain gorillas in East Africa at about 380,000 years, indicating that the split did not coincide with the last glacial maximum of 18,000 years ago, but was probably either due to an earlier Pliocene or Pleistocene arid phase, or associated with vicariance resulting from tectonic or volcanic activity along the rift. Groves & Stott (1979), citing volcanic data suggest that the dispersal of gorillas from west to east took place much earlier than 100,000 years ago. Finally, Schaller (1963) suggests that the eastern and western gorillas maintained contact until recently, but the level of divergence seen in this study precludes this suggestion.

Size

Large size is the distinguishing hallmark of hominoids of modern aspect. It is a character that can be used by direct observation to differentiate the African apes. Bonobos are smaller than chimpanzees in some respects, which in turn are smaller than gorillas. Western gorillas are smaller than eastern gorillas. Size is an also an important criterion used in differentiating Miocene ape species (*e.g*., species of *Proconsul*, Walker *et al.*, 1993; and *Sivapithecus*, Ward, 1997). Considering its utility for fossil species differentiation it is instructive to examine how size affects patterns of dental diversity in the African apes.

In differentiating the species of chimpanzees in this study when untransformed dental variables were used, the two species were classified with an accuracy of about 91%. The single discriminant function had a high correlation with overall dental size. When the variables were transformed into shape variables, thus excluding the differences in absolute size, classification accuracy fell to 79% and the correlation of the discriminant function with tooth size was considerably weaker (Table 3.9). This indicates that in molar dimensions it is absolute (isometric) rather than allometric size that differentiates the species. In average dental dimensions *P. troglodytes* is about 18% larger than *P. paniscus*. In dimensions of canines however, *P. troglodytes* is about 30% larger. The sexual dimorphism ratio (male:female canine height) does not differ between the species but bonobos have much smaller canines than chimpanzees. Dental size presents an important criterion for differentiating chimpanzee species, however size differences

are not maintained isometrically throughout the dentition. When shape transformed variables were used in differentiating the four subgroups of chimpanzees (three subspecies of *P. troglodytes* and *P. paniscus*), intergroup distances separating the western chimpanzee from the others were greater than that separating bonobos from the subspecies of chimpanzee. Thus, while size differences are useful for differentiating the two species, the other distinctive subgroup, the western chimpanzee is most clearly differentiated by shape factors.

Tooth type	**Discriminant Accuracy**	**Explained variance**	**Correlation with GM**
Raw Variables			
LM1	86%	0.71	0.50
LM2	86%	0.73	0.45
LM3	85%	0.67	0.47
UM1	91%	0.76	0.24
UM2	89%	0.74	0.18
UM3	82%	0.66	0.19
Average	**87%**	**0.71**	**0.34**
	Discriminant Accuracy	**Explained variance**	**Correlation with GM**
Shape variables			
LM1	82%	0.66	0.09
LM2	79%	0.64	0.19
LM3	80%	0.61	0.08
UM1	90%	0.74	0.02
UM2	85%	0.67	-0.15
UM3	83%	0.67	-0.13
Average	**83%**	**0.67**	**0.02**

Table 5.1 Summary of discriminant analysis of eastern and western gorillas using raw and shape variables

Size is not as important for differentiating gorillas dentally. If we consider the eastern and western subgroups as separate species (so as to provide a comparison with chimpanzees), dental dimensions can help classify them with an

accuracy of 87% (Table 5.1), but the disciminant function does not have a high correlation with overall tooth size (0.34). When the raw variables are changed to shape variables, classification accuracy falls only slightly to 83%, the percentage of variance explained is not much different (drops from 71% to 67%), but the discriminant function has a non-significant and weaker correlation with the Geometric Mean. Size plays some role in differentiating the two groups but its influence is not strong. Moreover, the two groups are just as easily differentiated using only shape variables, signaling the role of this factor in influencing separation. Sexual dimorphism in canine size is high in gorillas, but molar sizes are maintained in isometric proportion between the sexes.

In conclusion, although size is an important biological criterion for maintaining variation, and it is useful in differentiating the African apes at the supraspecific level it is not very influential at the infraspecific level.

Diet

Teeth being intimately connected with mastication it is expected that dental morphology reflects dietary preference. This is a valid assumption and a useful one for reconstructing the paleodiet of extinct forms. To assist in this reconstruction, Kay (1975, 1977), Hylander (1975a, 1975b) and Kay & Hylander (1978) studied the dentition of living primates with known dietary preferences and outlined morphological features on the dentition that are associated with diet. Their studies suggest that, compared with frugivorous primates, folivores have (1) smaller

incisors (2) well-developed shearing crests on molars (3) taller molar cusps (4) wider mesiobuccal development grooves on lower molars (5) mesiobuccally oriented anterior transverse crest on upper molars, and (6) long and buccally placed cristid obliqua on lower molars.

Many of these morphological features are visible on the dentition of the African apes, and can be used to infer the role of diet in causing differences in dental pattern. Dental features differentiating bonobos from chimpanzees include a wide mesiobuccal development groove on lower molars, a buccally placed cristid obliqua making a wide angle with the distal cusps, a mesiobuccally oriented anterior transverse crest on UM1, and mesiodistally and buccolingually narrower incisors. Kinzey (1984) has suggested that dental characters such as these imply a more folivorous diet for bonobos. However, similar characters differentiate the West African, *P. t. verus* from the other subspecies. In particular, a buccally placed cristid obliqua and a wide mesiobuccal development groove are found in the lower molars of this chimpanzee.

It is curious that folivory-related characters are visible on the dentition of the bonobo, although it is predominantly frugivorous in dietary preference, but incorporates a small herbaceous component to its diet as a fall back food (Badrian & Malenky, 1984). Yet, these characters do not help to distinguish the mountain gorilla from the other gorillas, although the former is an obligate folivore and consumes high-quality terrestrial herbs throughout the year (Schaller, 1963; Watts, 1996; Fossey & Harcourt, 1977; Doran & McNeilage, 1998). Mountain gorilla

incisors are narrower than western lowland gorilla incisors (Table 4.14), which is presumably related to the seasonal frugivory of the western gorilla (Remis, 1997). However, other dental characters that signal folivory, such as a buccally oriented anterior transverse crest on the upper molars, wide mesiobuccal development on the lower molars, long shearing crests and high cusps are manifest more strongly in the molars of the western lowland gorilla. The only folivory-related character exhibited to a greater degree by the mountain gorilla is a buccally placed cristid obliqua on all lower molars. This provides an important shearing crest in the chewing cycle of folivores (Kay, 1975). As argued in Chapter Four, the lack of dental characters signaling extreme folivory could be due to the fact that gorillas are predominantly folivorous and therefore such characters cannot be used to differentiate them at the infraspecific level.

When dental traits of chimpanzees and gorillas are compared (Table 5.2), it is seen that gorillas have wider developmental grooves on the lower molars, but other dental traits related to folivory are not prominent. On the whole, establishing dietary correlation using discrete dental traits seems tenuous.

Drift

Discrete dental traits are of immense utility in taxonomy and phylogenetic reconstruction. In this study, quantitative and qualitative dental measurements, although constituting independent sets of data, showed similar results regarding patterns of population differentiation in the African apes. Following a multivariate cluster analysis using such discrete traits, I was able to use a univariate chi-square

Character	Gorilla	Chimpanzee	Chi-square probability
UM1cta buccally directed	14%	42%	.00000
UM2cta buccally directed	14%	25%	.00041
UM3cta buccally directed	7%	9%	.00631
LM1 wide mesiobuc dev groove	99%	67%	.00000
LM1 wide distobuc dev groove	43%	4%	.00000
LM2 wide mesiobuc dev groove	98%	60%	.00000
LM2 wide distobuc dev groove	85%	15%	.00000
LM3 wide mesiobuc dev groove	96%	58%	.00000
LM3 wide distobuc dev groove	42%	2%	.00000

Table 5.2 Frequencies of discrete dental traits that show dietary correlation in chimpanzees and gorillas.

test to identify the traits that differentiated subgroups of African apes. Several of these "affinity-indicator" traits have no apparent functional value or selective advantage (some such traits are described in detail in Chapter Six). I assume, therefore, that the manner in which they vary and covary within populations is driven by the random forces of genetic drift. Drift is a powerful evolutionary force that influences phenotypic variability, and can be indicative of isolated populations that have experienced a bottleneck.

In this study the role of drift is invoked, in particular, to explain the fluctuating frequencies of discrete dental traits in chimpanzees from West Africa. Several traits (from the anterior dentition, and accessory cuspules on the molars) are found at a higher frequency within this subgroup than the species, *P. troglodytes* (Table 3.17). This finding, coupled with the finding that overall dental

diversity is lower within this subgroup than the species point to a reduction in the gene pool following a population bottleneck and subsequent isolation of the group.

Discrete dental traits that differentiate bonobos from chimpanzees are also presumably driven by genetic drift. As in *P. t. verus* several differences are seen on the anterior dentition (Table 3.11). It is remarkable, however, that despite a long history of isolation and lack of contact between them (molecular studies place the split between these two species at about 2.5 million years ago, Ruvolo, 1996), the traits do not have a discrete pattern of appearance. Rather, they are polymorphic in nature within both species, the difference being in the frequency of occurrence of traits. This is indicative of the high levels of diversity inherent in this genus (and probably all hominoids) and suggests that the founder population that migrated and dispersed along the south of the Congo River was probably large.

Among gorillas discrete dental traits most clearly separate the eastern and western lineages (Table 4.11). The eastern populations also differ from each other in several traits, and each display low levels of dental diversity as calculated using the CV and R%. These finding are indicative of isolation and drift within these populations. However sample sizes for some of the populations are small and often the subspecies and population are identical. Therefore, these results could be due to sampling.

Phylogeny

It is inevitable that at least some aspects of their shared evolutionary history will be reflected in the patterns of dental diversity of the African apes. In chimpanzees and gorillas, for example, canine size dimorphism is high. Gorilla male upper canines are about double the height of female upper canines and male lower canines are about 60% taller than their counterpart from the lower jaw (Table 4.14). In length and breadth dimensions the difference is also marked (male dimensions are 30% to 40% greater). Sexual dimorphism is not as marked in the other teeth.

Bonobos are smaller than chimpanzees in all dental dimensions, but canine dimorphism index is about the same in both species (Table 3.10). Upper canine dimensions are about 20% greater in males and in the lower canine the dimensions are about 17% greater. Compared to gorillas, chimpanzees show reduced canine dimorphism. This reduced dimorphism could signify a trend culminating in the reduced dimorphism seen in modern humans. Conversely, it could suggest that gorilla canines show a trend towards increased dimorphism compared to chimpanzees. Just as in gorillas, dimorphism in premolar and molar dimensions do not differ markedly between the sexes in chimpanzees.

Intragroup variation and modes of speciation

Gorillas and chimpanzees differ markedly in the partitioning of variation within the taxon. Figure 5.4 displays the contrast in the CV of LM2 dimensions. CVs were calculated by averaging the values across populations, subspecies and

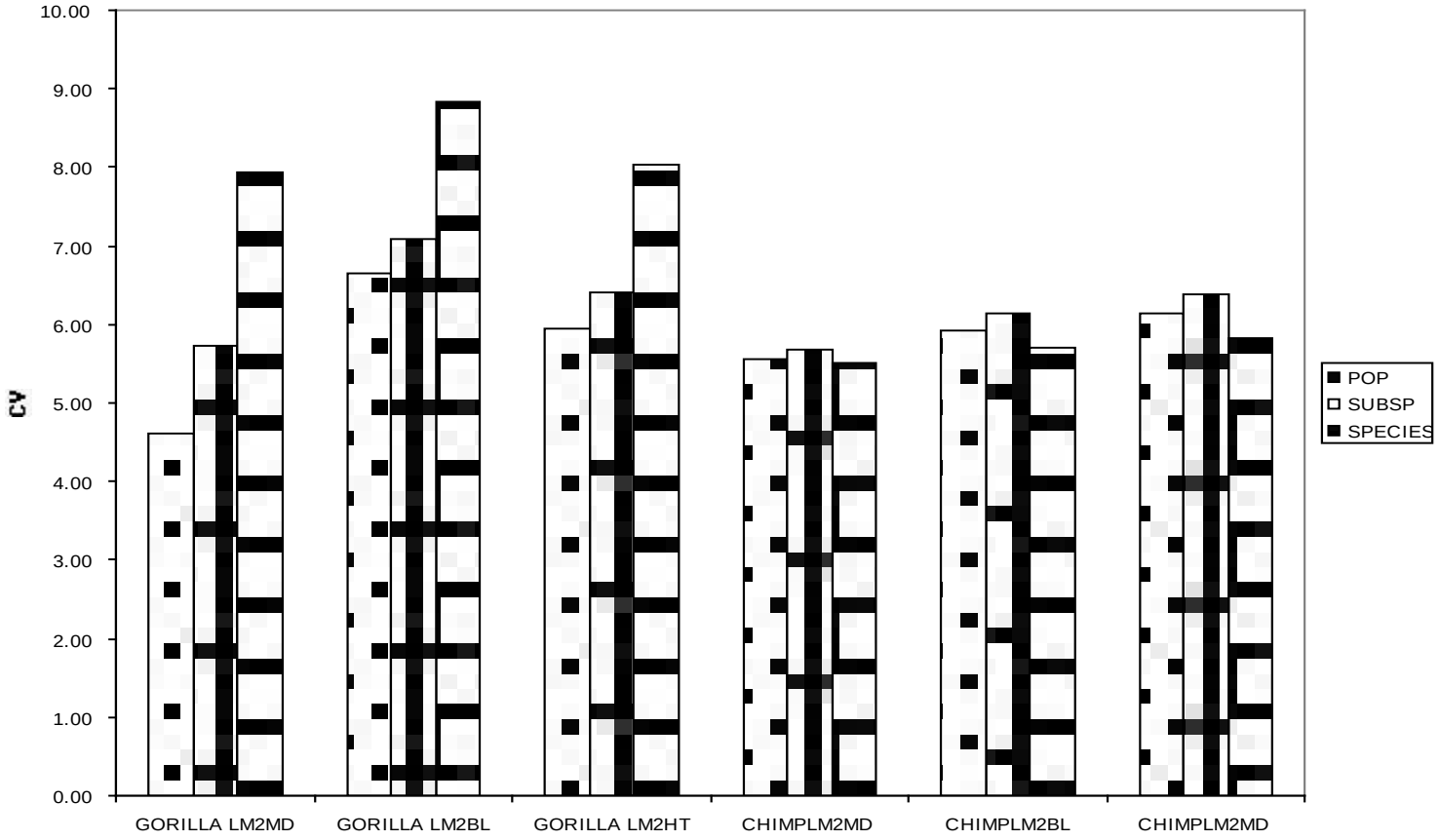


Figure 5.4 Comparison of variation in chimpanzees and gorillas

species. In chimpanzees, in general, the population is extremely diverse and most of the variation within the species is visible at the level of population. Variation does not increase significantly up the hierarchical ladder (Figure 3.7). Ranges of diversity in non-metric dental traits are also high within populations (Table 3.17). Gorilla patterns of variation follow an expected trend, whereby ranges of variation are lowest at the level of the population, but increase sequentially in the subspecies and species (Figure 4.5). In addition, the frequency of non-metric traits differs significantly between populations (Table 4.11). The levels of within group diversity are lower in the east African populations, and since the population is often synonymous with subspecies, variation does not increase with taxonomic level.

The unusual pattern of variation in chimpanzees has been alluded to previously. Shea & Coolidge (1988) remarked that in their craniometric study interdemic distances between chimpanzee subspecies were lower than comparable distances in gorillas and orangutans. To them this suggested that chimpanzees have "maintained higher levels of contact among populations than gorillas and orangutans increasing gene flow and inhibiting differentiation (Shea & Coolidge, 1988: 680). Recently Gagneux *et al.* (1999) noted that chimpanzees exhibit greater levels of variation in mtDNA haplotypes than the entire human species. This agrees with the assumption that modern humans underwent a population bottleneck resulting in a restriction of the gene pool and therefore present-day levels of variation are low (Harpending, 1994; Rogers, 1995). Gagneux *et al.* also found that variation in mtDNA haplotypes was high in a population from the Taï forest. They

suggest that the high diversity in mtDNA can be explained by the chimpanzee social structure of female-biased dispersal.

Patterns of female dispersal differ in gorillas and chimpanzees. Chimpanzee females migrate from their natal group while males remain in the group (Pusey & Packer, 1987), so that the social core is made up of related males. Sugiyama (1999) has said that although males do not commonly emigrate, male dispersal is sometimes seen. Gagneux *et al.* (2001), are of the opinion, based on the levels of genetic diversity encountered, that males must travel between groups and cause mixing of gene pools. The pattern of dental variation encountered in this study would imply that there is considerable admixture of the gene pool. It is possible that females travel extensively during their reproductive lifetime and transfer between groups more than once. However, Mitani *et al*. (2002) have said that secondary female transfer is rare in chimpanzees. The levels of diversity in all populations in this study and the panmictic nature of variation in the genus indicate extreme vagility and constant contact between populations.

The pattern of dispersal in *Gorilla* is more localized compared to chimpanzees – males either stay in their natal group, or move out and find another group to move into but do not emigrate once settled in a new group (Doran *et al.,* 1998*). Gorilla* females move out of the natal group and join another group. They transfer more than once during their reproductive lifetime (Watts, 1996), but most likely do not go far (Harcourt, 1978). As a result of this pattern of dispersal the *Gorilla* gene pool is constrained and localized causing isolation of populations, low

levels of variation within groups and high levels of diversity between groups. The gorilla pattern of dental variation agrees with this manner of dispersal. It presumably explains why gorillas have been affected by climatic fluctuations of the Plio-Pleistocene causing fragmentation of their habitat, isolation of populations, their present impoverished state and vulnerability to threats by hunters and poachers. The difference in patterns of variation suggest that chimpanzees are more versatile compared to gorillas and more likely to adjust to adverse circumstances.

In conclusion, biomechanical and social adaptations help to understand differences in patterns of dental variation between chimpanzees and gorillas.

Morphology versus molecules

Many of the patterns of population structure recognized by this study are also recognized by mtDNA studies. To provide some examples, the separation of the East and West African gorillas (Ruvolo *et al*., 1994), the distinctiveness of the West African chimpanzees (Morin *et al.*, 1994), the singularity of the chimpanzees North of the Sanaga River (Gonder *et al.*, 1997), and the separation of the Kahuzi-Biega and Tshiaberimu gorillas from the Virunga and Bwindi gorillas (Jensen-Seaman and Kidd, 2001), based on mtDNA studies, are supported by the patterns of dental variation in this study. This agreement between two unrelated datasets suggests that there is an underlying pattern of population diversification that is being revealed by these data.

Recently there has been a surge of opinion in anthropology suggesting that molecules are capable of reconstructing historical processes of divergence and

diversification, and are therefore useful for phylogeny reconstruction, whereas craniodental morphology has little value in this regard (Pilbeam, 1996, 2000; Collard & Wood, 2000). The molecules versus morphology debate has been simmering in anthropology since Goodman's (1963) molecular phylogeny of the extant hominoids opposed well-entrenched morphological opinions (exemplified in Simons & Pilbeam, 1965) and proposed that chimpanzees and humans are more closely related to each other than either is to gorillas or orangutans. Subsequent molecular studies (Sarich & Cronin, 1976; Sibley & Ahlquist, 1984; Templeton, 1984) supported Goodman's phylogeny, and cast further doubts on the morphological phylogeny, while newly emerging fossils (Pilbeam, 1979; 1982) showed that the traditional morphology-based phylogeny was flawed. Whereas new molecular phylogenies continued to show excellent concordance, simultaneous attempts at reconstructing hominoid phylogeny using morphological data did not. As emphasized by Pilbeam (2000) in a recent commentary, "During the 1980s and 1990s at least six major phylogenetic studies of living hominoids were completed by using dominantly hard and soft tissue morphological data (Andrews & Martin, 1987; Kluge, 1983; Schwartz, 1984; Groves, 1986; Hartwig-Scherer, 1993; Braga, 1995). They reached five different conclusions as to the relationships among the hominoids!" (Pilbeam, 2000: 10684). This lack of concordance between molecular and morphological phylogenies was also demonstrated with other taxa (*e.g.*, Disotell, 1996). The debate snowballed, until the original advocates of the morphological phylogeny of the extant hominoids swung their opinion in the

opposite direction and proclaimed that the value of a morphological phylogeny can only be evaluated by comparing it with a molecular phylogeny (Pilbeam, 1996, 2000, 2002). A logical extension of this viewpoint, expressed by several scholars is that morphological data are unreliable for phylogeny reconstruction and since this is the predominant type of data in reconstructing fossil phylogeny, fossil phylogenies are unreliable (Hartman, 1988; Collard & Wood, 2000; Gibbs *et al.*, 2000). In apparent support of this viewpoint Harrison (1993) pointed out that reconstructing the phylogeny of fossil species is not equivalent to that of neontological species, because in reconstructing a fossil phylogeny, one takes into account the unfolding of its phylogenetic history (*i.e.*, subsequent taxa that are phylogenetically related), but this is not (and cannot be) be considered when reconstructing the phylogeny of neontological species.

The utility of craniodental morphology for phylogeny reconstruction has been put to the test. Tattersall (1993) used craniodental characters to examine the phylogeny of the lemurs and found that the most parsimonious cladograms failed to support the established phylogeny. Hartmann (1988) attempted a cladistic analysis of extant hominoids using molars but found the functional signal to be so strong as to obscure the phylogeny. Molar characters did not support the otherwise robust molecular phylogeny.

Several explanations have been put forth to account for the poor performance of phenotypic data, and conversely the strength of molecular data, in phylogeny reconstruction (Collard & Wood, 2000; Pilbeam, 2000). As spelled out

by Pilbeam (2000) problems lie, on the one hand, in the selection of phylogenetically relevant morphological characters that are homologous, and on the other hand in attempting to reconstruct phylogenetic relationships that are "genetic relationships" using phenotypic characters.

In this study, as outlined above, conclusions regarding the population structure and patterns of diversification of chimpanzees and gorillas match the conclusions of mtDNA studies. This would suggest that dental morphology is capable of reconstructing such historical processes accurately. Most of the characters used in the study were measured on the occlusal surface of molars and care was taken to select characters that are used in recognizing fossil species. Given the general lack of confidence in dental, especially molar, characters in paleontological systematics the results of this study need to be comprehended.

Several reasons can be proposed to justify the robustness of my results: (1) Level of analysis: In contrast with previous studies, this study was performed at the infraspecific level. All units of analysis at this level are part of the primary evolutionary unit, the species, and are therefore subject to the same selective pressures. "Function" no longer has the power to obfuscate phylogeny because the functional signal affects all units uniformly. To provide an example, on the whole, it was difficult to identify the role of diet in separating populations because characters related to diet are ubiquitous for the entire group and are therefore phylogenetically uninformative. Significantly, none of the dental characters differentiating mountain gorillas from lowland gorillas could be correlated with

extreme folivory because the entire genus has a preference for folivory.

Size provided an important criterion for separating groups. The most striking difference between bonobos and chimpanzees was related to size. This is not surprising since it signals a divergence due to migration or isolation and a break away from the common forces of selection.

(2) Vastness of the data set: This results of this study were based on multivariate analyses of about 200 quantitative measurements, most taken on the occlusal surface of the molars, and about 200 qualitatively coded characters studied throughout the dentition. Unlike the case with molecular data, problems with determining homology are known to pervade morphological data (Cartmill, 1994; Lieberman, 1999). Problems with character definition and replicability result in poor resolution of phylogeny (Pilbeam, 2000). There seems to be no simple solution for circumventing this problem in morphology, apart from isolating the genes for morphological characters. One possible solution, adopted here, is to use a large enough data set so that the phylogenetic signal will prevail over the din of homoplasy. As shown in this study, dental characters differentiating subgroups can be identified in most teeth. Taxa are differentiated, however, not merely by the presence or absence of particular dental characters but by the frequency of occurrence of variable states. Given the high levels of diversity, especially in the African apes, attempting to isolate characters that are phylogenetically relevant at the outset of the study may be futile. It is significant that by using a large number of soft-tissue characters Gibbs *et al.* (2000) were able to build a robust phylogeny

for the modern hominoids that matched the molecular phylogeny.

(3) Representative samples: The patterns of dental variation were studied using representative samples from the entire range of distribution of the African apes. This provides an understanding of the entire gamut of diversity within each group. Subgroups with a unique pattern of variation that diverge from the norm are easily identified. For example, although it suffers from a poor sample size, this study recognized populations bounded by the Kasai and Lomani rivers on the south of the Congo River as being distinct from other populations of *P. paniscus*. These centers have independently been identified as Centers of Endemism. The West African chimpanzees also showed remarkable divergence from all other populations. Given the reduced diversity within the West African chimpanzees, if only these were used to represent the species (and this is entirely plausible since more than 400 craniodental specimens for this group are available in museums) this will lead to a biologically inaccurate interpretation of the levels of diversity within the species.

Ultimately, however, the results of this study indicate that a phylogeny using morphological or molecular data can be deemed robust or weak not by fiat based on the whether morphological or molecular data was used in reconstructing it, but by judging its merits on a case by case basis, by empirically comparing the phylogeny with other independent phylogenies.

Patterns of dental variation and levels of differentiation

It is common practice in mtDNA studies to take genetic distance from one group to justify taxonomic revision in another group. Ruvolo *et al.*, (1994), for example, found that the genetic distance between the East and West African gorillas is greater than the distance between the two species of chimpanzees, and therefore proposed that the gorillas should be recognized as distinct species. Morin *et al.* (1994) suggested elevating *P. t. verus* to the rank of a species (*P. verus*) based on their finding that genetic distance between this and the other subspecies of *P. troglodytes* is far greater than the distance separating the other subspecies from each other. They indicate that, "*P. t. verus* is more differentiated from the other two subspecies than are some full species of mammals" (Morin *et al.*, 1994: 1199).

This yard stick approach, where distance between two distinct taxa is used as a comparative guideline for judging distances between two other taxa, is problematic. Avise (1994) has cautioned against such an approach stating that no consistent standard can be found among vertebrates. As explained by Jolly *et al.* (1995), "From a 'frog's point of view,' the genetic distinctness of the western chimpanzee would appear trivial, while from a 'bird's eye view,' it would suggest separation at the family level" (Jolly *et al.*, 1995: 185).

So how does one account for this pattern of unequal levels of differentiation in taxa that are at the same taxonomic level? If *P. t. verus* is well separated from the other subspecies, while *P. t. troglodytes* and *P. t. schweinfurthii* show a close affinity, as was found in this study, are we justified in regarding them all as

subspecies? In *Gorilla* several populations in East Africa were found to be distinct from one another and they are often regarded as subspecies. The West African gorilla populations are not so distinct from one another. Should all the East African populations be designated subspecies?

Part of the answer lies in understanding the subspecies as a taxonomic category. Whereas a species is considered to be a discrete entity well diverged and easily identified, the examples in this study would suggest that a subspecies is a taxonomic unit of convenience – a category that holds groups with varying levels of diversity and distinctness, that are not distinct enough to be called a species. It could be a population that is well-diverged (the West African chimpanzee) or populations barely diverged from each other (West-central and Central African chimpanzee). There is no implicit assumption that the subspecies will evolve into the species. Given the difficulty in determining whether a taxon has a cohesive gene pool and can therefore be considered a species, a distinctive population is likely to be recognized as a species only by consensus opinion. That is, the hallmark of a species is convergence of opinion, based on several systems of data, whereas when opinions regarding distinctiveness are not unanimous it could signify a subspecies.

An understanding of what constitutes a subspecies can also be gained by looking at the history of the species. Gorillas are inherently restricted in their range of movement, are faced with habitat fragmentation, and are more likely to get isolated and diverge from other populations. Consequently the level of

differentiation seen in gorilla populations cannot be compared with chimpanzee populations that maintain contact and are not easily differentiated. A yardstick approach that takes the level of differentiation from one group and uses it to suggest taxonomic separation in another group (*e.g.*, Ruvolo *et al.*, 1994) suffers from a lack of appreciation of the unique evolutionary and biogeographical history of the group.

If subspecies are fluid and variable categories in the neontological context, can they be used to recognize subspecies in fossil context? Should subspecies be diagnosed in the fossil context? A simple answer to this question is that subspecies are not reliable categories in the extant context and therefore should not be used as models for paleontological subspecies. Subspecies do however serve a purpose in the extant context of providing a holding stage for populations that are differentiating but are not distinct. As explained by Mayr (2000) subspecies convey the concept of close relationship and allopatry. Although it is not advisable to use extant subspecies to determine ranges of variation in fossil subspecies, subspecies in the fossil context could serve the same purpose as in the extant context and be diagnosed in the same manner – a taxonomic category below the level of the species that is different but not distinct enough to be a species. The lack of complete differentiation signifies a pattern of mosaic evolution (Mayr, 2000). Translated into the fossil context, a lack of consensus among researchers about the proposed species status for fossil population could signify mosaic evolution.

Utility as models

Patterns of dental variation differ strikingly between chimpanzees and gorillas. The differences can be tied to differences in modes of speciation and the unique evolutionary history of the apes. If these taxa are used as models and applied to understanding patterns of variation in fossil species, a different understanding regarding the nature of variation in fossil species is likely to emerge depending on whether a chimpanzee or a gorilla model is used. In general, if a gorilla model is used, specimens from different localities are likely to be recognized as distinct species. The high level of intergroup variation in gorillas predicts that there will be little debate regarding taxonomic schemes. With a chimpanzee model, on the other hand, paleontologists are likely to overestimate species numbers initially. Fossils from different geographical localities are likely to be designated as separate species when first discovered, but with the discovery of additional material and a greater display of within-group diversity there is likely to be disagreement regarding the taxonomy.

Interdemic distances between humans have been reported to be low in craniometric studies (Howells, 1973). Humans also exhibit high levels of variation within populations (Nei, 1975; Lasker & Crews, 1996), and are similar to chimpanzees in this respect. If chimpanzee levels of diversity can be related to their social structure, which promotes a panmictic nature of gene flow, it suggests that in order for humans to maintain such levels of diversity the social behavior of early hominids was the similar to chimpanzees. Ghiglieri (1987), and Di Fiore & Rendall

(1994) completed a phylogenetic analysis of social organization in primates and posited that early hominin social organization was based on female exogamy and male retention in the natal group, a social organization similar to *Pan*. It is quite possible, therefore, that high levels of variability in *Pan* and *Homo* are retentions from a last common ancestor. This, in turn, indicates that a chimpanzee model of dental variation will be especially suitable for applying to fossil hominin species. A gorilla model on the other hand is likely to result in an overestimation of the number of fossil hominin species.

Application to Miocene hominoids

This study has shown that patterns of dental variation within extant species vary according to principles that are intimately connected with the phylogenetic and biogeographic history of the species. Ackermann (2002) studied patterns of craniometric variation in the African apes and humans and found, likewise, that patterns of variation differ in these taxa, but reflect the phylogenetic history of the apes. Considering the unique evolutionary pathways of all modern taxa, the utility of individual models from the extant context for applying to fossil species recognition is limited. Taxa that are phylogenetically related are likely to be more efficacious for reconstructing fossil patterns of variation than taxa that show structural and adaptive similarity. For understanding patterns of variation in the Miocene hominoids, therefore, common principles and generalities regarding patterns of dental variation in all extant hominoids are likely to serve as a more useful models than any one modern hominoid group. Future work documenting

patterns of dental variation in orangutans and gibbons will help build such models. Until then, although the extant African apes can be used to make hypotheses regarding the taxonomy of the Miocene apes, these will probably be deficient. In the next chapter patterns of dental variation in all four extant hominoid genera, *Pan*, *Gorilla*, *Pongo* and *Hylobates* are applied to examining the utility of a single taxonomic character, lingual incisor morphology, that demonstrates such an approach for differentiating Miocene hominoid species.

CHAPTER SIX

Assessing the utility of incisor morphology for discriminating fossil species

Introduction

Patterns of dental diversity in the African apes differ in ways that reflect their unique modes of speciation, related to their particular evolutionary trajectories. Their utility for understanding patterns of variation in fossil species is limited, therefore, especially since fossil species could likewise differ in patterns of variation. Given this situation, it was suggested in the previous chapter that drawing common themes from several extant taxa is likely to be of greater use in developing models for applying to assessing the taxonomy of Miocene hominoid species. Accordingly, in this chapter, all four extant apes (gibbons and three great apes) are used for understanding the nature of diversity in incisor morphology.

Background

Due to the complexity of molar crowns and the greater representation of molars in the fossil record, molar morphology is traditionally used in differentiating fossil species. The morphology of the anterior dentition has not received as much attention, although there are notable exceptions (Hrdlicka, 1920; Dahlberg, 1949; Coon, 1962; Trinkaus, 1983; Trinkaus & Howells, 1979; Harrison, 1986; 1988; Simons, 1986). In the last decade the morphology of the lingual side of the upper central incisor has been made a prominent taxonomic characteristic in Miocene hominoid systematics. Begun (Begun *et al.*, 1990; Begun, 1992) differentiated the late Miocene Spanish hominoids *Dryopithecus crusafonti* from *Dryopithecus*

laietanus mainly on the basis of lingual incisor morphology. *Dryopithecus crusafonti*, he claimed, was characterized by narrow and high-crowned upper central incisors with well developed median and mesial lingual pillars separated from each other and the distal cingulum by deep fissures. *Dryopithecus laietanus*, on the other hand, had a low-crowned I^1 without a lingual pillar. Martin & Andrews (1993) suggested that lingual incisor morphology could be used to recognize two species of hominoids at the middle Miocene site of Pasalar in Turkey. A lingual pillar, according to them, characterized the most commonly occurring species, *Griphopithecus alpani*, while the lack of pillar distinguished the other, rarer species. More recently, Ward *et al.* (1999) used lingual incisor morphology to recognize *Equatorius*, a new genus from Kenya and differentiate it from *Kenyapithecus*. *Kenyapithecus*, they said, has a derived pattern of incisor morphology with upper central incisors having marginal ridges on the lingual side, but no foveae, while *Equatorius* has the more primitive lingual morphology comprised of median lingual tubercle flanked by foveae. A difference in morphology was also recognized in the upper lateral incisors. Ward *et al.* (1999) claimed that since lingual incisor morphology of *Kenyapithecus* was similar to that seen in the less common, unnamed species from Pasalar, there was a phylogenetic relationship between the two to the exclusion of *Equatorius*. If *Equatorius* were placed in the same genus as *Kenyapithecus* it would constitute a paraphyletic grouping. They, therefore, placed *Equatorius* in a distinct genus.

This focus on lingual incisor morphology for taxonomic purposes marks a departure from the usual focus on molars in Miocene hominoid systematics. Miocene hominoids are notorious for having homogeneous molar morphology (Kelley & Pilbeam, 1986), and attempts at using linear dimensions of molars for identifying species numbers (Kay, 1982b) have proved to be unsatisfactory (Cope & Lacy, 1992; Plavcan, 1993). However, the utility of lingual incisor morphology as a taxonomic character has not gone without criticism. Harrison (1991) criticized Begun *et al*.'s (1990) diagnosis of *D. crusafonti* arguing that the lingual incisor morphology differentiating the two species was likely to be due to intraspecific variation, probably stemming from inter-populational differences. Ribot *et al.* (1996) conducted a comparative study of lingual incisor morphology in *Pan* and *Pongo* and found that lingual cingulum and median pillars show a high level of variation in these taxa. Taken in combination, relative crown height, development of cingulum, and development of lingual pillar encompassed the range of variation seen in *D. crusafonti* and *D. laietanus*. Kelley *et al.* (1995) likewise found, from a comparative study of 20 gorillas from Cameroon, that disparate lingual incisor morphologies are observable within a population. Benefit & McCrossin (2000) critiquing Ward *et al.*'s (1999) recognition of *Equatorius* cited Hooijer's (1948) study in support of the contention that the incisor variation observed in *Kenyapithecus* and *Equatorius* is found within single populations of subfossil orangutans.

Given this interest in the morphology of the lingual side of incisors, it is timely to assess the utility of lingual incisor morphology for taxonomic discrimination. Based on the premise that patterns of variation in fossil taxa should correspond to those seen in modern taxa, the purpose of this chapter is to study the patterns of variation in lingual incisor morphology among extant hominoids. These are the closest modern counterparts of the Miocene hominoids, large numbers of specimens from known localities are available in museums around the USA and Europe, and the alpha-taxonomy is well-established on the basis of molecular and morphological studies.

There have been at least three hypotheses regarding the nature of variation in lingual incisor morphology in the Miocene hominoids. Begun (1992), Martin & Andrews (1993) and Andrews *et al.* (1996) have demonstrated that incisors with lingual pillars are taller and narrower than incisors without pillars suggesting that there is a correlation between relative incisor size (height and length) and the presence of lingual pillars in the Miocene hominoids. Begun (1992) has tentatively suggested that the differences in incisor morphologies in *Dryopithecus* could be related to different dietary specialization, and the presence of lingual pillars in *D. crusafonti* implies incisal preparation of food. And finally, Martin & Andrews (1993) assert that the lingual incisor morphology seen in the Miocene hominoids is unique and unlike anything seen in modern hominoids. These three hypotheses are taken as avenues for exploring the nature of variation in incisor morphology in modern hominoids, and have helped in formulating the following questions:

(1) what types of morphological features are encountered on the lingual aspect of incisors in extant hominoids (2) what is the nature of variation in species, subspecies and populations in such characters; and (3) what is the correlation between variable morphological patterns and sex, size and diet?

Materials and Methods

All four genera of extant hominoids were included. The comparative sample was made up of 341 chimpanzees, 319 gorillas, 171 orangutans and 321 gibbons. The specimens were sorted into populations, subspecies and species as explained in Chapter Two.

Lingual incisor morphology on the upper and lower incisors was examined and notes were taken on the observable variants. Based on these observations, discrete character states were defined and specimens were scored for these states. A detailed description of the variable morphological patterns is provided in the following section. In addition to qualitative data, linear measurements were taken. Using sliding calipers calibrated to the nearest 0.01mm, mesio-distal length (at incisive edge), labio-lingual breadth (at median point of cervical-apical axis) and labial height (from incisive edge to cemento-enamel junction) were measured. These univariate dimensions were reduced to nominal categories in order to permit comparison with the qualitatively coded morphological characters. This was done by sorting the specimens into species and within each species by sex. The measurements from each sex-pooled sample were divided into three percentiles: the top 30^{th} percentile was assigned to the first category, the next 35^{th} was assigned to

the second category and the final 35th percentile to the third category. Using contingency tables and chi-square statistics, with associated probabilities of <0.01, the correlation between morphology, taxonomic category (i.e., population, subspecies or species), sex and size was studied. A t-test was also used to analyze difference in means. Dietary associations were difficult to assess accurately because there are few data that directly compare dental form with regional differences in diet and food preparation in the hominoids (for exception, see Ungar, 1994a, 1994b). Dietary correlations could be examined only by association.

Description of incisor morphology

Gibbons

Despite the great diversity in species numbers in *Hylobates* (13 species recently recognized - Groves, 2001), lingual incisor morphology is remarkably consistent, especially when compared to the great apes. The upper central incisors are spatulate and the upper lateral incisors are, on average, smaller than the central, although the size disparity is slightly less than in the great apes (Table 6.1). The I^1 is mesiodistally long when indexed against height, but this is not the case for the I^2 and the lower incisors (Table 6.2).

Taxon	Average I^1MD/I^2MD (n)	Average I_1MD/I_2MD (n)
Hylobates	1.24 (239)	0.93 (252)
Gorilla	1.42 (172)	0.87 (166)
Pan	1.35 (216)	0.93 (215)
Pongo	1.60(119)	1.00 (121)

Table 6.1 Average I1/I2 size difference (in mesiodistal length) in extant hominoids. Sample size in parentheses.

The most prominent morphological feature on the lingual side is the presence of a ridge-like cingulum along the lingual border of the upper incisors (Figure 6.1). It is a common feature in all species and is observed in about 90% of the specimens (Table 6.3). The cingulum is confined to the cervical margin of the lingual face and does not extend onto the mesial and distal margins. Even along the cervical margin it has an asymmetric appearance because the thickness is not uniform throughout, but it increases in thickness towards the mesial end of the cervical margin. This thickening has variable manifestations: at times it is only a thin ledge slightly stronger than the adjoining cingulum (Figure 6.1A), but at other times it has the appearance of a broad shelf (Figure 1B), which has prompted the description of gibbon incisors as being chisel-like (Gregory, 1922) and two-cusped (Maier, 1984). Skirting the cingulum, at its apical end, a wide sulcus is often present in mesiodistal orientation. This transverse sulcus is not as common as the cingulum and was observed at a frequency of 55% in the I^1 and 30% in the I^2. The sulcus could provide a guide for interlocking the lower incisors because when the incisors begin to wear, an obliquely oriented facet appears on the cingular ledge (or lingual cusp) and the transverse sulcus is worn down to a deep groove. When worn, the upper incisors look as though they are two-cusped in lingual view, with the groove-like transverse sulcus separating the lingual cusp from the rest of the lingual face (Figure 6.2). Another feature of the upper incisors is a fovea at the distal end of the lingual face. This distal fovea is placed at the midpoint of the cervical-apical

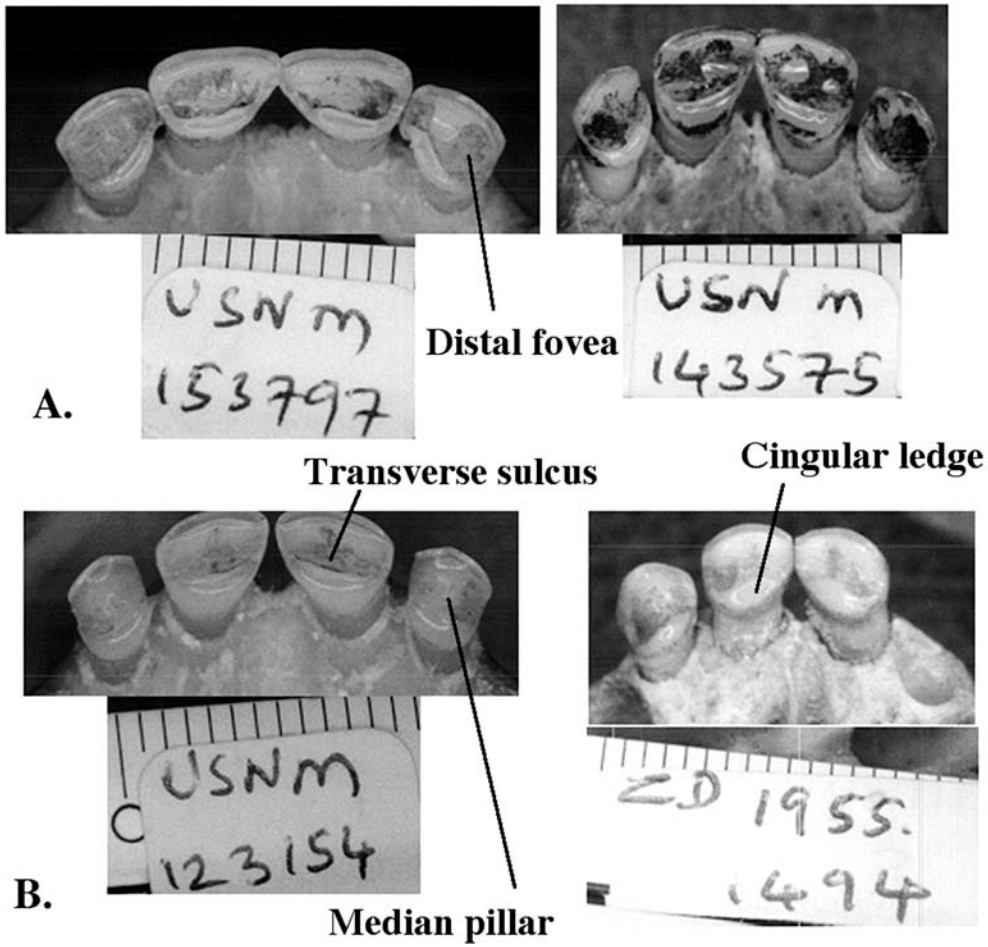


Figure 6.1 Gibbon upper incisors A. Moderate development of cingular swelling B. Prominent cingular swelling. Scale = 1mm divisons

axis on the distal margin of the tooth and does not extend down to the cervical margin as is seen in great apes (Figure 6.1). The fovea is not common on the central incisor (seen in 30% of the specimens) but it is much more common on the lateral incisor (86%), where it often occupies the entire distal half of the lingual side (Table 6.3). The fovea is most often found along with the transverse sulcus, and is formed by a widening of the sulcus at the distal end (Figure 6.1).

Taxon	I^1MD/I^1HT (n)[1]	I^2MD/I^2HT (n)	I_1MD/I_2HT (n)	I_2MD/I_2HT (n)
Hylobates	1.04 (40)	0.92 (58)	0.71 (69)	0.70 (78)
Gorilla	1.01(41)	0.84 (55)	0.74 (153)	0.68 (62)
Pan	0.90 (48)	0.77 (64)	0.70 (58)	0.71 (72)
Pongo	0.90 (38)	0.72 (57)	0.65 (38)	0.62 (41)

Table 6.2 Average mesiodistal/height index in modern hominoids. Sample size in parentheses.

The tuberculum dentale, a thin ridge of cingulum rising towards the apex, a feature commonly observed in the great apes, is rarely observed in gibbons. On the I^1 this enamel pillar (also referred to as median lingual pillar) is observed at a frequency of 3%. It is more frequently encountered on the I^2, at a frequency of 53%, but the configuration of the pillar differs in the I^2. The crown is mesiodistally compressed; the lingual pillar is formed by the posterior bulge of lingual face (Figure 6.1 B). When the median pillar is present, the incisal border of the I^2 slopes towards the cervix, both mesially and distally, causing the I^2 to have a conical appearance. In brief, the central and lateral incisors are heteromorphic in *Hylobates* (Swindler, 1976).

Figure 6.2 Gibbon upper incisors showing wear and groove-like transverse sulcus.

The lower incisors have a less complex morphology compared to the uppers. The lower lateral incisors are mesiodistally longer, on average, than the central incisors, a characteristic shared with *Pan* and *Gorilla*, but not with *Pongo* (Table 6.1), and the distal half of the incisal border of the I_2 often tapers towards the cervix (Figure 6.3). A shallow concave sulcus occupies the lingual side of the lower incisors (Swindler, 1976), and a thin cingulum borders the lingual face (23% on I_1 and 30% on I_2). The cingulum, when present, is not confined to the cervical margin but runs along the entire lingual side from the mesial margin around the cervical margin and up to the distal margin of the tooth.

Based on these observations, the following morphological characters, and discrete states were defined for *Hylobates* (Table 6.3):

I^1 and I^2: Cingular ledge, transverse sulcus, distal fovea, and median lingual pillar.

I_1 and I_2: Lingual cingulum

Character states: 0: Absent, 1: Present.

Character (n)	Absent	Present
Cingular ledge I^1 (176)	8%	92%
Cingular ledge I^2 (258)	10%	90%
Transverse sulcus I^1 (192)	45%	55%
Transverse sulcus I^2 (260)	70%	30%
Distal fovea I^1 (198)	70%	30%
Distal fovea I^2 (261)	14%	86%
Median lingual pillar I^1 (190)	97%	3%
Median lingual pillar I^2 (206)	47%	53%
Lingual cingulum I_1 (270)	77%	23%
Lingual cingulum I_2 (282)	63%	37%

Table 6.3 Frequency of occurrence of variable morphological patterns in *Hylobates*. Sample size in parentheses.

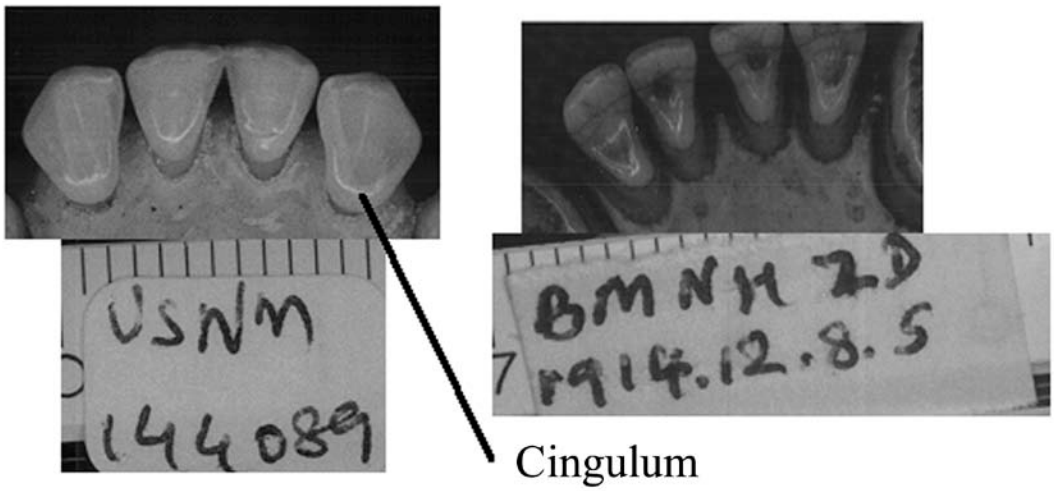


Figure 6.3 Lower incisors of gibbons showing lingual sulcus and cingulum. Scale = 1mm

Great Apes

Great ape incisors, while displaying differences from gibbon incisors in shape and morphology, share several features in common with each other. On the whole, in the great apes the incisors are tall relative to mesiodistal length (Table 6.2), and the upper lateral incisors are much smaller than the central (Table 6.1).

The upper central incisors are concave in lingual view, but this concavity is restricted to the incisive edge of the crown. The cervical end of the lingual side has a convex topography formed by a thick swelling at the cervical base. The swelling is most prominent at the median part of the cervical margin; it is reduced in prominence at the mesial and distal ends and slopes gently towards the apex of the tooth (Figure 6.4). A cingulum is not found skirting the cervical edge when the lingual swelling is seen, although well-developed ridges run along the mesial and distal margins of the crown and foveae are found adjoining the ridges (Figure 6.4). This morphology of the upper central incisors, with basal swelling, is commonly found in all three great ape taxa, and was observed at a frequency of 82% in *Pan*, 84% in *Gorilla* and 80% in *Pongo* (Table 6.4).

A morphological pattern resembling the great apes, with a broad, smoothly sloping cervical bulge, has not been noted for fossil hominoids, providing some justification for the claim that upper central lingual incisor morphology differs in the fossil and modern hominoids (Martin & Andrews, 1993). Frequently, however, the lingual swelling is compressed mesiodistally as it proceeds apically and, in this case, it forms a robust, centrally placed, enamel pillar. The foveae on the mesial

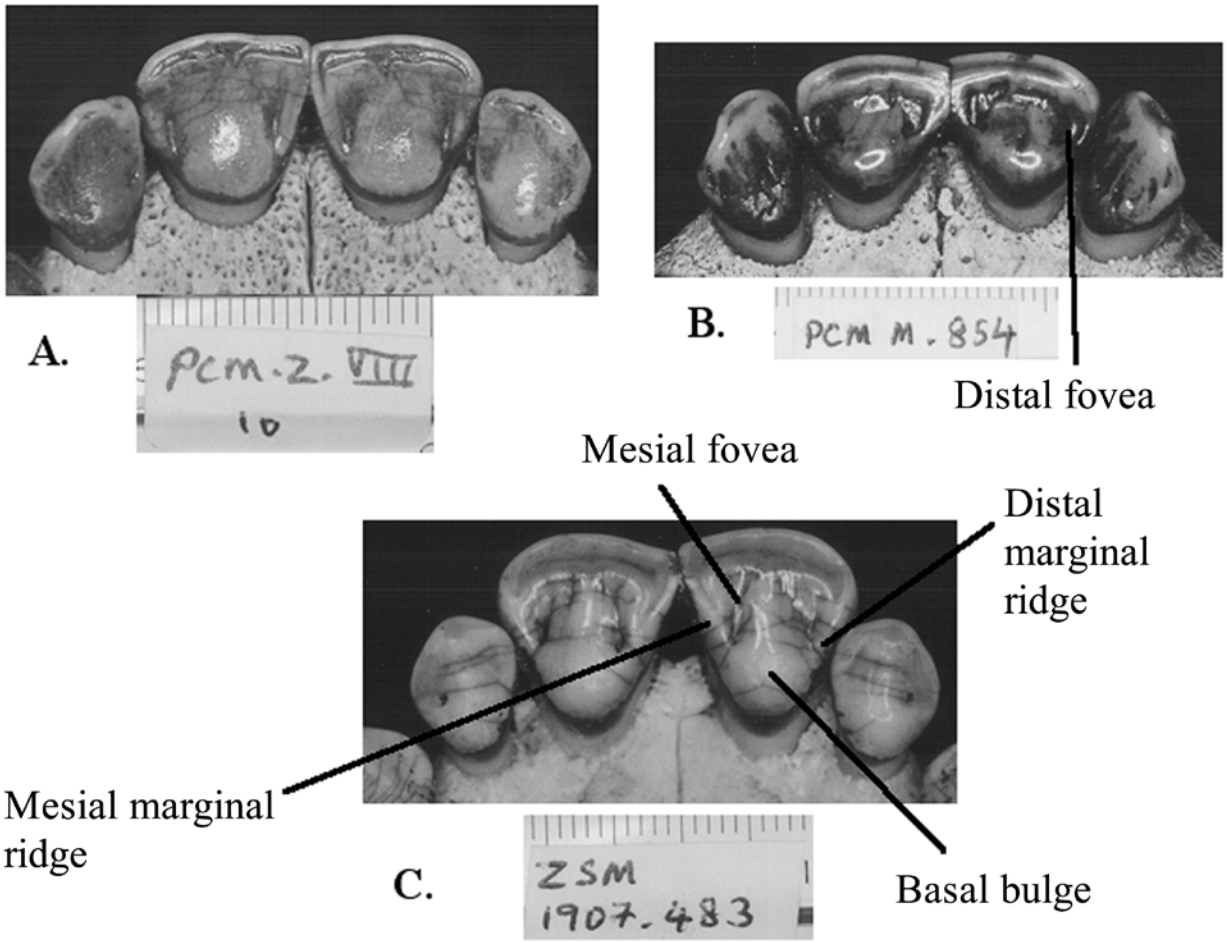


Figure 6.4 Great ape upper incisors showing predominant morphological pattern of basal bulge. A: *Pan*, B: *Gorilla*, C: *Pongo*. Scale = 1mm.

Table 6.4 Frequency of occurrence of variable morphological patterns in great apes. Sample size in parentheses. Frequencies presented in order of character states from column 2. Character states as defined in text.

Tooth type	Character	State	*Pan*	*Gorilla*	*Pongo*
I^1	**Cingulum**	0	0%	2%	0%
		1	9%	11%	1%
		2	82%	84%	80%
		3	9%	3%	19%
Sample size			**206**	**161**	**95**
I^2	**Cingulum**	0	7%	31%	7%
		1	20%	46%	13%
		2	63%	22%	49%
		3	10%	1%	31%
Sample size			**228**	**200**	**89**
I_1	**Cingulum**	0	3%	18%	7%
		1	20%	71%	7%
		2	52%	10%	82%
		3	25%	1%	4%
Sample size			**225**	**175**	**119**
I_2	**Cingulum**	0	2%	13%	9%
		1	18%	67%	6%
		2	52%	18%	82%
		3	28%	2%	3%
Sample size			**232**	**206**	**128**
I^1	**Median lingual pillar**	0	43%	68%	18%
		1	57%	32%	82%
Sample size			**195**	**158**	**89**
I^2	**Median lingual pillar**	0	67%	86%	47%
		1	33%	14%	53%
I_1	**Median lingual pillar**	0	30%	90%	55%
Sample size			**224**	**200**	**127**
		1	70%	10%	45%
Sample size			**223**	**173**	**116**
I_2	**Median lingual pillar**	0	19%	65%	51%
		1	81%	35%	49%
Sample size			**228**	**205**	**127**
I^1	**Mesial marginal ridge**	0	39%	49%	18%
		1	61%	51%	82%
Sample size			**195**	**158**	**89**
I^2	**Mesial marginal ridge**	0	61%	68%	55%
		1	39%	32%	45%
Sample size			**222**	**200**	**127**
I_1	**Mesial marginal ridge**	0	69%	64%	69%

Table 6.4 Continued

Tooth type	Character	State	*Pan*	*Gorilla*	*Pongo*
		1	31%	36%	31%
Sample size			**224**	**173**	**116**
I_2	**Mesial marginal ridge**	0	68%	66%	68%
		1	32%	34%	32%
Sample size			**228**	**201**	**127**
I^1	**Distal marginal ridge**	0	27%	49%	20%
		1	73%	51%	80%
Sample size			**190**	**146**	**93**
I^2	**Distal marginal ridge**	0	43%	60%	52%
		1	57%	40%	48%
Sample size			**205**	**185**	**124**
I_1	**Distal marginal ridge**	0	67%	58%	66%
		1	33%	42%	34%
Sample size			**210**	**155**	**108**
I_2	**Distal marginal ridge**	0	39%	42%	68%
		1	61%	58%	32%
Sample size			**220**	**189**	**119**
I^1	**Mesial fovea**	0	45%	47%	35%
		1	55%	53%	65%
Sample size			**204**	**159**	**96**
I^2	**Mesial fovea**	0	66%	80%	75%
		1	34%	20%	25%
Sample size			**227**	**182**	**124**
I_1	**Mesial fovea**	0	69%	92%	80%
		1	31%	8%	20%
Sample size			**225**	**155**	**116**
I_2	**Mesial fovea**	0	61%	84%	72%
		1	39%	16%	27%
Sample size			**232**	**189**	**127**
I^1	**Distal fovea**	0	7%	3%	32%
		1	93%	97%	68%
Sample size			**208**	**164**	**97**
I^2	**Distal fovea**	0	41%	67%	41%
		1	59%	33%	59%
Sample size			**227**	**200**	**126**
I_1	**Distal fovea**	0	26%	77%	81%
		1	74%	23%	19%
Sample size			**225**	**152**	**116**
I_2	**Distal fovea**	0	6%	15%	83%
		1	94%	85%	17%
		Sample size	**232**	**206**	**127**

and distal ends are much stronger in the presence of the pillar, often more prominent on the distal end than the mesial. Mesial and distal marginal ridges are also seen adjoining the foveae (Figure 6.5). The median lingual pillar on the upper central incisor has a high frequency of occurrence in *Pongo* (82%) and *Pan* (57%), but it is less frequent in *Gorilla* (32%).

This latter morphological pattern, with enamel pillar, marginal ridges and foveae resembles that described for several Miocene hominoid taxa, including *Proconsul* (Andrews, 1978), *Dryopithecus* (Begun, 1992; Andrews *et al.*, 1996) and *Griphopithecus* (Martin & Andrews, 1993). Andrews has suggested that upper central incisors with lingual pillars constitutes the ancestral morphological pattern for hominoids (Andrews, 1985; Martin & Andrews, 1993; Andrews *et al.*, 1996). A variant of this morphological pattern, as reviewed here, is to be seen in the modern great apes.

It should be noted that *Proconsul* and the European Miocene hominoids differ in upper central lingual pillar morphology. In *Proconsul*, most often, a continuous, well-defined cingulum is present, and the lingual pillar, which is just as frequent, is clearly separated from the cingulum; in the European hominoids the lingual cingulum gradually forms the lingual pillar and there is no separation of the mesial and distal moieties (personal observation). The European morphological pattern is most commonly seen in the modern great apes, as reviewed above; the African variant can also be observed, at a frequency of 19% in *Pongo* (Figure 6.5 C), but much more seldom in *Pan* (9%) and *Gorilla* (3%). A morphological pattern

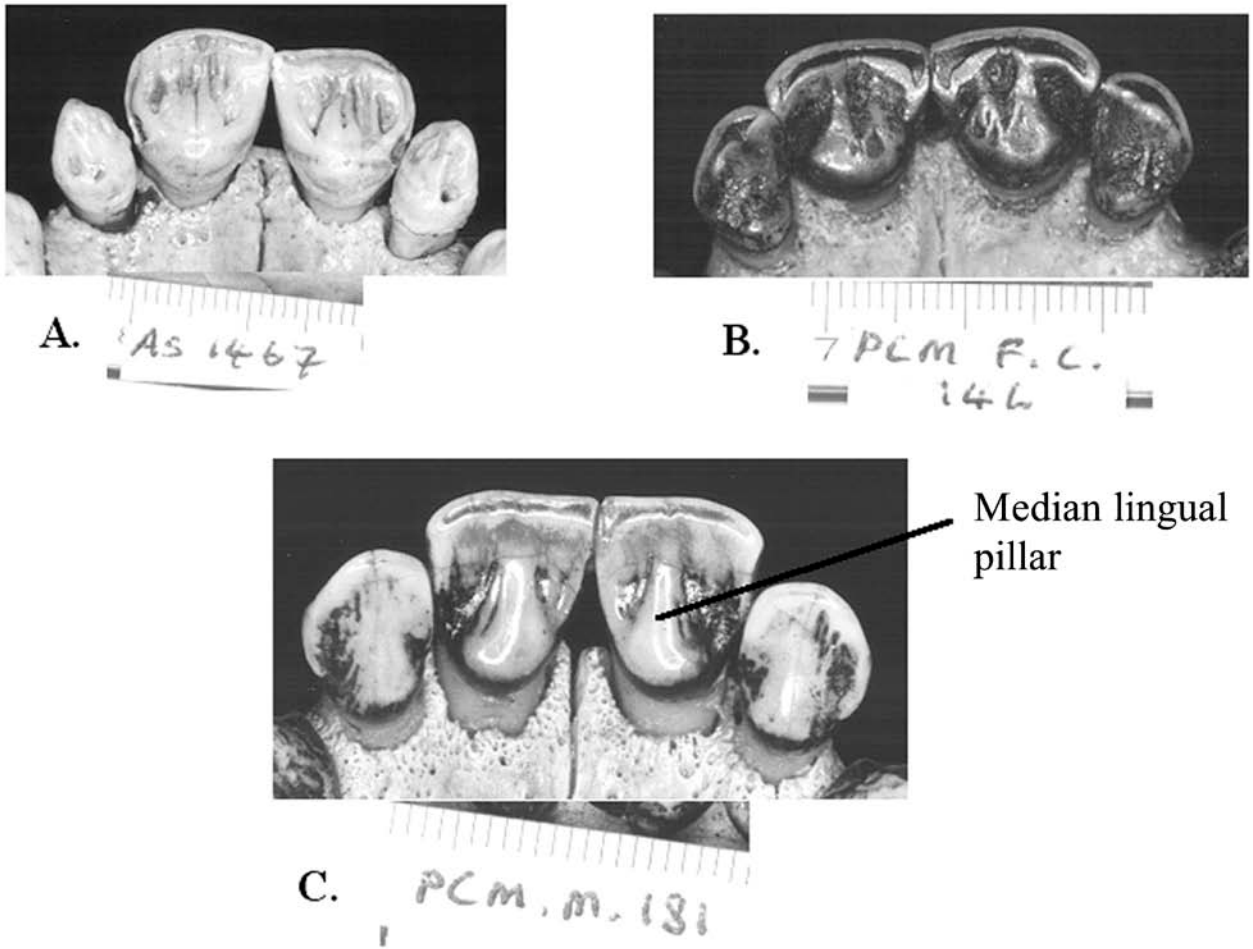


Figure 6.5 Great ape upper incisors showing configuration of median lingual pillar. A: *Pongo*, B: *Gorilla*, C: *Pan*. Scale = 1mm.

which is relatively rarely seen in the Miocene hominoids - a continuous lingual cingulum, without a pillar, or basal bulge, is not commonly encountered in the great apes either: 9% in *Pan*, 11% in *Gorilla* and 1% in *Pongo* (Figure 6.6).

The upper lateral incisors are smaller than the central incisors in the extant great apes (Table 6.1), but the morphological variants are the same, with basal swelling, median lingual pillar, mesial and distal foveae and marginal ridges. I^1s and I^2s do not always share the same morphological pattern, however, and a basal bulge in the central is often accompanied by a cingulum without a bulge in the lateral incisor (Figure 6.4). The frequency of occurrence of the various patterns also differs in the central and lateral incisors. The basal bulge, for example, is not as common in the lateral as the central incisor (63% in *Pan*, 22% in *Gorilla* and 49% in *Pongo*), but there is a higher frequency of continuous cingulum without a lingual pillar in I^2 (20% in *Pan*, 46% in *Gorilla* and 13% in *Pongo*). The morphological variant of continuous cingulum and lingual pillar separated from the cingulum is, like in the upper central incisors, more commonly observed in the UI2s of *Pongo* (31%) than in *Pan* (10%) or *Gorilla* (1%).

The lower incisors in the modern hominoids have tall crowns relative to mesiodistal length (Table 6.2). Unlike their counterparts in the upper jaw, the lower lateral incisors are slightly wider than the central incisors (Table 6.1), except in *Pongo*, where the two teeth are, on average, more equal in size. The incisal edge is wide and horizontal, although frequently, the distal half of the lateral incisor tilts towards the cervix. In comparison to gibbon lower incisors great ape lower incisors

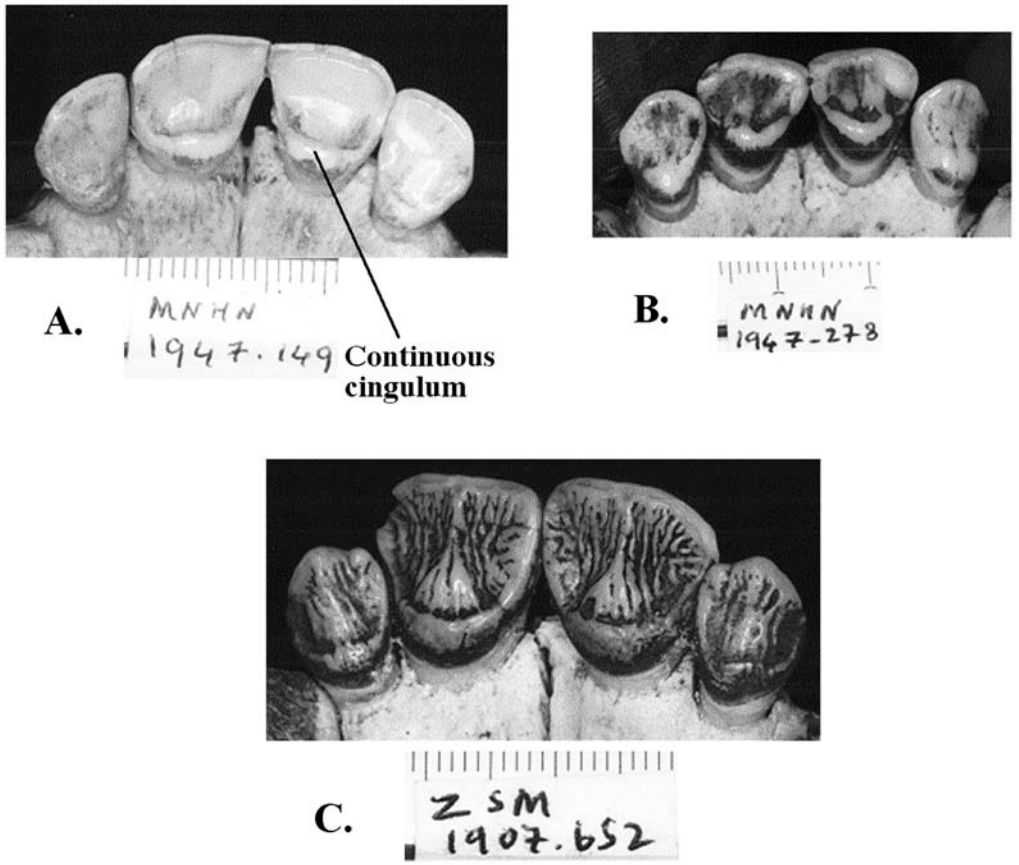


Figure 6.6 Great ape upper incisors showing continuous cingulum. A. *Pan,* B. *Gorilla,* C. *Pongo*. Scale = 1mm.

have a greater diversity of morphological patterns; all the morphological patterns from the upper incisors, including the basal swelling, mesial and distal marginal ridges, lingual pillar, lingual cingulum and mesial and distal foveae are observed on the lingual side of the lower incisors. Unlike the upper incisors, however, no single morphological pattern can be used to characterize all three taxa. *Gorilla* lower incisors are predominantly characterized by a continuous cingulum skirting the cervical base without an enamel pillar rising from the cingulum (71% occurrence in LI1, 67% in LI2), and there is a high incidence of a distal fossa, or fovea on the LI2 (Table 6.4; Figure 6.7). In *Pan* and *Pongo*, in contrast, a continuous cingulum is less frequently encountered – 20% of LI1 and 18% of LI2 in *Pan*, 7% of LI1 and 6% of LI2 in *Pongo*. Lower incisors of *Pongo* commonly present a basal swelling gently rising towards the apex (82%) and a median lingual pillar is also seen (Table 6.4; Figure 6.7). In *Pan* too, the most commonly occurring pattern is the basal bulge, although it is not as frequently seen as in *Pongo* (only 52%). The median lingual pillar is much more frequent in the lower incisors of *Pan* (70% LI1; 81% LI2). In addition, the morphological configuration of continuous cingulum and median lingual pillar separated from the cingulum has a higher occurrence in *Pan* than in the other two taxa (Table 6.4).

A morphological feature not observed in the upper incisors is seen in the lower incisors: it consists of a thickening of the cingulum at the median part of the cervical base, described by Swindler (1976) as a lingual tubercle. It is morphologically similar to the swelling seen in the upper incisors of *Hylobates*, but

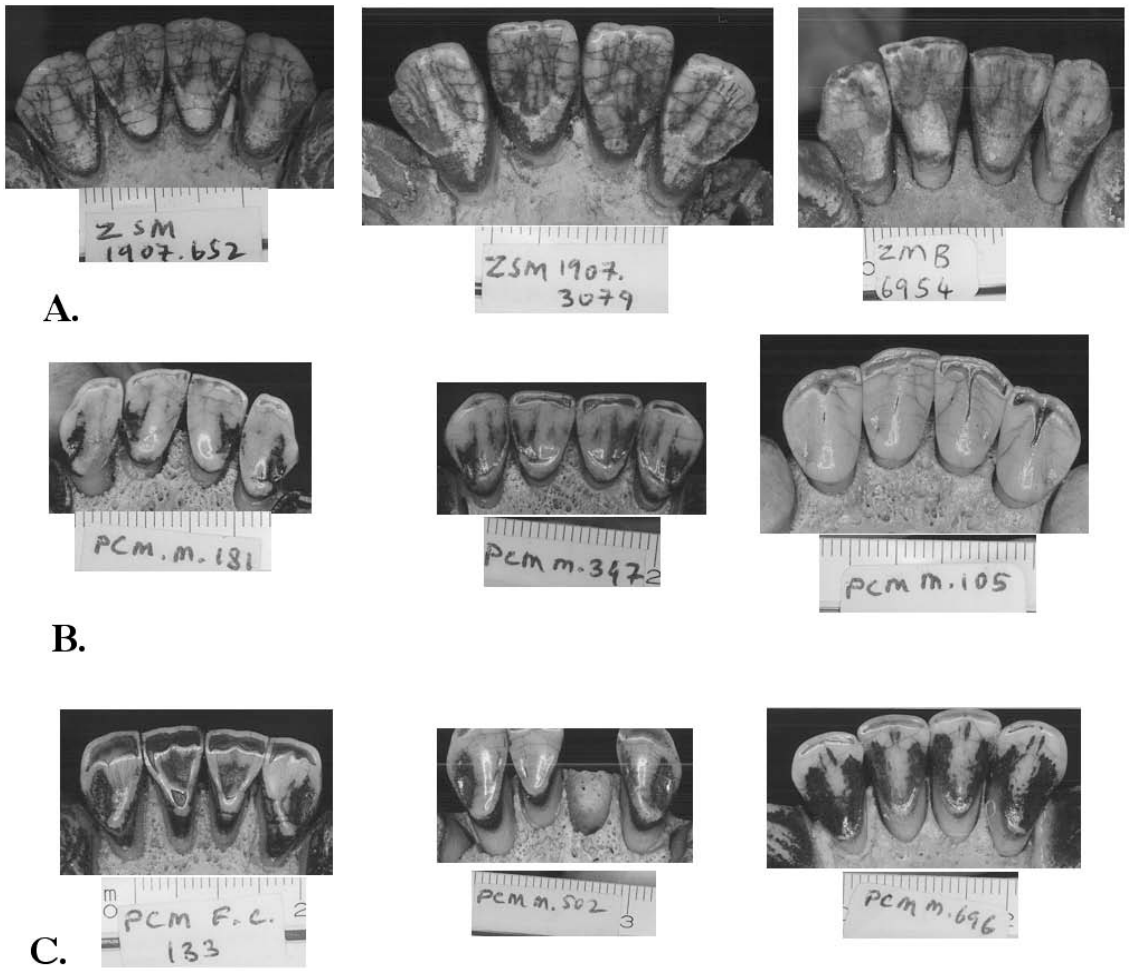


Figure 6.7 Great ape lower incisors showing variable morphological patterns. First row: *Pongo*, Second row: *Pan*, Third row: *Gorilla*. Scale = 1mm

it has a more median placement in the great apes. This feature is observed in all extant great apes (Figure 6.7) but it is not a frequent occurrence. Other morphological patterns other than the prominent patterns described here are also observed in each of the great apes, as shown in Figure 6.7. Finally, mesial marginal ridges are not common on great ape lower incisors; distal marginal ridges are more common, especially in *Pan* and *Gorilla* (Table 6.4).

An inspection of table 6.4 reveals that several differences in lingual incisor morphology and in the frequency of occurrence of morphological features in the great apes (Table 6.4). Underlying morphological patterns are similar, however, and these were used to define the following morphological characters, and discrete states:

Cingulum: 0: No cingulum, 1: Continuous cingulum confined to cervical margin, 2: Basal bulge sloping towards apex, 3: Continuous cingulum and median lingual pillar, separated.

Median lingual pillar: 0: Absent, 1: Present

Mesial marginal ridge: 0: Absent, 1: Present

Distal marginal ridge: 0: Absent, 1: Present

Mesial fovea: 0: Absent, 1: Present

Distal fovea: 0: Absent, 1: Present

Apportionment of variation in species, subspecies and populations

In order to examine the taxonomic utility of lingual incisor morphology, the nature of variation in species and lower order taxonomic categories of the modern hominoids needs to be studied. Consequently, in this section, the four genera of modern hominoids are subdivided into species, where pertinent, and subsequently into subspecies and populations and the differences in patterns of variation in each of these groupings is described.

Species

The patterning of variation was examined in two species of *Pan, P. troglodytes* and *P. paniscus,* and five species of *Hylobates, H. concolor, H. syndactylus, H. agilis, H. lar* and *H. muelleri*. Adequate samples were obtained only for these five *Hylobates* species. No morphological pattern was found to occur exclusively in any of these species, but all morphological patterns were found represented in each. Species could be differentiated based on morphological features, but the differences were in the frequency of occurrence of variable features. Differences that were statistically significant, based on Pearson's significance of chi-square statistics, were noted.

Features that are significantly different in the two species of *Pan* are outlined in Table 6.5. When compared with *P. troglodytes, P. paniscus* is characterized by a low incidence of mesial foveae in the incisors, a lower representation of the median lingual pillar in the lower incisors and a higher frequency of type 1 (or discontinuous) cingulum in the I^2. *P. troglodytes* more

Character	*Character* States	*P. troglodytes*	*P. paniscus*	Pearson's Significance
I^2 cingulum	0,1,2,3	8,17,66,9 (194)	0, 38,47,15 (34)	.00900
I^2 mesial marginal ridge	0,1	65,35 (188)	41,59 (34)	.00899
I_1 median lingual pillar	0,1	25,75 (189)	53,47 (34)	.00120
I_2 median lingual pillar	0,1	15,85 (191)	40,60 (37)	.00023
I^1 mesial fovea	0,1	41,59 (172)	69,31 (32)	.00341
I_1 mesial fovea	0,1	64,36 (191)	94,6 (34)	.00056
I_2 mesial fovea	0,1	54,46 (195)	97,3 (37)	.00000

Table 6.5 Differences in lingual incisor morphology between *P. troglodytes* and *P. paniscus*. (Chi-square test, p<0.01). Sample size in parentheses. Frequencies (%) presented in order of character states from column 2. Character states as defined in text.

frequently has a basal bulge in the I_2, and mesial foveae and median lingual pillars in the lower incisors are more common.

Table 6.6 shows the differences between the species of *Hylobates*. Of the five species, *H. syndactylus* diverges most strongly from the other species. I_2s in *H. syndactylus* lack a transverse sulcus (in the specimens examined) and a ledge-like cingulum and distal fovea are less frequently encountered. *H. concolor* is similar to *H. syndactylus* in this respect, while the *lar* group (*H. agilis*, *H. lar* and *H. muelleri*) are similar to each other in character frequencies. It should be mentioned that although the results reported here are based on disparate sample sizes, simulations studies were also carried out, randomly drawing smaller samples from

the larger group so as the equalize sample sizes. The results did not differ significantly.

Character	Character states	*H. concolor*	*H. syndactylus*	*H. agilis*	*H. lar*	*H. muelleri*
I^1 cingular ledge	O,1	39,61 (13)	6,94 (18)	0,100(22)	4,96 (51)	10,90 (51)
I^2 cingular ledge	O,1	30,70 (20)	39,61 (23)	8,92 (26)	5,95 (85)	3,97 (70)
I^2Median lingual pillar	O,1	21,79(14)	58,42 (19)	57,43 (21)	32,68 (63)	61,39(66)
I^2Distal fovea	O,1	15,85(20)	48,52 (23)	8,92 (26)	3,97 (89)	19,81 (69)
I^2 Transverse sulcus	O,1	85,15 (20)	100,0 (23)	52,48(25)	61,39 (88)	70,30(70)

Table 6.6 Characters showing statistically significant differences between species of *Hylobates*. (Chi-square test, p<0.01). Sample size in parentheses. Frequencies presented in order of character states from column 2. Character states as defined in text.

Subspecies

Incisor morphology shows greater variability in the subspecies of the recent great apes than in gibbon subspecies. Sample sizes for the subspecies of *Hylobates* vary markedly, making it difficult to compare subspecies. Subspecies for which sample sizes of greater than 20 individuals were available, for example, *H. m. funereus* and *H. m. abbotti* show no significant differences in any of the lingual incisor characters. Subspecies of *H. agilis*, *H. a. unko, H. a. agilis* and *H. a. albibarbis* differ significantly in the frequency of cingulum in the lower incisors, but sample sizes are too small (15, 4 and 7 individuals, respectively) to place much confidence in the differences. Of the subspecies of *H. lar,* the cingular ledge is

present in the I^1 in *H. l. entelloides* in all of 42 specimens examined, and in 71 of 73 specimens in the I^2. In contrast, 2 of 5 individuals of *H. l. lar* do not present the cingular ledge in the I^1, and 2 out of 7 specimens lack the cingular ledge in the I^2 of *H. l. vestitus*.

The two subspecies of *Pongo pygmaeus*, *P. p. pygmaeus* and *P. p. abelii* differ in their patterns of cingulum development and the presence/absence of mesial and distal marginal ridges, but since sample sizes for *P. p. abelii* were small (varying between 10 and 20 individuals depending on the character studied), caution needs to be exercised when interpreting these results (Table 6.7). The mesial and distal marginal ridges and the cingulum are more often absent in the incisors of *P. p. abelii*.

Character	Character states	*P. p. pygmaeus*	*P. p. abelii*	Pearson's Significance
I^1 Mesial marginal ridge	0,1	14,86 (79)	50,50 (10)	.00513
I^2 Mesial marginal ridge	0,1	50,50 (107)	85,15 (20)	.00342
I^1 Distal marginal ridge	0,1	16,84 (83)	60,40 (10)	.00102
I^2 Cingulum	0,1,2,3	4,11,51,34 (107)	25,20,40,15 (20)	.00273
I_1 cingulum	0,1,2,3	3,7,85,5 (102)	29,6, 65,0 (17)	.00078
I_2 cingulum	0,1,2,3	5,7,84,4 (109)	32,0,68,0 (19)	.00098

Table 6.7 Differences in character frequencies in subspecies of *Pongo pygmaeus* (Chi-square test, $p<0.01$). Sample size in parentheses. Frequencies presented in order of character states from column 2. Character states as defined in text.

The subspecies of *P. troglodytes* display several differences in the frequency of lingual incisor morphologies (Table 6.8). The upper incisors in *P. t. verus* show greater variability in morphological patterns of the cingulum: *P. t. troglodytes* and *P. t. schweinfurthii* most commonly display a basal bulge in the upper incisors, but in *P. t. verus* a continuous cingulum is regularly observed, sometimes without pillar and other at times with the pillar separated from the cingulum. The three subspecies also differ in the presence/absence of mesial and distal marginal ridges.

Character	Character States	*P. t. verus*	*P. t. troglodytes*	*P. t. schweinfurthii*	Significance
I^1 Cingulum	0,1,2,3	0,23,51,26 (35)	0,3,97,0 (87)	0,4,88,8 (51)	.00000
I^2 Cingulum	0,1,2,3	11,39,22,28 (36)	7,12,78,3 (101)	7,13,71,9 (56)	.00000
I_1 Cingulum	0,1,2,3	3,24,55,18 (33)	5,18,60,17 (101)	0,23,34,43 (56)	.00400
I^2 Distal marginal ridge-	0,1	24,76 (34)	48, 52 (87)	57,43 (53)	.00868
I_1 Mesial marginal ridge	0,1	73,27 (33)	77,23 (101)	53,47 (55)	.00589
I_2 Mesial marginal ridge	0,1	60,40 (35)	77,23 (101)	52,48 (54)	.00383

Table 6.8 Differences between subspecies of *P. troglodytes*

The most striking differences in the patterns of lingual incisor morphology is to be seen in gorillas. The three subspecies show highly significant differences in

most of the morphological features of the incisors (Table 6.9). The two East African subspecies, *G. g. graueri* and *G. g. beringei* display a high frequency of mesial and distal marginal ridges in the upper and lower incisors compared to the west African subspecies, *G. g. gorilla*. The West African subspecies, in turn, has a higher frequency of mesial and distal foveae on the I_2. And *G. g. graueri* has a higher frequency of the type 1 cingulum (continuous cingulum skirting cervical margin).

Populations

In all four modern hominoid genera, on the whole, populations within a subspecies do not display significant differences in the morphological patterns displayed by incisors. In *Hylobates* interpopulational differences could only be tested from two adjacent localities of *H. l. entelloides* (Chiang Dao and Doi Angka in Chiang Mai, Thailand), since these were the only two localities with large enough sample sizes. Character state frequencies were not significantly different in these two localities. In chimpanzees, gorillas and orangutans, several populations from the most commonly represented subspecies were selected and compared.

Two populations of *P. p. pygmaeus*, one from Batang Bara in western Sarawak and the other from Sampit in western Borneo (Röhrer-Ertl, 1984) showed no significant differences in incisor morphology, but individuals from Skalau from eastern West Borneo (north of the Kapuas River) differed significantly from the Sampit population in the configuration of the distal fovea of the I_1. Within the subspecies of *P. troglodytes* several populations were compared with one another

Character	Character states	*G. g. gorilla*	*G. g. graueri*	*G. g. beringei*	Pearson's Significance
I^1 cingulum	0,1,2,3	2,5,93,0 (113)	7,33,53,7 (30)	0,11,78,11 (18)	.00001
I^2 cingulum	0,1,2,3	40,30,29,1 (135)	8,90,2,0 (39)	23,61,12,4 (26)	.00000
I_1 cingulum	0,1,2,3	24, 63,13,0 (124)	3,94,0,3(34)	0,88,12, 0 (17)	.00079
I_2 cingulum	0,1,2,3	16,65,17,2 (138)	2,84,12,2 (44)	17,42,42,0 (24)	.00552
I^1 lingual pillar median	0,1	80,20 (110)	50,50 (30)	28,72 (18)	.00000
I_2 lingual pillar median	0,1	69,31 (137)	39,61(44)	87,13 (24)	.00005
I^1 mesial marginal ridge	0,1	64,36 (111)	14,86 (29)	17,83 (18)	.00000
I^2 mesial marginal ridge	0,1	78,22 (135)	51,49 (39)	38,62 (26)	.00001
I_1mesial marginal ridge	0,1	79,21 (122)	33,67 (34)	18,82 (17)	.00000
I_2 mesial marginal ridge	0,1	75,25 (137)	41,59 (44)	62,38 (24)	.00014
I^1distal marginal ridge	0,1	67,33 (101)	7,93 (27)	11,89 (18)	.00000
I^2Distal marginal ridge	0,1	72,28 (123)	43,57 (37)	20,80 (25)	.00000
I_1distal marginal ridge	0,1	76,24 (108)	20,80 (30)	12,88 (17)	.00000
I_2Distal marginal ridge	0,1	55,45 (123)	9,91 (42)	29,71 (24)	.00000
I^1 Mesial fovea	0,1	55,45 (112)	41,59 (29)	6,94 (18)	.00035
I_2 Mesial fovea	0,1	78,22 (123)	93,7 (42)	100,0 (24)	.00572
I^2 Distal fovea	0,1	57,43 (134)	90,10 (40)	81,19 (26)	.00012

Table 6.9 Differences between subspecies of *G. gorilla*.

but no significant differences were noted between populations.

In *G. g. gorilla*, two adjacent populations – one from the coastal region of Cameroon (south of the Sanaga River, including the localities of Bipindi, Campo, Lolodorf) and the other from coastal region of Gabon (including Cap Lopez and Libreville, see Groves, 1970b) displayed significant differences in the frequency of four morphological characters: I_1 mesial marginal ridge, I_1 distal marginal ridge, I_2 distal marginal ridge and I_2 cingulum. In *G. g. graueri*, on the other hand, the Utu population was not significantly different from the Mwenga-Fizi. It appears that the inter-populational differences are random in nature occurring through processes of migration and divergence, and of no particular taxonomic significance.

Incisor morphology, sex and size

All morphological features on the lingual side of incisors occur with equal frequency in both sexes in the modern hominoids. In other words, no statistically significant correlation can be established between sex and incisor morphology using chi-square statistics (Table 6.10).

Trait	**Male**	**Female**
I^1 median lingual pillar	49%	51%
I^1 mesial marginal ridge	52%	48%
I^1 distal marginal ridge	50%	50%
I^1 mesial fovea	48%	52%
I^1 distal fovea	53%	47%
Average	**50%**	**50%**

Table 6.10. Frequency of lingual incisor traits in the two sexes of *Pongo*.

To study the association between incisor size and incisor morphology, two analyses were carried out. First, length, breadth and height dimensions within each sex in a species were transformed into three nominal categories and the individuals were sorted into small, medium and large sizes. The association between morphological variants and size was then studied using simple contingency tables and chi-square statistics. An inspection of these tables revealed that none of the morphological characters display a significant correlation with size.

The other analysis used was a more direct parametric test. Upper centrals incisors in the four great ape species (two species of *Pan*, one each of *Gorilla* and *Pongo)* were sorted by the presence or absence of the median lingual pillar and differences in the mean linear dimensions of these two groups were tested using a t-test. This was done so as to compare the modern hominoids with the Miocene hominoids and find out if incisors with lingual pillars are taller and mesiodistally longer than incisors without pillars. The results are displayed in Table 6.11.

It reveals that in all species, except *Pongo,* I^1s with pillars have longer dimensions than I^1s without pillars. The negative t-value is merely a reflection of the fact that the second variable in the comparison (incisors with pillars) has a higher mean than the first variable (incisors without pillars). The standard deviations for the means are quite high, however, and the differences are not significant. The only exception is *Gorilla* – in this group mean breadth and height dimensions of individuals with lingual pillars are significantly higher than individuals without pillars.

TAXA	Length	Pillar absent	SD	Pillar present	SD	t-value	Df	2-tailed Significance
P. troglodytes	I^1 MD	11.70	.98	11.86	.80	-1.19	158	.237
	I^1 BL	9.31	.53	9.37	.64	-.61	158	.543
	I^1 HT	11.91	1.41	12.34	1.17	-2.05	154	.042
Pan paniscus	I^1 MD	10.32	.78	10.70	.70	-1.39	30	.268
	I^1 BL	7.64	.51	7.72	.46	-.43	30	.670
	I^1 HT	10.79	1.38	11.16	1.55	-.70	29	.530
Pongo pygmaeus	I^1 MD	13.95	.98	13.55	1.04	1.23	66	.224
	I^1 BL	12.20	.93	12.06	.99	.44	65	.661
	I^1 HT	15.01	1.74	14.35	1.71	1.20	60	.237
Gorilla gorilla	I^1 MD	13.49	.91	13.51	1.09	-.09	143	.932
	I^1 BL	10.63	.70	11.03	.77	-3.28	143	**.001**
	I^1 HT	12.65	1.28	13.38	1.30	-3.20	134	**.002**

Table 6.11 t-test results comparing mean linear dimensions of great ape upper central incisor with and without lingual pillar. Two tests with significant results are highlighted.

Incisor morphology and diet

Long-term field research has demonstrated that there is a great deal of variability in food availability and dietary strategies in the modern hominoids (e.g., Wrangham *et al.*, 1994; Schaller, 1963; Boesch & Boesch, 2000; Remis, 1997). Following this demonstration there have been suggestions that differences in dental morphology can be explained by differential dietary strategies. One example that is particularly relevant for the present study is Kinzey's (1984) dietary hypothesis. Kinzey suggested that the differences between bonobos and chimpanzees in the length and positioning of crests on molars and the degree of wear on incisors could be related to a greater proportion of tough herbaceous foods in the bonobo diet, as reported by Badrian & Malenky (1984). In support of this hypothesis McCollum & McGrew (2001) have demonstrated recently that the pattern of incisor wear and

incisor size in *P. paniscus* is consistent with incisal preparation of *Haumania liebrechtsiana*, a tough fibrous plant commonly consumed by bonobos.

Kinzey's (1984) hypothesis is particularly instructive because Begun (1992) has similarly proposed for *Dryopithecus* from Spain that lingual pillars on the maxillary central incisors of *D. crusafonti* might have played a role in the incisal preparation of food. It is possible to suggest based on Begun's and Kinzey's hypotheses, that it is the processing of specialized food by incisors that accounts for the difference between bonobos and chimpanzees in incisor morphology. Unfortunately, it is difficult to evaluate this hypothesis because bonobos present a greater variability in incisor morphology when compared with chimpanzees and no morphological pattern occurs at a high enough frequency to characterize the group. Compared to chimpanzees, bonobo incisors have a lower frequency of median lingual pillars, higher frequency of cingulum confined to cervical margin and lower frequency of mesial and distal fovea (Table 6.5). In other words, bonobos have a lower frequency of characters thought by Begun (1992) to suggest specialized preparation of food by incisors.

Like Kinzey (1984), Wrangham (1986a) has suggested that bonobos are differentiated from chimpanzees by their reliance on Terrestrial Herbaceous Vegetation (THV), and that the bonobo diet is similar to gorillas in this respect. If incisal features in bonobos and gorillas are compared, some similarities in incisor morphology are apparent, for example, in the low frequency of median lingual pillars in both taxa (Table 6.4). On the whole, however, gorillas differ from

bonobos and share similarities with chimpanzees in most features of the upper central incisors (Table 6.4). Moreover, gorillas as a group do not share homogenous incisor morphology, but character frequencies differ markedly between subspecies (Table 6.9). Ultimately, the degree of variability in incisor morphology is high in the modern hominoids both within and between groups and even within single localities. It is therefore difficult to conclusively demonstrate any association between incisor morphology and diet. It is significant in this regard that Ungar (1994b) studied incisor use in some Sumatran primates by direct observation of dietary behavior, and concluded that dietary differences explain only part of the differences in incisor use. Other factors such as positional behavior and anatomical specializations also account for differences in incisor use.

Discussion

This study has demonstrated that modern hominoids exhibit a wide diversity in details of lingual incisor morphology, encompassing the diversity seen in the Miocene forms. Variable morphological patterns are found with equal frequency in males and females, and different morphological types do not correlate strongly with size. The nature of diversity in morphological patterns also precludes attempts at establishing a correlation between incisor morphology and diet. It is plausible, based on the patterns of wear, that *Hylobates* incisors play a role in food handling. In the absence of any known advantage to lingual incisor morphology, the balance of the argument would suggest that lingual incisor morphology, particularly in the modern great apes, does not have adaptive significance. It would

appear, based on the results of this study that morphological features of the incisors are nonselective in nature, and differences in morphological patterns are driven by the random forces of genetic drift.

Great ape incisors are similar, in diversity of form, to the incisors of modern humans. It has been suggested that variable dental traits in modern human populations may have had functional value (Dahlberg, 1963; Brace, 1967). The consensus opinion, summarized in Scott & Turner (1997) suggests that dental traits, such as shoveled incisors and carabelli's cusp do not confer particular dietary or functional advantages, but differences in types of observable variants are driven by forces of genetic drift and reflect patterns of population divergence and reconnecting.

Incisor traits, such as shovel shaped incisors, in recent humans have immense utility as racial and population markers because differences in frequency of variable morphological types can be used in assessing population affinities and migration patterns (e.g., Turner, 1983; Hanihara, 1990). Modern hominoid species and subspecies, as shown in this study differ significantly in the frequency of occurrence of variable types of incisor morphologies. It is of significance to note that differences in frequency of occurrence of incisor patterns successfully align *H. syndactylus* with *H. concolor* and separate them from the *lar* group; that the two east African subspecies of *Gorilla gorilla* (*G. g. graueri* and *G. g. beringei*) are closely allied and well-separated from the west African subspecies (*G. g. gorilla)*; that the west African subspecies of *P. t. verus* is clearly separated from the other

two subspecies of *P. t. troglodytes* and *P. t. schweinfurthii* – all conclusions that are verified based on other molecular and morphological data. The differences, however, are in the proportional representation of morphological types and therefore, of a qualitative nature. It is possible through more detailed studies, such as those done by dental anthropologists with recent human populations (*e.g.*, Turner *et al.*, 1991) to develop sophisticated scoring procedures and establish frequencies for variable lingual incisor patterns in the recent great apes. These can then be used in studying patterns of divergence in these apes.

Lingual incisor morphology does have the potential to serve as population markers for modern hominoids, and therefore can be said to have taxonomic utility, at least in the recent context. The utility of this morphology for paleontological systematics is limited, however, because fossil samples are most often meager and the large samples needed to assess the nature of variability in incisor morphology are not available. Incisor morphology in the modern hominoids is only important when considered from a relational perspective, that is, when differences in frequency of occurrence are calculated. Given this situation, although incisor morphology may have only limited utility in fossil taxonomy when used as a single character, its value can be enhanced if it is used in conjunction with other taxonomic features. As an illustration an attempt was made to classify the two species of *Pan* by using the differences in incisor morphology tabulated in Table 6.5. When the two groups were sorted by the absence of mesial fovea on the I_2 (a characteristic most prominent in *P. paniscus*), only 25% of the resulting sample

was made up of *P. paniscus* reflecting the fact that the same character is also often encountered in *P. troglodytes*. When lack of mesial fovea on I_1 was added to the previous character, the representation of *P. paniscus* in the sorted sample rose to 26%. When a dentral trait from the upper molar (absence of sulcus obliquus on the M^2, Table 3.8.) was added to the list of diagnostic characters 67% of the sample was made up of *P. paniscus* and finally when a fourth trait, from the lower molar (absence of tuberculum sextum on the M_2) was added, 75% of the sample comprised *P. paniscus*. The two molar traits do not have mutually exclusive representation in the two species, either, and cannot be used to differentiate the species, but when the four traits were taken in conjunction classification accuracy increased considerably.

This simple exercise demonstrates that significance of incisor morphology as a taxonomic indicator increases when associated with other dental variables, and it suggests a possible use for this morphology in fossil species discrimination. It also suggests that associated material needs to be discovered in order to substantiate claims for taxonomic discrimination based on lingual incisor morphology. Finally, large samples of fossil specimens need to be made available so as to examine the nature of variability in these characters. These are extremely stringent requirements, especially for fossil species whose hallmark characteristics are fragmentary material in small numbers. But if we are to assume that fossil and recent species are equivalent concepts these requirements need to be met. An

alternative, of course, is to break away from the strict adherence to concepts of equivalence but there are sound theoretical reasons for maintaining it.

Implications for fossils

The morphology of the lingual aspect of incisors of modern hominoids is complex. In all great apes a basal swelling on the lingual side of the UI1 is the dominant morphological pattern. Several other morphological patterns, such as marginal ridges and foveae are also found. The manner of co-occurence of the variable traits does not follow a predictable pattern. A basal swelling may be found with or without foveae or marginal ridges. Most importantly, although there is a predominant morphological pattern, variations about this morphology are found at all taxonomic levels – from the population to the species. This demonstration of the nature of variation in this morphology in the extant context, whereby variable morphotypes are found within all populations in all extant hominoid genera, suggests an underlying pattern of inherent diversity in the expression of this morphology. That this is a pattern is strengthened by the demonstration of similar diversity in modern human populations (Scott & Turner, 1997). This has definite implications for the taxonomy of the middle-Miocene apes.

In middle-Miocene locality of Pasalar in Turkey, two central incisor morphs are seen from the same locality (Martin & Andrews, 1993). The dominant morph, with a prominent lingual pillar, represented by about 90% of the population, corresponds with the basal bulge morph in the extant context. The rarer morph, with a cingulum skirting the cervical margin, has a similar counterpart in the extant

context, with a similar level of representation within modern hominoid populations. The Pasalar pattern falls within the expected range of variation of modern populations for this morphology. The overwhelming demonstration of this pattern of variation in all populations in the modern context suggests that lingual incisor morphology cannot be used to promote the presence of two species at Pasalar. Martin & Andrews (1993) have suggested that there are additional features of the molar dentition that indicate the presence of two possible species. As demonstrated above, incisor traits if used in conjunction with molar traits can be used to strengthen the argument of two species at Pasalar. However, associated material with large samples are required for this purpose. In conclusion, based on the material as presented from Pasalar, this study does not suggest the presence of two ape species from this region.

Equatorius, from Africa is differentiated from *Kenyapithecus* at the level of the genus based on similarity in incisor morphology between this material and Pasalar (Ward *et al.*, 1999). The available fossil material of *Equatorius* is not large enough to demonstrate the nature of variation in this morphological pattern. Since this study does not support the presence of two species at Pasalar, based on incisor morphology alone, the status of *Equatorius* as distinct from *Kenyapithecus* is also cast in doubt. Unless additional fossil material shows that the alleged incisor morphology lies outside the range of variation for this morphology in modern hominoids, a situation that is unlikely given the robust demonstration of this pattern

in the extant context, the status of *Equatorius* as distinct from *Kenyapithecus* is not supported.

Dryopithecus crusafonti is differentiated from *D. laietanus* on the basis several molar features, but the most striking difference is in the morphology of incisors (Begun, 1992). *Dryopithecus crusafonti*, from Can Ponsic is represented by only three incisors, all of which have a median lingual pillar. *Dryopithecus laietanus*, from Can Llobaters, about 15 km away, is represented by four incisors, which have a cingulum skirting the cervical margin. This discrete and non-overlapping pattern of incisor morphology has been used to suggest the presence of two species in these localities (Begun *et al*., 1990). Assessing this taxonomic attribution from the point of view of variation in this morphology in extant hominoids, is difficult, given the small sample size. The occurrence of 3 incisors with a median lingual pillar in Can Ponsic is within the expected range of variation for this morphology in modern hominoids. Central incisors with a median lingual pillar (or a basal bulge) are represented at a high frequency (about 80%, Table 6.4) in modern great ape populations. This is also the dominant morph in Pasalar, also from the middle Miocene, where sample sizes for central incisors are considerably larger.

From Can Llobateres all four incisors (albeit from three individuals) exhibit a lingual incisor morphology that is both invariable and different from Can Ponsic. A morphological pattern similar to that, with the cingulum restricted to the cervical margin occurs at a frequency of only about 10% in the extant apes. Given that

representation, randomly drawing a sample of three of this morph from the extant sample is statistically unlikely (although not improbable). Ultimately, the patterns of variation within extant great apes in lingual incisor morphology cannot be used to convincingly falsify the hypothesis of two *Dryopithecus* species in Spain. Yet, given the nature of variability in the modern context, with such sample sizes no great confidence can be placed in this hypothesis.

Conclusions

Extant hominoids exhibit a wide variety of morphological features on the lingual face of incisors. The morphological patterns displayed by the hylobatids differ markedly from those seen in the great apes. Great ape lingual incisor morphology has several features that are unlike that seen in the hominoids from the Miocene, but the range of variability in incisor morphology in the great apes encompasses that seen in the Miocene hominoids. In species, subspecies and in some cases, populations of hominoids, significant differences are detected in the frequency of occurrence of morphological traits. The differences cannot be correlated with sex or size, however, and dietary associations, if present, cannot be substantiated. In the absence of known adaptive significance it is concluded that incisor morphology at least in the modern great apes is nonselective in nature and differences in morphological patterns are driven by drift.

If the patterns of variation in the modern hominoids can be used as models it suggests that incisor morphology can be of significant use as a taxonomic indicator only when supplemented by other dental characters and when adequate

sample sizes are available to appreciate the nature of variation in incisor morphology. On its own incisor morphology has limited utility as a taxonomic indicator, but using associated dental material in taxonomic reconstruction can enhance its utility.

CHAPTER SEVEN

Summary and Conclusions

Introduction

In this dissertation I have sought to establish a correspondence between paleontological and neontological systematics. Since teeth are commonly preserved as fossils, I have focused on documenting patterns of variation throughout the dentition in chimpanzees and gorillas, as well as of variation in incisor morphology in all extant hominoids. My proximate goals were to seek answers to the following questions: (1) what, if any, dental characters can be used to differentiate subgroups within African apes, (2) what is the nature of variation in such characters, and (3) do population divisions recognized using dental material correspond with the divisions established using other kinds of data? Answers to these questions are crucial for understanding the relationship between neontological species and paleospecies, especially if we seek to use models based on neontological species for recognizing species in the fossil context.

As described in Chapter One, there is a significant qualitative difference in the types of data used by neontologists and paleontologists when recognizing species. Neontologists have access to aspects of behavior, ecology, external morphology and the molecular structure of extant forms. Paleontologists generally have to be content with hard-tissue anatomy, mostly teeth, and typically deal with small sizes and incomplete preservation. Despite differences in the tools of their trade, the quest of both groups of systematic biologists in recognizing species is the

same; namely, to identify populations which have a cohesive gene pool and form a single evolutionary lineage. As outlined in Chapter One, the differences in kinds of data have spurred the development of alternative concepts of species and how to recognize them. In attempting to balance the two main criteria of a well-defined concept – theoretical compactness (ontology) and ease of application (epistemology) – species concepts have been put forth that, although unintentional, are applicable only to particular kinds of data. Thus, there is the Biological Species Concept (Mayr, 1942) and the Recognition Concept (Paterson, 1985), which are formulated with extant taxa in mind, and there is the Phylogenetic Species Concept (Nelson & Platnik, 1981) and the Hennigian Species Concept (Hennig, 1966) that are best applied to fossil taxa. Both types of concepts have their strengths and weaknesses, in both theory and applications. As emphasized in Chapter One, despite fundamental differences in their conceptions of what constitutes a species, the actual means for recognizing species is the same for all of the concepts, namely, by using indirect phenotypic criteria, whether molecules or morphology. There is an implicit assumption that the populations that share a common gene pool also share phenotypic distinctiveness. It is assumed, in addition, that species in the neontological and paleontological context are equivalent. My ultimate goal in this thesis was to test this assumption of equivalence, and then make suggestions regarding the use of extant species as models for the ranges and patterns of variation in fossil species.

In this chapter I would like to summarize the main findings of my research. Based on these findings I would like to comment, first, on the assumption of equivalence between neontological and paleontological species, second, on the efficacy of the alternative species concepts in recognizing species in the modern and fossil context, and finally, on the utility of models from the extant context for recognizing fossil species.

Summary of findings

(1) **Dental data are capable of differentiating species and subspecies of extant hominoids.** Using quantitative and qualitative dental characters the two species of *Pan*, and the eastern and western lineages of *Gorilla* were differentiated with a high level of accuracy. The four subgroups of *Pan* (three subspecies of *P. troglodytes* and *P. paniscus*), and the four main subgroups of *Gorilla* (Nigerian, Western lowland, Eastern lowland and Eastern highland) were also readily differentiated. Using only incisor morphology, I was able to differentiate all species and subspecies of extant hominoids with similar levels of success.

(2) **Not all subspecies are equally well-differentiated using dental data.** Of the subspecies of *P. troglodytes*, *P. t. verus* was clearly divergent, but *P. t. troglodytes* and *P. t. schweinfurthii* were not easily separated. Several isolated populations of *Gorilla* were distinguished in East Africa, but in West Africa gorilla populations were not easily distinguishable in dental morphology.

(3) **Dental differences are of degree rather than kind.** Dental differences were detected in nearly all tooth types, and these could be used to differentiate the

known species and subspecies of African apes. However, the differences were of a qualitative nature. Species and subspecies were differentiated on the basis of the frequency of occurrence of dental traits, rather than the presence or absence of traits. In lingual incisor morphology the species of *Pan* and *Hylobates*, and the subspecies of all extant hominoids were readily differentiated, but in every case, the difference lay in the frequency at which the traits were manifest within each group. This attests to the high levels of diversity in dental morphology in extant hominoids.

The morphology of the lingual face of incisors differs in gibbons and great apes in a non-overlapping manner. Gibbon upper central incisors commonly have a ridge-like cingulum bordering the cervical margin. Great ape incisors display a basal swelling or a median lingual pillar.

(4) **Dental differences can be related to size, shape and genetic drift, but the role of diet is difficult to demonstrate.** The two species of *Pan* were mainly differentiated by overall dental size. When the dental variables were transformed to remove the effect of overall tooth size, the species were not as clearly differentiated. In *Gorilla* size (isometric or allometric) was not an important factor in causing separation. The groups were differentiated based on a combination of dental traits suggesting the role of shape in causing group separation. For several of the dental traits, functional underpinnings could not be established, and therefore it was assumed that genetic drift was the primary influence in driving differences. Lingual incisor morphology in the extant great

apes is one such example. Morphological features on the lingual side of upper central incisors differ between species and subspecies of extant great apes, but they do not correlate with size, sex or diet. In modern humans, upper central incisor traits similarly differ in frequency of occurrence between populations and serve as population markers.

It is commonly assumed that dental morphology can be used to reconstruct dietary patterns. In this study, several attempts were made to establish a correlation between dental morphological patterns and dietary behaviors. However, such a correlation could not be substantiated with any degree of confidence. Features related to folivory were seen in the dentition of all gorillas, but these could not be used to differentiate mountain gorillas from lowland gorillas based on their greater reliance on folivory.

(5) **Populational structuring of dental variation differs in chimpanzees and gorillas.** Chimpanzees were characterized by a pattern of dental variation where most of the variation within the species was visible at the level of the local population. In gorillas dental variation increased sequentially up the taxonomic hierarchy. This pattern can be related to the biogeographic history and the pattern of dispersal of the apes. *Gorilla* habitats, especially in East Africa, are affected by tectonic movements, isolating several populations. Chimpanzee habitats are continuous, except where interrupted by geographical barriers, such as rivers. Chimpanzee females disperse out of their natal group and join another group. There is a high level of contact between groups. Gorilla

males move out of their natal group, and then move into a new group, but since there is no contact between isolated groups there is no gene flow. The social structure and patterns of dental diversity suggest a difference in modes of speciation between the two African ape taxa.

(6) **On their own chimpanzee and gorilla patterns of diversity have limited utility as models against which patterns of variation in fossil hominoid species can be compared.** Patterns of dental diversity in chimpanzees and gorillas showed remarkable differences. The differences reflect their unique evolutionary history, and ecological and social adaptive strategies. Used as models these taxa will lead to differences in hypotheses regarding patterns of diversity in fossil forms. A chimpanzee model will allow high levels of diversity with a low power for recognizing distinct morphs, whereas a gorilla model will suggest low levels of diversity with a higher likelihood of recognizing distinct morphs as independent taxonomic units.

(7) **Patterns of diversity in lingual incisor morphology can be used to reassess the alpha-taxonomy of Miocene hominoid species.** The nature of variability in lingual incisor morphology in the modern great apes suggests that the two incisor morphs from the middle Miocene locality of Pasalar fall within the expected range of variation for a single population. The extant data do not support the presence of two species at this locality. They consequently also do not support the generic distinction of *Equatorius* from *Kenyapithecus*. The presence of two distinct non-overlapping lingual incisor morphs at Can Ponsic

and Can Llobateres in Spain could indicate taxonomic separation but this will need to be substantiated with larger samples.

(8) **Associated material, with a combination of characters from the anterior and posterior dentition have greater utility in differentiating species than incisor morphology alone.** Because of the level of diversity in extant great apes, incisor morphology alone cannot be used to differentiate the two species of *Pan*. When combined with dental characters from the posterior dentition the two species were easier to differentiate.

Implications for species concepts and fossil species recognition

The findings of this study suggest that all extant hominoids exhibit high levels of diversity in dental morphology. Dental traits are useful for differentiating species and subspecies but, as explained above, the most important differences are found in the frequency of occurrence of traits. Such levels and patterns of diversity make it problematic for recognizing species in the paleontological context. Fossils, with incomplete material and small samples, do not display the levels of diversity seen in modern samples. In addition, patterns of diversity that result from gene flow, such as that seen in chimpanzees are unlikely to be detected at small sample sizes. Species concepts that use unique combinations of character states for recognizing species, such as the Hennigian or the Phylogenetic Species concept could lead to erroneous counts of species numbers in the fossil context. At small sample sizes the chimpanzee and gorilla dental material used in this study is likely to be divided into several distinct morphs. With an increase in sample size, and the

demonstration of variation, there will be difficulty in selecting a unique combination of characters for differentiating species, and the number of species recognized could be fewer than that commonly recognized.

The Biological Species Concept or the Recognition Concept, which also use phenotypic differences in recognizing species, are likewise likely to overlook the levels and patterns of diversity in extant hominoids if encountered as fossils. In general, no matter which species concept is used as a guiding principle, a display of diversity is used either as an argument to lump together fossil specimens into a single taxonomic category, or to disregard the character that displays diversity. Without an appreciation of how the diversity is partitioned, and an understanding that frequency differences could be pertinent, the types of dental characters that differentiate subgroups of extant hominoids are likely to have little value in the paleontological context.

Ultimately, it appears that there is a lack of congruence between the concept of a species and the means for recognizing species. This is true both in the neontological and paleontological context. In so far as phenotypic criteria are uniformly used by all species concepts for recognizing species, and none provide means for appreciating the nature of diversity in recognizing species, there is no justifiable reason for supporting any one species concept over another. However, if similar patterns of population structure can be diagnosed using different types of data, it will provide justification for recognizing those patterns. This suggests that species, or lower order taxonomic groups can be recognized not so much by what

concept is used in the endeavor but whether there is unanimity of opinion from disparate datasets and methodologies regarding the taxonomic categories recognized. This approach of reciprocity between datasets could also help in understanding the nature of diversity encountered. If a similar pattern of diversity is displayed using variable types of data, it would strengthen the presence of the pattern and perhaps permit an explanation for the underlying pattern. Thus, high levels of diversity within chimpanzee populations were demonstrated using craniometric (Shea & Coolidge, 1988), molecular (Morin *et al.*, 1994) and dental (this study) data, strengthening hypotheses of extensive gene flow.

If validity from multiple fronts provides the only means for recognizing species in the recent context, this is also a useful approach in the fossil context. A convergence of opinion based on, for example, cranial, dental and postcranial data, would imply that there is justification for recognizing the underlying pattern. Because of meager samples, however, one must test hypotheses for fossil patterns of diversity based on similar patterns of diversity in modern forms. The evidence from this study suggests that patterns of diversity in modern forms are influenced by their unique modes of speciation, questioning the utility of such models for recognizing the patterns of diversity in fossil species.

In this study chimpanzees and gorillas were found to have differences in patterns of diversity, resulting in the likelihood that they would offer disparate hypotheses for explaining patterns of diversity in fossil forms. This presents a conundrum for utilizing models from the extant context for partitioning the

diversity in fossil forms. It is also seen, however, that similar patterns of diversity are encountered in modern humans as in chimpanzees. Given their phylogenetic affinity, established using several independent lines of evidence, it is possible that this similarity in pattern of diversity comes from their shared phylogenetic history. This makes chimpanzee models (along with modern humans) uniquely appropriate for applying to appraising patterns of diversity in fossil hominines. Jolly (2001) has proposed that baboons offer an appropriate model for assessing patterns of diversity in fossil hominines, because the patterns of reticulation and gene flow displayed by baboons are similar to that in modern humans, and was therefore likely to have been the case with extinct hominines. This study suggests that chimpanzees are similar in this regard, but in their case the similarity is because of a shared phylogenetic history.

Extant taxa that have similar patterns of diversity, either due to shared phylogenetic history or similar modes of speciation are likely to be more appropriate as models for recognizing fossil species. For understanding patterns of diversity in Miocene hominoids, therefore, appropriate models need to be drawn from all modern hominoids. Kelley (1993) has argued that modern hominoids are similar to the hominoids from the Miocene period in that they are characterized by a reduction in taxonomic diversity in any single locality. Therefore, modern hominoids provide the only and best model for differentiating Miocene hominoid species. The findings of this study would suggest that modern hominoids are also influenced by their unique evolutionary trajectories, and their patterns of diversity

differ because of that. It is important, when building models based on extant species, therefore to situate them firmly within their own adaptive and evolutionary context. While extant hominoids may provide the most appropriate models for Miocene hominoid fossil recognition, underlying themes of diversity that bind all extant hominoids are likely to be of greater utility than any single extant hominoid species.

The models developed in this thesis provide a starting point for recognizing species in the fossil context. Such an approach, which situates the models firmly within the modern context, and explains their unique patterns of diversity prior to applying them for recognizing fossil species, is essential for recognizing the nature and patterns of diversity in extinct taxa.

APPENDIX 1

Mean linear dental dimensions, CV and R% of *Pan* populations, subspecies and species. Sex pooled.

Pop 1: South of River Gambia to West of River Sassandra							
Variable	Mean	Std Dev	Minimum	Maximum	N	CV	R%
UI1MD	11.87	0.63	10.81	13.22	18	5.30	20.30
UI1BL	9.48	0.38	8.59	10.01	18	4.06	14.99
UI2MD	8.99	0.65	7.94	10.30	19	7.18	26.25
UI2BL	8.83	0.67	7.74	10.62	19	7.57	32.53
UCMD	12.47	1.52	9.99	15.48	20	12.20	44.04
UCBL	10.04	1.55	8.15	14.56	20	15.38	63.57
UP3MD	8.36	0.62	7.40	9.95	30	7.42	30.40
UP3BL	10.44	0.70	7.96	11.40	30	6.76	33.02
UP4MD	7.50	0.60	6.23	8.52	28	7.95	30.68
UP4BL	10.29	0.56	9.09	11.32	28	5.47	21.65
UM1MD	10.70	0.47	9.85	11.72	26	4.40	17.41
UM1BLMES	11.02	0.45	10.28	12.06	26	4.10	16.23
UM1BLDIS	10.82	0.56	9.86	11.94	26	5.18	19.21
UM2MD	10.15	0.61	9.16	11.46	30	5.99	22.66
UM2BLMES	11.10	0.66	10.04	12.71	30	5.93	24.11
UM2BLDIS	10.04	0.74	8.62	11.54	30	7.32	29.05
UM3MD	9.25	0.77	7.97	11.42	28	8.29	37.31
UM3BLMES	10.41	0.80	9.17	12.34	28	7.65	30.41
UM3BLDIS	8.72	0.81	7.12	10.65	28	9.26	40.47
LI1MD	7.99	0.47	7.21	8.81	17	5.89	20.00
LI1BL	8.69	0.51	8.05	9.89	16	5.82	21.15
LI2MD	8.68	0.68	7.40	10.14	19	7.88	31.57
LI2BL	9.25	0.45	8.59	10.17	19	4.86	17.09
LCMD	12.15	1.56	10.00	15.26	19	12.86	43.32
LCBL	10.19	1.20	8.26	12.64	19	11.80	42.94
LP3MD	11.06	0.60	9.66	12.00	25	5.46	21.20
LP3BL	8.71	0.57	7.84	9.82	25	6.50	22.74
LP4MD	8.06	0.61	6.92	9.61	26	7.52	33.38
LP4BL	9.37	0.71	8.14	10.76	26	7.55	27.95
LM1MD	11.20	0.49	10.32	12.25	25	4.35	17.23
LM1BLMES	9.59	0.47	8.75	10.54	25	4.86	18.61
LM1BLDIS	10.08	0.48	9.15	11.19	25	4.77	20.21
LM2MD	11.05	0.57	10.15	12.20	25	5.19	18.61
LM2BLMES	10.46	0.60	9.24	11.80	25	5.74	24.52
LM2BLDIS	10.17	0.49	9.30	11.00	25	4.84	16.71
LM3MD	10.42	0.66	9.35	11.73	26	6.32	22.82
LM3BLMES	9.83	0.64	8.48	11.00	26	6.50	25.67
LM3BLDIS	9.29	0.59	8.28	10.37	26	6.39	22.53

Pop 6: South of R. Sanaga, East of R. Dja and West of R. Ubangi							
Variable	Mean	Std Dev	Minimum	Maximum	N	CV	Range
UI1MD	11.87	0.68	10.31	12.93	23	5.71	22.13
UI1BL	9.44	0.67	8.08	11.09	23	7.14	31.88
UI2MD	8.79	0.71	7.04	9.75	24	8.08	30.88
UI2BL	8.47	0.59	7.21	9.75	24	7.00	29.96
UCMD	12.59	1.84	9.84	16.72	27	14.60	54.58
UCBL	10.12	1.33	8.41	14.02	27	13.07	55.39
UP3MD	8.14	0.78	6.57	9.71	28	9.61	38.55
UP3BL	10.36	0.83	8.32	12.12	28	7.99	36.63
UP4MD	7.32	0.65	6.22	8.85	28	8.91	35.96
UP4BL	9.98	0.59	8.50	11.22	28	5.93	27.25
UM1MD	10.10	0.51	9.00	11.06	26	5.03	20.35
UM1BLMES	10.42	0.60	9.03	11.43	26	5.72	23.05
UM1BLDIS	10.29	0.60	9.11	11.42	26	5.82	22.41
UM2MD	10.10	0.67	8.69	11.25	29	6.62	25.29
UM2BLMES	10.76	0.63	9.59	11.99	29	5.85	22.24
UM2BLDIS	10.04	0.80	8.26	11.62	29	7.95	33.38
UM3MD	9.35	0.59	8.22	10.61	27	6.34	25.51
UM3BLMES	10.28	0.70	8.98	12.31	27	6.80	32.32
UM3BLDIS	8.97	0.76	7.64	10.65	27	8.49	33.59
LI1MD	7.61	0.52	6.13	8.51	24	6.86	31.39
LI1BL	8.66	0.55	7.64	9.75	24	6.31	24.41
LI2MD	8.26	0.54	7.03	9.27	23	6.53	27.16
LI2BL	9.08	0.55	7.99	10.32	23	6.04	25.70
LCMD	11.80	1.36	9.91	14.91	25	11.54	42.35
LCBL	10.48	1.22	8.40	12.98	25	11.62	43.71
LP3MD	10.96	0.71	9.13	12.29	27	6.49	28.83
LP3BL	8.57	0.62	7.42	10.00	27	7.27	30.10
LP4MD	7.64	0.60	6.61	9.02	27	7.80	31.60
LP4BL	8.53	0.71	7.32	10.10	27	8.37	32.64
LM1MD	10.77	0.54	9.78	12.01	24	5.01	20.71
LM1BLMES	9.13	0.57	8.11	10.20	24	6.22	22.91
LM1BLDIS	9.58	0.59	8.51	10.75	24	6.17	23.36
LM2MD	11.22	0.60	10.08	12.23	27	5.33	19.15
LM2BLMES	9.84	0.53	8.63	10.98	27	5.38	23.88
LM2BLDIS	9.96	0.55	8.89	11.02	27	5.55	21.32
LM3MD	10.62	0.57	9.38	11.70	26	5.38	21.83
LM3BLMES	9.46	0.61	8.37	11.05	26	6.50	28.26
LM3BLDIS	9.37	0.56	8.36	10.77	26	5.96	25.66

Pop 10, 11, 12: South of R. Uele, East of R. Zaire, North of L. Tanganiyika							
Variable	Mean	Std Dev	Minimum	Maximum	N	CV	Range
UI1MD	11.64	0.92	9.64	13.42	24	7.90	32.51
UI1BL	9.18	0.51	8.03	10.05	24	5.51	22.01
UI2MD	8.70	0.85	7.19	10.76	25	9.75	40.99
UI2BL	8.48	0.62	7.23	9.58	25	7.30	27.76
UCMD	12.93	2.11	10.01	17.05	27	16.34	54.44
UCBL	10.40	1.59	8.20	14.06	27	15.32	56.32
UP3MD	7.81	0.53	6.91	8.94	28	6.82	25.98
UP3BL	10.39	0.82	8.65	11.84	28	7.87	30.67
UP4MD	7.60	0.69	6.47	9.17	27	9.08	35.56
UP4BL	10.04	0.52	8.91	11.05	27	5.14	21.33
UM1MD	10.56	0.54	9.36	11.61	28	5.09	21.33
UM1BLMES	10.73	0.56	9.60	11.96	28	5.23	22.06
UM1BLDIS	10.38	0.58	9.17	11.55	28	5.62	22.93
UM2MD	10.31	0.57	9.00	11.42	29	5.56	23.49
UM2BLMES	10.79	0.62	9.47	12.01	29	5.72	23.56
UM2BLDIS	10.20	0.67	8.74	11.36	29	6.53	25.72
UM3MD	9.38	0.90	7.61	11.21	24	9.61	38.34
UM3BLMES	10.14	0.69	8.59	11.76	24	6.82	31.23
UM3BLDIS	8.85	0.85	7.30	10.95	24	9.60	41.30
LI1MD	7.67	0.48	6.54	8.59	25	6.25	26.74
LI1BL	8.63	0.53	7.44	9.47	25	6.12	23.45
LI2MD	8.16	0.71	7.16	10.10	24	8.70	36.01
LI2BL	8.83	0.54	7.72	9.80	24	6.06	23.58
LCMD	11.93	1.43	9.78	14.91	25	11.98	43.00
LCBL	10.54	1.24	8.19	12.82	25	11.76	43.94
LP3MD	10.63	0.86	9.02	12.39	27	8.13	31.75
LP3BL	8.48	0.61	7.21	9.87	27	7.23	31.42
LP4MD	7.75	0.62	6.52	8.92	27	8.01	31.02
LP4BL	8.94	0.69	7.69	10.18	27	7.67	27.85
LM1MD	10.97	0.61	9.86	12.34	25	5.59	22.64
LM1BLMES	9.49	0.54	8.43	10.55	25	5.68	22.38
LM1BLDIS	9.64	0.58	8.58	10.99	25	5.99	24.91
LM2MD	11.44	0.70	9.95	12.50	28	6.16	22.28
LM2BLMES	10.08	0.60	9.02	11.09	28	5.93	20.51
LM2BLDIS	10.01	0.60	8.85	11.22	28	6.00	23.68
LM3MD	10.95	0.73	9.53	12.15	22	6.65	23.97
LM3BLMES	9.62	0.53	8.40	10.57	22	5.49	22.62
LM3BLDIS	9.34	0.68	8.10	10.44	22	7.24	25.09

Pop15: South and West of R. Zaire, East of R. Lomani							
Variable	Mean	Std Dev	Minimum	Maximum	N	CV	Range
UI1MD	10.34	0.89	8.52	11.95	22	8.58	33.20
UI1BL	7.71	0.47	7.03	8.99	22	6.10	25.37
UI2MD	7.47	0.71	5.86	8.76	22	9.56	38.75
UI2BL	7.08	0.52	6.29	8.27	22	7.28	27.91
UCMD	9.88	1.16	8.17	12.00	23	11.69	38.70
UCBL	7.73	1.10	6.36	10.26	23	14.21	50.51
UP3MD	7.37	0.63	6.24	8.70	29	8.56	33.40
UP3BL	9.26	0.50	8.47	10.27	29	5.43	19.44
UP4MD	6.35	0.72	4.37	7.83	28	11.33	54.51
UP4BL	8.69	0.52	7.64	10.11	28	6.04	28.40
UM1MD	8.86	0.42	8.02	9.56	24	4.77	17.42
UM1BLMES	9.49	0.57	8.40	10.95	24	6.03	26.80
UM1BLDIS	9.38	0.34	8.58	10.02	24	3.66	15.28
UM2MD	9.00	0.46	7.80	10.04	28	5.10	24.91
UM2BLMES	9.62	0.48	8.72	10.93	28	4.95	23.02
UM2BLDIS	8.89	0.65	7.88	10.64	28	7.35	31.10
UM3MD	8.35	0.56	7.57	9.31	19	6.66	20.83
UM3BLMES	9.25	0.61	8.30	10.45	19	6.61	23.22
UM3BLDIS	7.73	0.72	6.52	9.23	19	9.37	34.96
LI1MD	7.24	0.60	6.11	8.53	22	8.24	33.46
LI1BL	6.96	0.46	6.08	7.97	22	6.58	27.14
LI2MD	7.50	0.65	6.08	8.47	22	8.69	31.85
LI2BL	7.00	0.37	6.45	8.05	22	5.30	22.84
LCMD	9.04	0.91	7.39	10.82	25	10.11	38.04
LCBL	7.71	0.83	6.38	9.20	25	10.76	36.61
LP3MD	8.99	0.50	7.85	10.23	28	5.55	26.38
LP3BL	7.36	0.48	6.26	8.23	28	6.56	26.85
LP4MD	6.95	0.58	5.69	8.36	28	8.41	38.46
LP4BL	7.85	0.61	6.58	9.03	28	7.73	31.22
LM1MD	9.99	0.46	9.16	10.81	23	4.64	16.54
LM1BLMES	8.64	0.44	7.75	9.44	23	5.05	19.58
LM1BLDIS	8.77	0.39	7.86	9.53	23	4.49	19.06
LM2MD	10.29	0.58	8.95	11.33	27	5.61	23.13
LM2BLMES	8.97	0.51	7.68	10.11	27	5.63	27.10
LM2BLDIS	8.81	0.50	7.80	10.05	27	5.68	25.52
LM3MD	9.19	0.51	8.05	10.06	20	5.57	21.85
LM3BLMES	8.27	0.57	7.18	9.34	20	6.88	26.19
LM3BLDIS	8.11	0.52	7.18	9.30	20	6.42	26.10

P. t. verus: South of R. Gambia to west of R. Niger							
Variable	Mean	Std Dev	Minimum	Maximum	N	CV	Range
UI1MD	11.97	0.66	10.85	13.22	16	5.49	19.79
UI1BL	9.50	0.41	8.63	10.11	16	4.28	15.59
UI2MD	9.05	0.66	7.99	10.28	16	7.30	25.26
UI2BL	8.86	0.64	7.80	10.43	16	7.25	29.62
UCMD	12.55	1.48	10.11	15.49	19	11.77	42.89
UCBL	10.05	1.47	8.18	14.16	20	14.58	59.27
UP3MD	8.36	0.63	7.21	9.94	30	7.59	32.66
UP3BL	10.45	0.73	8.09	11.58	30	6.97	33.48
UP4MD	7.56	0.70	6.25	9.52	28	9.27	43.12
UP4BL	10.22	0.75	7.77	11.29	28	7.35	34.49
UM1MD	10.72	0.46	9.89	11.68	26	4.28	16.72
UM1BLMES	11.02	0.44	10.31	12.01	26	3.95	15.38
UM1BLDIS	10.82	0.53	9.90	11.91	26	4.88	18.59
UM2MD	10.20	0.58	9.19	11.42	29	5.73	21.83
UM2BLMES	11.14	0.64	10.06	12.64	29	5.74	23.16
UM2BLDIS	10.08	0.71	8.68	11.48	29	7.00	27.72
UM3MD	9.32	0.73	8.02	11.27	27	7.87	34.84
UM3BLMES	10.46	0.76	9.20	12.25	27	7.25	29.15
UM3BLDIS	8.73	0.76	7.19	10.49	27	8.68	37.77
LI1MD	8.03	0.48	7.24	8.80	15	5.92	19.43
LI1BL	8.73	0.50	8.08	9.83	15	5.67	19.99
LI2MD	8.72	0.67	7.46	10.06	17	7.64	29.80
LI2BL	9.28	0.43	8.60	10.13	17	4.68	16.45
LCMD	12.19	1.55	10.04	15.20	18	12.72	42.37
LCBL	10.16	1.15	8.34	12.53	18	11.35	41.20
LP3MD	11.02	0.73	8.85	11.99	23	6.68	28.60
LP3BL	8.82	0.72	7.86	10.87	23	8.19	34.06
LP4MD	8.06	0.59	6.98	9.49	23	7.30	31.12
LP4BL	9.38	0.68	8.17	10.69	23	7.20	26.79
LM1MD	11.23	0.48	10.37	12.19	22	4.25	16.18
LM1BLMES	9.63	0.47	8.77	10.51	22	4.87	18.05
LM1BLDIS	10.12	0.48	9.20	11.14	22	4.76	19.19
LM2MD	11.12	0.60	10.16	12.18	23	5.39	18.22
LM2BLMES	10.51	0.61	9.30	11.81	23	5.83	23.88
LM2BLDIS	10.23	0.50	9.34	11.12	23	4.85	17.43
LM3MD	10.45	0.64	9.38	11.66	23	6.08	21.81
LM3BLMES	9.87	0.62	8.56	10.96	23	6.24	24.31
LM3BLDIS	9.34	0.60	8.30	10.42	23	6.37	22.68

P. t. troglodytes: South of R. Sanaga to West of R. Ubangi							
Variable	Mean	Std Dev	Minimum	Maximum	N	CV	Range
UI1MD	11.80	0.83	9.81	13.22	20	7.05	29.04
UI1BL	9.38	0.64	8.26	10.86	20	6.86	27.65
UI2MD	8.73	0.68	7.24	9.90	22	7.79	30.57
UI2BL	8.50	0.58	7.35	9.74	22	6.86	28.03
UCMD	12.83	1.82	10.08	16.56	25	14.19	50.48
UCBL	10.29	1.37	8.36	13.69	25	13.30	51.70
UP3MD	8.11	0.75	6.63	9.61	28	9.27	36.76
UP3BL	10.40	0.75	8.77	12.01	28	7.19	31.20
UP4MD	7.28	0.62	6.20	8.80	28	8.56	35.65
UP4BL	10.11	0.60	8.84	11.48	28	5.92	26.21
UM1MD	10.13	0.56	9.05	11.31	25	5.56	22.33
UM1BLMES	10.48	0.67	9.18	11.94	25	6.40	26.27
UM1BLDIS	10.31	0.60	9.21	11.58	25	5.83	22.96
UM2MD	10.13	0.69	8.79	11.51	29	6.77	26.82
UM2BLMES	10.84	0.74	9.49	12.48	29	6.82	27.61
UM2BLDIS	10.11	0.78	8.41	11.79	29	7.76	33.50
UM3MD	9.31	0.66	8.13	10.72	26	7.06	27.85
UM3BLMES	10.38	0.82	8.85	12.35	26	7.92	33.66
UM3BLDIS	8.99	0.83	7.67	10.97	26	9.29	36.74
LI1MD	7.66	0.59	6.09	8.60	21	7.69	32.94
LI1BL	8.69	0.55	7.64	9.74	21	6.38	24.19
LI2MD	8.39	0.75	7.12	10.45	21	8.88	39.38
LI2BL	9.13	0.62	8.07	10.62	21	6.78	27.90
LCMD	12.00	1.39	9.96	14.85	22	11.60	40.70
LCBL	10.62	1.23	8.56	13.04	22	11.62	42.18
LP3MD	10.90	0.80	8.71	12.34	25	7.39	33.40
LP3BL	8.59	0.70	7.34	10.22	25	8.09	33.51
LP4MD	7.69	0.64	6.59	9.18	25	8.35	33.67
LP4BL	8.76	0.79	7.42	10.61	25	9.04	36.37
LM1MD	10.73	0.56	9.55	11.81	21	5.20	21.01
LM1BLMES	9.14	0.55	8.11	10.18	21	5.98	22.55
LM1BLDIS	9.49	0.57	8.41	10.57	21	5.96	22.74
LM2MD	11.23	0.63	10.10	12.54	25	5.65	21.74
LM2BLMES	9.87	0.61	8.67	11.29	25	6.23	26.54
LM2BLDIS	10.00	0.61	8.91	11.39	25	6.14	24.74
LM3MD	10.66	0.75	9.15	12.31	23	7.02	29.58
LM3BLMES	9.55	0.68	8.33	11.10	23	7.15	29.04
LM3BLDIS	9.37	0.73	7.95	10.95	23	7.74	31.97

P. t. schweinfurthii: East of R. Ubangi, North and East of R. Zaire							
Variable	Mean	Std Dev	Minimum	Maximum	N	CV	Range
UI1MD	11.64	0.88	9.77	13.27	21	7.57	30.09
UI1BL	9.13	0.54	8.02	10.01	21	5.91	21.86
UI2MD	8.70	0.79	7.28	10.54	22	9.10	37.44
UI2BL	8.46	0.58	7.35	9.51	22	6.83	25.54
UCMD	13.19	2.10	10.10	16.87	24	15.90	51.32
UCBL	10.56	1.52	8.25	13.74	24	14.42	51.93
UP3MD	7.89	0.62	6.82	9.36	27	7.87	32.11
UP3BL	10.47	0.78	8.67	11.74	27	7.43	29.34
UP4MD	7.60	0.79	6.07	9.48	26	10.35	44.89
UP4BL	10.01	0.63	8.30	11.06	26	6.26	27.61
UM1MD	10.51	0.57	9.41	11.62	27	5.40	21.10
UM1BLMES	10.66	0.64	9.22	11.88	27	6.03	24.95
UM1BLDIS	10.33	0.64	9.15	11.58	27	6.23	23.47
UM2MD	10.24	0.63	8.80	11.39	29	6.11	25.31
UM2BLMES	10.83	0.63	9.56	12.15	29	5.79	23.96
UM2BLDIS	10.17	0.76	8.28	11.55	29	7.48	32.17
UM3MD	9.38	0.87	7.53	11.04	24	9.28	37.43
UM3BLMES	10.14	0.77	8.62	11.97	24	7.59	33.00
UM3BLDIS	8.91	0.95	7.10	11.07	24	10.62	44.54
LI1MD	7.64	0.49	6.50	8.54	21	6.45	26.74
LI1BL	8.60	0.53	7.52	9.52	21	6.21	23.22
LI2MD	8.20	0.66	7.22	9.91	21	8.06	32.81
LI2BL	8.84	0.53	7.78	9.77	21	6.02	22.52
LCMD	11.99	1.41	9.86	14.74	22	11.76	40.63
LCBL	10.63	1.29	8.30	12.92	22	12.14	43.53
LP3MD	10.69	0.80	9.12	12.27	24	7.50	29.46
LP3BL	8.51	0.61	7.27	9.85	24	7.22	30.31
LP4MD	7.74	0.63	6.60	8.98	24	8.14	30.66
LP4BL	8.97	0.69	7.66	10.25	24	7.69	28.92
LM1MD	10.89	0.59	9.85	12.17	23	5.46	21.24
LM1BLMES	9.40	0.57	8.33	10.47	23	6.10	22.78
LM1BLDIS	9.59	0.58	8.60	10.84	23	6.06	23.42
LM2MD	11.44	0.71	10.04	12.59	25	6.17	22.31
LM2BLMES	10.06	0.62	9.06	11.14	25	6.17	20.73
LM2BLDIS	10.01	0.61	8.90	11.21	25	6.06	23.06
LM3MD	10.94	0.73	9.58	12.14	21	6.67	23.44
LM3BLMES	9.58	0.59	8.37	10.61	21	6.17	23.35
LM3BLDIS	9.32	0.67	8.12	10.41	21	7.22	24.64

P. troglodytes: South of R. Gambia and along North of R. Zaire							
Variable	Mean	Std Dev	Minimum	Maximum	N	CV	Range
UI1MD	11.78	0.82	9.96	13.20	20	6.95	27.58
UI1BL	9.33	0.58	8.22	10.53	20	6.25	24.70
UI2MD	8.77	0.71	7.36	10.16	21	8.12	31.86
UI2BL	8.55	0.60	7.43	9.84	21	7.01	28.10
UCMD	12.88	1.85	10.11	16.50	23	14.39	49.62
UCBL	10.31	1.44	8.28	13.73	23	13.91	52.72
UP3MD	8.11	0.70	6.78	9.61	28	8.69	34.97
UP3BL	10.43	0.74	8.62	11.85	28	7.13	31.02
UP4MD	7.42	0.69	6.19	9.12	27	9.30	39.46
UP4BL	10.11	0.63	8.50	11.32	27	6.26	27.91
UM1MD	10.36	0.59	9.18	11.55	26	5.73	22.89
UM1BLMES	10.65	0.65	9.27	11.93	26	6.12	25.02
UM1BLDIS	10.43	0.63	9.23	11.70	26	6.08	23.68
UM2MD	10.17	0.64	8.87	11.44	29	6.32	25.22
UM2BLMES	10.91	0.69	9.60	12.43	29	6.36	26.00
UM2BLDIS	10.11	0.76	8.45	11.66	29	7.49	31.69
UM3MD	9.32	0.73	7.91	10.89	26	7.78	31.96
UM3BLMES	10.34	0.80	8.88	12.23	26	7.72	32.40
UM3BLDIS	8.91	0.85	7.39	10.91	26	9.52	39.51
LI1MD	7.72	0.55	6.41	8.65	20	7.17	29.08
LI1BL	8.67	0.53	7.67	9.68	20	6.14	23.23
LI2MD	8.40	0.73	7.20	10.21	20	8.61	35.62
LI2BL	9.07	0.58	8.00	10.34	20	6.43	25.69
LCMD	12.02	1.43	9.97	14.88	21	11.85	40.80
LCBL	10.53	1.24	8.49	12.94	21	11.80	42.31
LP3MD	10.86	0.79	8.84	12.23	24	7.28	31.22
LP3BL	8.61	0.68	7.38	10.24	24	7.88	33.20
LP4MD	7.78	0.64	6.64	9.20	24	8.28	32.84
LP4BL	8.94	0.78	7.54	10.56	24	8.71	33.76
LM1MD	10.87	0.58	9.71	11.98	22	5.33	20.91
LM1BLMES	9.32	0.57	8.23	10.35	22	6.10	22.67
LM1BLDIS	9.65	0.60	8.53	10.81	22	6.27	23.65
LM2MD	11.26	0.66	10.10	12.52	24	5.82	21.47
LM2BLMES	10.05	0.65	8.86	11.43	24	6.49	25.59
LM2BLDIS	10.04	0.59	8.96	11.24	24	5.88	22.70
LM3MD	10.67	0.73	9.27	12.15	23	6.86	27.05
LM3BLMES	9.62	0.65	8.40	10.95	23	6.78	26.43
LM3BLDIS	9.34	0.68	8.04	10.72	23	7.31	28.77

P. paniscus: South of R. Zaire							
Variable	Mean	Std Dev	Minimum	Maximum	N	CV	Range
UI1MD	10.37	0.85	8.59	11.94	22	8.23	32.29
UI1BL	7.64	0.49	6.86	8.86	22	6.42	26.20
UI2MD	7.57	0.76	5.95	9.07	22	10.02	41.30
UI2BL	7.11	0.52	6.31	8.21	22	7.25	26.81
UCMD	9.90	1.19	8.19	12.07	24	11.97	39.27
UCBL	7.68	1.05	6.36	10.16	24	13.67	49.47
UP3MD	7.44	0.62	6.25	8.68	29	8.29	32.54
UP3BL	9.28	0.53	8.42	10.33	29	5.76	20.65
UP4MD	6.35	0.74	4.50	7.99	28	11.68	54.99
UP4BL	8.70	0.50	7.65	9.98	28	5.80	26.79
UM1MD	8.78	0.46	7.99	9.54	24	5.29	17.62
UM1BLMES	9.42	0.55	8.43	10.82	24	5.89	25.36
UM1BLDIS	9.28	0.42	8.37	9.99	24	4.51	17.53
UM2MD	8.94	0.47	7.82	9.97	28	5.23	24.04
UM2BLMES	9.56	0.48	8.73	10.82	28	4.97	21.88
UM2BLDIS	8.87	0.64	7.89	10.55	28	7.21	30.00
UM3MD	8.20	0.59	7.34	9.28	21	7.16	23.64
UM3BLMES	9.17	0.56	8.33	10.43	21	6.09	22.98
UM3BLDIS	7.74	0.67	6.55	9.14	21	8.60	33.50
LI1MD	7.20	0.59	6.06	8.48	22	8.21	33.66
LI1BL	6.92	0.47	6.06	7.91	22	6.80	26.61
LI2MD	7.47	0.70	6.08	8.80	23	9.37	36.40
LI2BL	6.98	0.40	6.14	7.96	23	5.76	26.07
LCMD	9.02	0.88	7.46	10.77	26	9.78	36.67
LCBL	7.74	0.88	6.17	9.53	26	11.32	43.38
LP3MD	9.03	0.49	7.90	10.18	28	5.43	25.20
LP3BL	7.42	0.50	6.28	8.27	28	6.75	26.73
LP4MD	6.92	0.60	5.73	8.34	27	8.73	37.81
LP4BL	7.75	0.64	6.49	9.00	27	8.29	32.35
LM1MD	9.85	0.54	8.73	10.78	24	5.50	20.82
LM1BLMES	8.56	0.45	7.75	9.40	24	5.25	19.22
LM1BLDIS	8.65	0.48	7.53	9.51	24	5.59	22.92
LM2MD	10.16	0.66	8.54	11.30	27	6.46	27.18
LM2BLMES	8.86	0.56	7.41	10.02	27	6.30	29.42
LM2BLDIS	8.76	0.51	7.83	9.97	27	5.77	24.44
LM3MD	9.16	0.50	8.04	10.01	22	5.45	21.55
LM3BLMES	8.17	0.58	7.19	9.29	22	7.07	25.65
LM3BLDIS	8.01	0.52	7.15	9.18	22	6.50	25.30

APPENDIX 2

Mean linear dental dimensions, CV and R% of *Gorilla* populations and subspecies. *G. g. diehli* not included because of limited samples.

Pop 4 males: Southern Gabon and Cabinda							
Variable	Mean	Std Dev	Minimum	Maximum	N	CV	R%
UI1MD	13.86	0.91	12.66	15.79	16	6.57	22.58
UI1BL	10.73	0.69	9.49	11.99	16	6.43	23.30
UI2MD	9.55	0.91	8.3	11.96	20	9.53	38.32
UI2BL	9.9	0.88	8.77	11.94	20	8.89	32.02
UCMD	20.54	1.54	16.97	23.79	28	7.50	33.20
UCBL	15.52	1.34	13.24	17.92	28	8.63	30.15
UP3MD	11.98	0.84	10.19	13.74	31	7.01	29.63
UP3BL	15.96	1.02	13.92	17.74	31	6.39	23.93
UP4MD	11.06	0.63	9.84	12.67	32	5.70	25.59
UP4BL	15.25	0.86	13.45	17.13	32	5.64	24.13
UM1MD	14.68	0.79	12.98	16.54	22	5.38	24.25
UM1BLMES	14.17	1.14	11.98	16.22	22	8.05	29.92
UM1BLDIS	13.78	1.02	12.09	15.88	22	7.40	27.50
UM2MD	15.65	0.8	14.06	17.27	31	5.11	20.51
UM2BLMES	15.11	1.1	12.81	17.99	31	7.28	34.28
UM2BLDIS	14.54	0.99	12.68	16.64	31	6.81	27.24
UM3MD	14.82	1.11	11.87	16.85	30	7.49	33.60
UM3BLMES	14.59	1.13	12.95	17.53	30	7.75	31.39
UM3BLDIS	12.77	1.24	9.4	15.4	30	9.71	46.99
LI1MD	7.68	0.44	7.1	8.27	16	5.73	15.23
LI1BL	9.06	0.53	8.02	9.7	16	5.85	18.54
LI2MD	8.83	0.69	7.71	10.42	23	7.81	30.69
LI2BL	10.56	0.62	9.56	12	23	5.87	23.11
LCMD	17.03	1.45	14.45	19.6	29	8.51	30.24
LCBL	14.08	1.18	12.3	16.65	28	8.38	30.89
LP3MD	17.14	1.18	14.2	19.22	31	6.88	29.29
LP3BL	13.78	1.03	11.33	16.09	31	7.47	34.54
LP4MD	11.76	1.29	10.15	15.35	31	10.97	44.22
LP4BL	13.15	1.09	11.48	15.29	31	8.29	28.97
LM1MD	15.36	0.77	13.62	16.8	17	5.01	20.70
LM1BLMES	12.54	0.79	11.16	14.07	17	6.30	23.21
LM1BLDIS	12.72	0.81	11.57	14.06	17	6.37	19.58
LM2MD	17.17	1.03	15.02	19.94	29	6.00	28.65
LM2BLMES	14.28	1.02	12.27	15.97	29	7.14	25.91
LM2BLDIS	14.17	0.91	12.13	15.75	29	6.42	25.55
LM3MD	17.26	1.2	15.36	19.53	31	6.95	24.16
LM3BLMES	13.87	1.16	11.55	16.5	31	8.36	35.69
LM3BLDIS	12.93	1.13	10.24	15.45	31	8.74	40.29

Pop 4 females: Southern Gabon and Cabinda							
Variable	Mean	Std Dev	Minimum	Maximum	N	CV	R%
UI1MD	12.66	0.39	12.38	13.1	3	3.08	5.69
UI1BL	9.66	0.72	8.95	10.38	3	7.45	14.80
UI2MD	7.9	0.73	7.06	8.76	4	9.24	21.52
UI2BL	8.23	0.98	6.91	9.26	4	11.91	28.55
UCMD	14.14	0.64	13.43	15.16	5	4.53	12.23
UCBL	11.75	1.2	10.12	12.96	5	10.21	24.17
UP3MD	10.64	0.81	9.46	11.35	6	7.61	17.76
UP3BL	15.12	0.58	14.25	15.73	6	3.84	9.79
UP4MD	10.58	0.43	9.87	11.04	6	4.06	11.06
UP4BL	14.07	0.44	13.69	14.76	6	3.13	7.60
UM1MD	13.92	0.61	13.34	14.77	4	4.38	10.27
UM1BLMES	13.11	0.29	12.83	13.49	4	2.21	5.03
UM1BLDIS	12.47	0.1	12.36	12.59	4	0.80	1.84
UM2MD	14.41	0.54	14.01	15.43	6	3.75	9.85
UM2BLMES	13.85	0.71	13.03	14.86	6	5.13	13.21
UM2BLDIS	13.04	0.91	11.64	14.22	6	6.98	19.79
UM3MD	13.14	0.5	12.44	13.58	6	3.81	8.68
UM3BLMES	13.1	0.63	12.5	14.04	6	4.81	11.76
UM3BLDIS	11.01	0.79	10.25	12.43	6	7.18	19.80
LI1MD	7.77	0.61	7.11	8.3	3	7.85	15.32
LI1BL	8.5	0.73	7.98	9.34	3	8.59	16.00
LI2MD	8.52	0.18	8.38	8.77	4	2.11	4.58
LI2BL	8.99	0.34	8.7	9.41	4	3.78	7.90
LCMD	12.43	0.2	12.13	12.59	4	1.61	3.70
LCBL	10.95	0.62	10.26	11.72	4	5.66	13.33
LP3MD	14.92	1.02	13.95	16.6	5	6.84	17.76
LP3BL	12.22	0.83	11.07	13.38	5	6.79	18.90
LP4MD	10.89	0.4	10.17	11.11	5	3.67	8.63
LP4BL	12.87	1.09	11.79	14.62	5	8.47	21.99
LM1MD	15.55	0.9	15	16.59	3	5.79	10.23
LM1BLMES	12.57	1.16	11.38	13.69	3	9.23	18.38
LM1BLDIS	12.62	0.68	11.83	13.06	3	5.39	9.75
LM2MD	16.22	0.79	15.39	17.31	5	4.87	11.84
LM2BLMES	13.19	1.58	11.78	15.27	5	11.98	26.46
LM2BLDIS	13.34	0.87	12.48	14.59	5	6.52	15.82
LM3MD	15.73	1.11	14.4	17.16	5	7.06	17.55
LM3BLMES	12.46	1.13	11.5	14.33	5	9.07	22.71
LM3BLDIS	11.54	0.6	10.77	12.12	5	5.20	11.70

Pop 7 males: Inland Cameroon							
Variable	Mean	Std Dev	Minimum	Maximum	N	CV	R%
UI1MD	14.2	1.28	11.89	16.43	21	9.01	31.97
UI1BL	10.96	0.67	10.02	12.42	21	6.11	21.90
UI2MD	9.99	1.04	8.36	12.06	22	10.41	37.04
UI2BL	10.3	0.75	8.64	11.44	22	7.28	27.18
UCMD	21.72	2.04	16.03	24.98	23	9.39	41.21
UCBL	16.12	1.51	12.62	18.2	23	9.37	34.62
UP3MD	12.08	0.82	9.96	13.85	30	6.79	32.20
UP3BL	15.7	0.95	13.76	17.41	30	6.05	23.25
UP4MD	11.08	0.79	9.4	12.53	30	7.13	28.25
UP4BL	15.18	0.85	13.5	16.52	30	5.60	19.89
UM1MD	15.12	0.92	13.56	16.71	25	6.08	20.83
UM1BLMES	14.52	0.98	13.17	16.66	25	6.75	24.04
UM1BLDIS	14.29	0.98	12.58	16.17	25	6.86	25.12
UM2MD	16.19	1.2	14.12	19.19	30	7.41	31.32
UM2BLMES	15.3	1	13.3	17.5	30	6.54	27.45
UM2BLDIS	14.82	1.14	13.04	17.23	30	7.69	28.27
UM3MD	14.94	1.12	12.39	17.08	29	7.50	31.39
UM3BLMES	14.77	1.19	12.27	17.46	29	8.06	35.14
UM3BLDIS	12.79	1.22	10.45	15	29	9.54	35.57
LI1MD	7.9	0.75	6.62	9.69	21	9.49	38.86
LI1BL	9.4	0.63	8.21	10.72	21	6.70	26.70
LI2MD	9.34	0.87	7.83	11.18	23	9.31	35.87
LI2BL	10.81	0.63	9.2	11.89	23	5.83	24.88
LCMD	18.6	1.78	14.44	21.04	22	9.57	35.48
LCBL	14.94	1.54	11.83	18.3	22	10.31	43.31
LP3MD	17.66	1.18	15.32	20.26	27	6.68	27.97
LP3BL	14.28	1.38	11.64	17.19	27	9.66	38.87
LP4MD	11.93	1.11	10.06	15.41	26	9.30	44.84
LP4BL	13.56	1.01	12.13	15.76	26	7.45	26.77
LM1MD	16.32	0.88	14.95	17.76	22	5.39	17.22
LM1BLMES	13.37	0.91	12.21	15.34	22	6.81	23.41
LM1BLDIS	13.18	0.82	11.5	14.58	22	6.22	23.37
LM2MD	17.81	1.09	15.99	19.72	27	6.12	20.94
LM2BLMES	14.98	1.18	12.66	16.95	27	7.88	28.64
LM2BLDIS	14.86	0.97	12.65	16.57	27	6.53	26.38
LM3MD	17.37	1.14	14.78	19.69	25	6.56	28.27
LM3BLMES	14.14	1.21	12.18	16.93	25	8.56	33.59
LM3BLDIS	13.41	0.94	10.82	15.06	25	7.01	31.62

Pop 7 females: Inland Cameroon							
Variable	Mean	Std Dev	Minimum	Maximum	N	CV	R%
UI1MD	13.45	0.56	12.07	14.39	13	4.16	17.25
UI1BL	10.24	0.59	9.57	11.25	13	5.76	16.41
UI2MD	9.34	1.03	7.14	11.63	13	11.03	48.07
UI2BL	9.16	0.84	7.73	10.78	13	9.17	33.30
UCMD	15.05	0.67	13.83	16.39	17	4.45	17.01
UCBL	11.89	1.02	10.03	13.52	17	8.58	29.35
UP3MD	11.12	0.74	9.61	12.92	19	6.65	29.77
UP3BL	14.64	0.72	13.31	15.75	19	4.92	16.67
UP4MD	10.59	0.53	9.62	11.75	19	5.00	20.11
UP4BL	14.36	0.7	13.06	15.87	19	4.87	19.57
UM1MD	14.35	0.57	13.62	15.35	13	3.97	12.06
UM1BLMES	13.33	0.6	12.29	14.45	13	4.50	16.20
UM1BLDIS	13.11	0.57	12.3	14.18	13	4.35	14.34
UM2MD	15.25	0.48	14.42	16.13	19	3.15	11.21
UM2BLMES	14.18	0.52	13.21	15.25	19	3.67	14.39
UM2BLDIS	13.85	0.59	13.04	15.16	19	4.26	15.31
UM3MD	13.53	0.63	12.02	14.55	17	4.66	18.70
UM3BLMES	13.22	0.55	12.23	14.23	17	4.16	15.13
UM3BLDIS	11.42	1	9.95	13.41	17	8.76	30.30
LI1MD	7.58	0.69	6.05	8.72	14	9.10	35.22
LI1BL	8.48	0.58	7.62	9.36	14	6.84	20.52
LI2MD	8.46	0.81	6.27	9.58	14	9.57	39.13
LI2BL	9.65	0.74	8.54	11.16	14	7.67	27.15
LCMD	13.33	0.94	11.93	14.73	16	7.05	21.01
LCBL	11.07	1.12	9.78	13.62	16	10.12	34.69
LP3MD	15.17	0.97	13.15	17.06	18	6.39	25.77
LP3BL	12.43	1.01	10.58	14.13	18	8.13	28.56
LP4MD	11.32	0.81	10.17	13.6	18	7.16	30.30
LP4BL	12.37	0.74	11.33	13.78	18	5.98	19.81
LM1MD	15.32	0.71	14.22	16.52	11	4.63	15.01
LM1BLMES	12.16	0.44	11.52	12.91	11	3.62	11.43
LM1BLDIS	12.38	0.54	11.76	13.63	11	4.36	15.11
LM2MD	16.72	0.79	15.76	18.32	17	4.72	15.31
LM2BLMES	13.63	0.71	12.52	15.56	17	5.21	22.30
LM2BLDIS	13.6	0.67	12.23	14.76	17	4.93	18.60
LM3MD	16.28	0.78	15.02	17.47	16	4.79	15.05
LM3BLMES	13.11	0.54	12.23	13.77	16	4.12	11.75
LM3BLDIS	12.22	0.64	11.25	13.49	16	5.24	18.33

Pop 8 males: Utu							
Variable	Mean	Std Dev	Minimum	Maximum	N	CV	R%
UI1MD	12.57	0.62	11.46	13.57	12	4.93	16.79
UI1BL	10.88	0.52	10.19	11.93	12	4.78	15.99
UI2MD	9.47	0.46	8.61	9.91	10	4.86	13.73
UI2BL	10.69	0.74	9.48	11.63	10	6.92	20.11
UCMD	21.04	1.12	18.92	22.49	15	5.32	16.97
UCBL	16.34	1	14.66	17.94	15	6.12	20.07
UP3MD	11.93	0.55	10.89	13.01	19	4.61	17.77
UP3BL	17.34	0.88	15.72	19.51	19	5.07	21.86
UP4MD	11.8	0.79	9.69	12.92	19	6.69	27.37
UP4BL	16.92	0.87	15.4	18.76	19	5.14	19.86
UM1MD	15.68	0.59	14.94	17.15	13	3.76	14.09
UM1BLMES	15.44	0.8	14.01	16.92	13	5.18	18.85
UM1BLDIS	15.67	0.8	14.54	17.21	13	5.11	17.04
UM2MD	17.57	0.96	15.19	19.05	17	5.46	21.97
UM2BLMES	16.62	0.72	15.54	18.29	17	4.33	16.55
UM2BLDIS	15.85	1.8	11.27	17.96	17	11.36	42.21
UM3MD	16.62	1.16	13.35	18.31	19	6.98	29.84
UM3BLMES	15.48	0.83	14.4	17.06	19	5.36	17.18
UM3BLDIS	14.11	1.19	11.54	16.38	19	8.43	34.30
LI1MD	7.68	0.43	7.04	8.34	7	5.60	16.93
LI1BL	9.65	0.46	9.05	10.27	7	4.77	12.64
LI2MD	8.86	0.79	7.47	10.36	12	8.92	32.62
LI2BL	10.89	0.6	10	11.99	12	5.51	18.27
LCMD	17.15	1.1	15.26	19.48	12	6.41	24.61
LCBL	14.2	0.83	13.17	15.96	12	5.85	19.65
LP3MD	17.35	0.97	16.08	19.31	17	5.59	18.62
LP3BL	14.18	0.73	13.1	15.52	17	5.15	17.07
LP4MD	11.98	0.72	10.81	14.24	17	6.01	28.63
LP4BL	14.44	0.85	12.91	15.45	16	5.89	17.59
LM1MD	16.99	0.38	16.3	17.59	12	2.24	7.59
LM1BLMES	14.16	0.54	13.05	14.85	12	3.81	12.71
LM1BLDIS	14.15	0.57	13.56	15.21	12	4.03	11.66
LM2MD	19.54	0.74	18.19	21.41	15	3.79	16.48
LM2BLMES	16.17	0.98	13.88	18.07	15	6.06	25.91
LM2BLDIS	15.87	0.9	14.09	17.57	15	5.67	21.93
LM3MD	19.32	1.46	16.86	22.45	15	7.56	28.93
LM3BLMES	14.73	1.24	12.36	16.87	15	8.42	30.62
LM3BLDIS	13.89	1.25	11.78	16.1	15	9.00	31.10

Pop 8 females: Utu							
Variable	Mean	Std Dev	Minimum	Maximum	N	CV	R%
UI1MD	12.15	0.89	11.01	13.61	8	7.33	21.40
UI1BL	10.08	0.46	9.4	10.91	8	4.56	14.98
UI2MD	8.79	0.53	8.28	9.81	8	6.03	17.41
UI2BL	9.61	0.49	8.96	10.21	8	5.10	13.01
UCMD	14.68	0.32	14.22	15.18	10	2.18	6.54
UCBL	12.05	0.75	11.15	13.18	10	6.22	16.85
UP3MD	11.35	0.74	10.33	12.83	11	6.52	22.03
UP3BL	16.41	0.69	15.49	17.65	11	4.20	13.16
UP4MD	11.09	0.91	9.46	13.19	11	8.21	33.63
UP4BL	15.74	0.75	14.85	16.99	11	4.76	13.60
UM1MD	14.97	0.49	14.46	15.76	9	3.27	8.68
UM1BLMES	14.6	0.83	12.9	15.86	9	5.68	20.27
UM1BLDIS	14.99	0.69	13.73	16.36	9	4.60	17.55
UM2MD	16.48	0.69	15.64	18	11	4.19	14.32
UM2BLMES	15.4	0.93	13.88	16.97	11	6.04	20.06
UM2BLDIS	15.22	0.6	13.65	15.85	11	3.94	14.45
UM3MD	15.24	0.85	13.88	16.42	8	5.58	16.67
UM3BLMES	14.78	0.81	13.97	16.5	8	5.48	17.12
UM3BLDIS	13.57	0.64	12.95	14.58	8	4.72	12.01
LI1MD	7.55	0.32	7.22	7.96	4	4.24	9.80
LI1BL	8.9	0.42	8.33	9.33	4	4.72	11.24
LI2MD	8.45	0.49	8.11	9.4	6	5.80	15.27
LI2BL	10.13	0.73	9.13	11.05	6	7.21	18.95
LCMD	13.2	0.63	12.49	14.22	7	4.77	13.11
LCBL	11.65	0.54	11.05	12.56	7	4.64	12.96
LP3MD	14.78	1.54	10.88	16.08	9	10.42	35.18
LP3BL	12.48	0.62	11.61	13.43	9	4.97	14.58
LP4MD	11.28	0.73	10.36	12.39	9	6.47	18.00
LP4BL	13.2	0.59	12.34	14.16	9	4.47	13.79
LM1MD	15.89	0.55	15.21	16.76	8	3.46	9.75
LM1BLMES	13.28	0.43	12.57	13.71	8	3.24	8.58
LM1BLDIS	13.27	0.56	12.54	14.09	8	4.22	11.68
LM2MD	18.31	0.78	17.46	19.52	9	4.26	11.25
LM2BLMES	14.82	0.84	13.88	16.42	9	5.67	17.14
LM2BLDIS	14.9	0.59	14.02	15.7	9	3.96	11.28
LM3MD	18.1	1.33	15.72	19.79	9	7.35	22.49
LM3BLMES	14	0.42	13.12	14.56	9	3.00	10.29
LM3BLDIS	13.56	0.78	12.56	14.63	9	5.75	15.27

Pop 11 males: Virunga Volcanoes							
Variable	Mean	Std Dev	Minimum	Maximum	N	CV	R%
UI1MD	13.03	0.57	12.32	13.87	10	4.37	11.90
UI1BL	11.85	0.55	11.02	12.67	10	4.64	13.92
UI2MD	10.07	0.56	9.19	11.15	13	5.56	19.46
UI2BL	11.86	0.85	10.7	13.39	13	7.17	22.68
UCMD	22.87	1.5	20.52	25.64	11	6.56	22.39
UCBL	17.84	1.55	14.95	20.51	11	8.69	31.17
UP3MD	13.15	0.86	11.99	15.01	15	6.54	22.97
UP3BL	16.81	0.83	15.3	18.1	15	4.94	16.66
UP4MD	12.3	1.07	10.63	13.96	15	8.70	27.07
UP4BL	16.11	1.76	10.59	17.94	15	10.92	45.62
UM1MD	15.72	0.72	14.71	16.98	11	4.58	14.44
UM1BLMES	14.76	1.12	12.75	16.29	11	7.59	23.98
UM1BLDIS	15.31	0.65	14.39	16.4	11	4.25	13.13
UM2MD	17.25	1.03	15.74	18.84	14	5.97	17.97
UM2BLMES	16.66	1.24	14.65	18.85	14	7.44	25.21
UM2BLDIS	16.34	0.79	15.33	17.7	14	4.83	14.50
UM3MD	15.86	1.43	13.99	18.61	13	9.02	29.13
UM3BLMES	15.32	1.15	13.59	17.52	13	7.51	25.65
UM3BLDIS	13.65	1.48	11.91	16.47	13	10.84	33.41
LI1MD	7.9	0.64	7.03	8.73	10	8.10	21.52
LI1BL	10.25	0.61	9.47	11.24	9	5.95	17.27
LI2MD	8.91	0.58	8.08	9.69	11	6.51	18.07
LI2BL	11.81	0.61	10.96	13.06	11	5.17	17.78
LCMD	18.98	0.98	17.49	20.59	13	5.16	16.33
LCBL	15.64	0.95	14.01	16.89	13	6.07	18.41
LP3MD	18.25	1.02	16.95	19.94	15	5.59	16.38
LP3BL	14.8	1.05	13.68	17.03	15	7.09	22.64
LP4MD	13.25	0.87	11.74	14.96	15	6.57	24.30
LP4BL	14.49	1.32	12.76	16.76	15	9.11	27.61
LM1MD	16.91	0.63	15.67	17.93	13	3.73	13.36
LM1BLMES	13.44	0.68	12.01	14.43	13	5.06	18.01
LM1BLDIS	14.14	0.52	13.34	15.37	13	3.68	14.36
LM2MD	18.64	1	17.45	20.74	15	5.36	17.65
LM2BLMES	15.77	1.03	14.61	18.02	15	6.53	21.62
LM2BLDIS	15.17	0.78	14.12	16.62	15	5.14	16.48
LM3MD	19.23	1.71	16.8	22.93	14	8.89	31.88
LM3BLMES	14.88	0.85	13.63	16.3	14	5.71	17.94
LM3BLDIS	14.21	0.97	12.95	16.36	14	6.83	24.00

Pop 11 females: Virunga Volcanoes							
Variable	Mean	Std Dev	Minimum	Maximum	N	CV	R%
UI1MD	12.87	0.56	12.17	13.49	7	4.35	10.26
UI1BL	11.04	0.43	10.24	11.58	7	3.89	12.14
UI2MD	9.59	0.52	8.69	10.27	10	5.42	16.48
UI2BL	10.53	0.66	9.53	11.45	11	6.27	18.23
UCMD	14.52	0.73	13.33	15.92	11	5.03	17.84
UCBL	12.24	0.79	11.22	13.7	11	6.45	20.26
UP3MD	11.72	0.75	9.92	12.79	12	6.40	24.49
UP3BL	15.81	0.72	14.96	16.85	12	4.55	11.95
UP4MD	11.67	0.98	10.43	13.32	11	8.40	24.76
UP4BL	15.51	0.62	14.41	16.44	12	4.00	13.09
UM1MD	14.59	0.62	13.62	15.34	11	4.25	11.79
UM1BLMES	13.9	0.83	12.28	14.98	11	5.97	19.42
UM1BLDIS	14.29	0.61	13.19	15.21	11	4.27	14.14
UM2MD	15.72	0.96	13.72	17.12	11	6.11	21.63
UM2BLMES	14.93	0.72	13.6	15.81	11	4.82	14.80
UM2BLDIS	14.67	0.7	13.06	15.56	11	4.77	17.04
UM3MD	14.35	1.01	12.66	15.75	11	7.04	21.53
UM3BLMES	13.89	0.98	12.46	15.41	11	7.06	21.24
UM3BLDIS	12.36	1	10.8	14.44	11	8.09	29.45
LI1MD	7.27	0.69	6.34	8.24	8	9.49	26.13
LI1BL	9.11	0.69	8.35	10.26	8	7.57	20.97
LI2MD	8.48	0.51	7.73	9.51	11	6.01	20.99
LI2BL	10.71	0.73	9.74	11.83	11	6.82	19.51
LCMD	13.1	0.77	12.17	14.07	9	5.88	14.50
LCBL	10.79	0.96	8.92	11.93	9	8.90	27.90
LP3MD	15.4	0.72	14.35	16.92	12	4.68	16.69
LP3BL	12.84	0.75	11.19	13.75	12	5.84	19.94
LP4MD	12.36	0.84	10.63	13.48	12	6.80	23.06
LP4BL	13.5	0.61	12.48	14.27	12	4.52	13.26
LM1MD	15.53	0.54	14.84	16.5	12	3.48	10.69
LM1BLMES	12.62	0.74	11.67	14.05	12	5.86	18.86
LM1BLDIS	13.05	0.56	12.06	14.1	12	4.29	15.63
LM2MD	17.1	0.86	15.19	17.95	12	5.03	16.14
LM2BLMES	14.25	1.13	12.14	16.44	12	7.93	30.18
LM2BLDIS	14.38	0.88	12.89	15.91	12	6.12	21.00
LM3MD	17.45	0.63	16.46	18.64	11	3.61	12.49
LM3BLMES	13.63	0.71	12.33	14.56	11	5.21	16.36
LM3BLDIS	13.14	0.59	12.36	14.2	11	4.49	14.00

G. g. gorilla males: South Of R. Sanaga To R. Congo and R. Sangha							
Variable	Mean	Std Dev	Minimum	Maximum	N	CV	R%
UI1MD	13.93	1.02	11.89	16.43	72	7.32	32.59
UI1BL	10.79	0.67	9.08	12.42	72	6.21	30.95
UI2MD	9.69	1.02	7.77	12.06	79	10.53	44.27
UI2BL	9.98	0.81	8.11	11.94	79	8.12	38.38
UCMD	21.08	1.77	16.03	24.98	91	8.40	42.46
UCBL	15.82	1.46	12.62	19.73	91	9.23	44.94
UP3MD	11.92	0.9	9.96	14.02	112	7.55	34.06
UP3BL	15.69	1.16	10.27	18.26	112	7.39	50.92
UP4MD	11.07	0.72	9.4	13.44	113	6.50	36.50
UP4BL	15.15	0.92	13.27	17.44	112	6.07	27.52
UM1MD	14.88	0.82	12.98	16.71	91	5.51	25.07
UM1BLMES	14.29	1	11.98	16.66	91	7.00	32.75
UM1BLDIS	13.95	0.92	12.09	16.31	91	6.59	30.25
UM2MD	15.89	1.01	14.06	19.19	112	6.36	32.28
UM2BLMES	15.13	1.05	12.81	18.59	112	6.94	38.20
UM2BLDIS	14.52	1.09	12.41	17.23	112	7.51	33.20
UM3MD	14.96	1.1	11.87	17.97	104	7.35	40.78
UM3BLMES	14.65	1.26	12.12	19.28	104	8.60	48.87
UM3BLDIS	12.71	1.18	9.4	15.4	104	9.28	47.21
LI1MD	7.79	0.66	6.29	9.69	70	8.47	43.65
LI1BL	9.2	0.65	7.68	10.77	71	7.07	33.59
LI2MD	9.07	0.78	7.71	11.18	82	8.60	38.26
LI2BL	10.64	0.7	8.79	12	82	6.58	30.17
LCMD	17.72	1.73	14.44	21.04	91	9.76	37.25
LCBL	14.48	1.31	11.83	18.3	90	9.05	44.68
LP3MD	17.38	1.13	14.2	20.61	106	6.50	36.88
LP3BL	14	1.32	9.84	17.19	106	9.43	52.50
LP4MD	11.82	1.05	9.76	15.41	105	8.88	47.80
LP4BL	13.29	1.04	11.36	15.76	105	7.83	33.11
LM1MD	15.88	0.79	13.62	17.76	80	4.97	26.07
LM1BLMES	12.89	0.89	11.16	15.34	80	6.90	32.43
LM1BLDIS	12.92	0.74	11.5	14.85	80	5.73	25.93
LM2MD	17.45	1.03	15.02	19.94	101	5.90	28.19
LM2BLMES	14.46	1.12	12.27	16.95	101	7.75	32.37
LM2BLDIS	14.38	1	12.13	16.57	101	6.95	30.88
LM3MD	17.41	1.27	14.15	20.11	101	7.29	34.23
LM3BLMES	14	1.21	11.54	16.93	101	8.64	38.50
LM3BLDIS	13.1	1.11	10.24	16.04	101	8.47	44.27

G. g. gorilla females: South Of R. Sanaga To R. Congo and R. Sangha							
Variable	Mean	Std Dev	Minimum	Maximum	N	CV	R%
UI1MD	13.18	0.8	11.36	15.2	42	6.07	29.14
UI1BL	10.08	0.64	8.71	11.5	42	6.35	27.68
UI2MD	8.91	0.97	7.06	11.63	42	10.89	51.29
UI2BL	8.82	0.88	6.91	10.78	42	9.98	43.88
UCMD	14.84	0.93	12.36	17.37	56	6.27	33.76
UCBL	11.82	0.91	10.03	13.6	56	7.70	30.20
UP3MD	11.15	0.89	9.46	13.73	63	7.98	38.30
UP3BL	14.79	0.8	13.31	16.78	63	5.41	23.46
UP4MD	10.66	0.72	8.82	12.85	63	6.75	37.80
UP4BL	14.29	0.74	12.7	15.87	63	5.18	22.18
UM1MD	14.34	0.74	12.22	16.45	47	5.16	29.50
UM1BLMES	13.34	0.86	11.39	15.38	47	6.45	29.91
UM1BLDIS	13.13	0.76	11.69	15.04	47	5.79	25.51
UM2MD	15.26	0.78	12.99	17.47	64	5.11	29.36
UM2BLMES	14.28	0.98	11.98	16.56	64	6.86	32.07
UM2BLDIS	13.61	0.78	11.64	15.43	64	5.73	27.85
UM3MD	13.72	1	11.36	17.29	59	7.29	43.22
UM3BLMES	13.28	0.9	11.43	15.96	59	6.78	34.11
UM3BLDIS	11.45	1.03	9.33	14.02	58	9.00	40.96
LI1MD	7.51	0.65	6.05	8.85	44	8.66	37.28
LI1BL	8.32	0.55	7.25	9.36	44	6.61	25.36
LI2MD	8.35	0.63	6.27	9.58	46	7.54	39.64
LI2BL	9.34	0.66	8.25	11.16	46	7.07	31.16
LCMD	13.09	0.82	11.6	14.76	51	6.26	24.14
LCBL	10.98	0.98	9.44	13.62	51	8.93	38.07
LP3MD	15.14	0.88	12.58	17.06	59	5.81	29.59
LP3BL	12.5	0.95	9.17	14.38	59	7.60	41.68
LP4MD	11.24	0.97	9.62	14.16	59	8.63	40.39
LP4BL	12.48	0.82	11.06	14.62	59	6.57	28.53
LM1MD	15.3	0.82	13.53	17.19	43	5.36	23.92
LM1BLMES	12.12	0.81	10.06	13.69	43	6.68	29.95
LM1BLDIS	12.31	0.61	11.24	13.63	43	4.96	19.42
LM2MD	16.8	0.95	14.02	19.15	58	5.65	30.54
LM2BLMES	13.61	1.02	11.61	15.89	58	7.49	31.45
LM2BLDIS	13.73	0.82	11.72	15.43	58	5.97	27.02
LM3MD	16.18	1.13	12.43	19.05	54	6.98	40.91
LM3BLMES	12.94	0.9	10.96	14.48	54	6.96	27.20
LM3BLDIS	12.22	1.04	9.96	15.62	54	8.51	46.32

G. g. graueri males: Utu and Mwenga-Fizi							
Variable	Mean	Std Dev	Minimum	Maximum	N	CV	R%
UI1MD	13.16	0.99	11.46	14.75	24	7.52	25.00
UI1BL	11.16	0.62	10.19	12.75	24	5.56	22.94
UI2MD	9.89	0.9	8.61	11.85	23	9.10	32.76
UI2BL	10.96	0.94	9.48	13.45	23	8.58	36.22
UCMD	21.3	1.4	18.92	24.96	26	6.57	28.36
UCBL	16.69	1.29	14.66	19.18	26	7.73	27.08
UP3MD	12.48	1.04	10.21	14.48	35	8.33	34.21
UP3BL	17.47	0.94	15.72	19.51	35	5.38	21.69
UP4MD	11.89	0.67	9.69	13.2	35	5.63	29.52
UP4BL	17.05	1.01	15.08	19.71	35	5.92	27.16
UM1MD	16.04	0.9	14.69	18.52	26	5.61	23.88
UM1BLMES	15.44	0.85	13.16	16.92	26	5.51	24.35
UM1BLDIS	15.94	0.95	14.01	17.87	26	5.96	24.22
UM2MD	17.99	1.12	15.19	20.73	31	6.23	30.79
UM2BLMES	16.72	0.93	14.95	19.07	31	5.56	24.64
UM2BLDIS	16.17	1.48	11.27	17.96	31	9.15	41.37
UM3MD	16.82	1.37	13.35	19.56	33	8.15	36.92
UM3BLMES	15.79	1	14.4	18.11	33	6.33	23.50
UM3BLDIS	14.55	1.3	11.54	17.29	33	8.93	39.52
LI1MD	8.23	0.73	7.04	9.47	20	8.87	29.53
LI1BL	9.87	0.62	8.54	10.67	20	6.28	21.58
LI2MD	9.14	0.84	7.47	10.58	27	9.19	34.03
LI2BL	11.31	0.91	9.82	13.14	27	8.05	29.35
LCMD	18.07	1.37	15.26	20.52	25	7.58	29.11
LCBL	14.96	1.05	13.17	16.85	25	7.02	24.60
LP3MD	17.74	1.13	16.08	20.75	34	6.37	26.32
LP3BL	14.54	0.94	12.95	16.52	34	6.46	24.55
LP4MD	12.21	0.87	10.29	14.24	34	7.13	32.35
LP4BL	14.67	1.21	11.71	17.44	33	8.25	39.06
LM1MD	17.23	0.72	15.79	18.86	26	4.18	17.82
LM1BLMES	14.16	0.63	12.79	15.06	26	4.45	16.03
LM1BLDIS	14.38	0.74	13.46	15.87	26	5.15	16.76
LM2MD	19.84	1.11	17	23.1	31	5.59	30.75
LM2BLMES	16.27	0.89	13.88	18.07	31	5.47	25.75
LM2BLDIS	16.11	0.95	14.09	19.01	31	5.90	30.54
LM3MD	19.93	1.45	16.86	23.34	30	7.28	32.51
LM3BLMES	15.1	1.08	12.36	16.87	30	7.15	29.87
LM3BLDIS	14.55	1.33	11.78	16.75	30	9.14	34.16

G. g. graueri females: Utu and Mwenga-Fizi							
Variable	Mean	Std Dev	Minimum	Maximum	N	CV	R%
UI1MD	12.55	0.84	11.01	13.71	15	6.69	21.51
UI1BL	10.37	0.53	9.4	11.09	15	5.11	16.30
UI2MD	9.12	0.59	8.28	10.56	20	6.47	25.00
UI2BL	10.08	0.7	8.96	11.82	20	6.94	28.37
UCMD	14.83	0.54	13.97	16.52	22	3.64	17.19
UCBL	12.49	1.38	11.15	17.94	22	11.05	54.36
UP3MD	11.79	0.7	10.33	13.07	25	5.94	23.24
UP3BL	16.48	0.69	15.42	17.68	25	4.19	13.71
UP4MD	11.52	0.76	9.46	13.19	25	6.60	32.38
UP4BL	15.86	0.68	14.85	16.99	25	4.29	13.49
UM1MD	15.23	0.6	14.46	16.6	19	3.94	14.05
UM1BLMES	14.57	0.71	12.9	15.86	19	4.87	20.32
UM1BLDIS	15.01	0.64	13.73	16.36	19	4.26	17.52
UM2MD	16.79	0.63	15.64	18	25	3.75	14.06
UM2BLMES	15.47	0.79	13.88	16.97	25	5.11	19.97
UM2BLDIS	15.23	0.59	13.65	16.18	25	3.87	16.61
UM3MD	15.52	0.81	13.88	17.07	18	5.22	20.55
UM3BLMES	15.07	0.84	13.97	16.63	18	5.57	17.65
UM3BLDIS	13.49	0.81	12.42	15.27	18	6.00	21.13
LI1MD	7.73	0.58	6.48	8.63	11	7.50	27.81
LI1BL	9.16	0.51	8.33	10.23	11	5.57	20.74
LI2MD	8.5	0.58	7.77	9.8	17	6.82	23.88
LI2BL	10.28	0.5	9.13	11.05	17	4.86	18.68
LCMD	13.31	0.62	12.35	14.38	16	4.66	15.25
LCBL	11.5	0.7	9.73	12.56	16	6.09	24.61
LP3MD	15.4	1.21	10.88	17.01	21	7.86	39.81
LP3BL	12.54	0.52	11.56	13.43	21	4.15	14.91
LP4MD	11.7	0.71	10.36	12.89	21	6.07	21.62
LP4BL	13.56	0.67	12.34	14.94	21	4.94	19.17
LM1MD	16.03	0.65	15	17.26	17	4.05	14.10
LM1BLMES	13.43	0.62	12.39	14.69	17	4.62	17.13
LM1BLDIS	13.49	0.75	12.26	15.33	17	5.56	22.76
LM2MD	18.38	0.72	17.1	19.76	21	3.92	14.47
LM2BLMES	15.04	0.66	13.88	16.42	21	4.39	16.89
LM2BLDIS	15.19	0.62	14.02	16.77	21	4.08	18.10
LM3MD	18.61	1.16	15.72	20.4	19	6.23	25.15
LM3BLMES	14.04	0.71	12.87	15.77	19	5.06	20.66
LM3BLDIS	13.61	0.76	12.41	14.78	19	5.58	17.41

G. g. beringei males: Virunga and Kayonza mountains							
Variable	Mean	Std Dev	Minimum	Maximum	N	CV	R%
UI1MD	13.03	0.57	12.32	13.87	10	4.37	11.90
UI1BL	11.85	0.55	11.02	12.67	10	4.64	13.92
UI2MD	10.07	0.56	9.19	11.15	13	5.56	19.46
UI2BL	11.86	0.85	10.7	13.39	13	7.17	22.68
UCMD	22.87	1.5	20.52	25.64	11	6.56	22.39
UCBL	17.84	1.55	14.95	20.51	11	8.69	31.17
UP3MD	13.15	0.86	11.99	15.01	15	6.54	22.97
UP3BL	16.81	0.83	15.3	18.1	15	4.94	16.66
UP4MD	12.3	1.07	10.63	13.96	15	8.70	27.07
UP4BL	16.11	1.76	10.59	17.94	15	10.92	45.62
UM1MD	15.72	0.72	14.71	16.98	11	4.58	14.44
UM1BLMES	14.76	1.12	12.75	16.29	11	7.59	23.98
UM1BLDIS	15.31	0.65	14.39	16.4	11	4.25	13.13
UM2MD	17.25	1.03	15.74	18.84	14	5.97	17.97
UM2BLMES	16.66	1.24	14.65	18.85	14	7.44	25.21
UM2BLDIS	16.34	0.79	15.33	17.7	14	4.83	14.50
UM3MD	15.86	1.43	13.99	18.61	13	9.02	29.13
UM3BLMES	15.32	1.15	13.59	17.52	13	7.51	25.65
UM3BLDIS	13.65	1.48	11.91	16.47	13	10.84	33.41
LI1MD	7.97	0.65	7.03	8.73	11	8.16	21.33
LI1BL	10.33	0.63	9.47	11.24	10	6.10	17.13
LI2MD	8.99	0.6	8.08	9.78	12	6.67	18.91
LI2BL	11.82	0.58	10.96	13.06	12	4.91	17.77
LCMD	18.94	0.95	17.49	20.59	14	5.02	16.37
LCBL	15.63	0.91	14.01	16.89	14	5.82	18.43
LP3MD	18.27	0.99	16.95	19.94	16	5.42	16.37
LP3BL	14.8	1.02	13.68	17.03	16	6.89	22.64
LP4MD	13.18	0.89	11.74	14.96	16	6.75	24.43
LP4BL	14.52	1.28	12.76	16.76	16	8.82	27.55
LM1MD	16.88	0.62	15.67	17.93	14	3.67	13.39
LM1BLMES	13.39	0.67	12.01	14.43	14	5.00	18.07
LM1BLDIS	14.13	0.51	13.34	15.37	14	3.61	14.37
LM2MD	18.71	1	17.45	20.74	16	5.34	17.58
LM2BLMES	15.8	1	14.61	18.02	16	6.33	21.58
LM2BLDIS	15.17	0.75	14.12	16.62	16	4.94	16.48
LM3MD	19.23	1.65	16.8	22.93	15	8.58	31.88
LM3BLMES	14.88	0.82	13.63	16.3	15	5.51	17.94
LM3BLDIS	14.21	0.94	12.95	16.36	15	6.62	24.00

G. g. beringei females: Virunga and Kayonza mountains							
Variable	Mean	Std Dev	Minimum	Maximum	N	CV	R%
UI1MD	12.87	0.56	12.17	13.49	7	4.35	10.26
UI1BL	11.04	0.43	10.24	11.58	7	3.89	12.14
UI2MD	9.65	0.54	8.69	10.31	11	5.60	16.79
UI2BL	10.6	0.68	9.53	11.45	12	6.42	18.11
UCMD	14.56	0.71	13.33	15.92	12	4.88	17.79
UCBL	12.31	0.8	11.22	13.7	12	6.50	20.15
UP3MD	11.69	0.73	9.92	12.79	13	6.24	24.55
UP3BL	15.86	0.71	14.96	16.85	13	4.48	11.92
UP4MD	11.62	0.96	10.43	13.32	12	8.26	24.87
UP4BL	15.57	0.64	14.41	16.44	13	4.11	13.04
UM1MD	14.61	0.59	13.62	15.34	12	4.04	11.77
UM1BLMES	13.95	0.8	12.28	14.98	12	5.73	19.35
UM1BLDIS	14.32	0.59	13.19	15.21	12	4.12	14.11
UM2MD	15.68	0.93	13.72	17.12	12	5.93	21.68
UM2BLMES	14.9	0.7	13.6	15.81	12	4.70	14.83
UM2BLDIS	14.75	0.72	13.06	15.58	12	4.88	17.08
UM3MD	14.34	0.97	12.66	15.75	12	6.76	21.55
UM3BLMES	13.96	0.97	12.46	15.41	12	6.95	21.13
UM3BLDIS	12.45	1	10.8	14.44	12	8.03	29.24
LI1MD	7.35	0.69	6.34	8.24	9	9.39	25.85
LI1BL	9.22	0.73	8.35	10.26	9	7.92	20.72
LI2MD	8.49	0.49	7.73	9.51	12	5.77	20.97
LI2BL	10.78	0.74	9.74	11.83	12	6.86	19.39
LCMD	13.2	0.79	12.17	14.1	10	5.98	14.62
LCBL	10.82	0.91	8.92	11.93	10	8.41	27.82
LP3MD	15.42	0.69	14.35	16.92	13	4.47	16.67
LP3BL	12.75	0.78	11.19	13.75	13	6.12	20.08
LP4MD	12.29	0.85	10.63	13.48	13	6.92	23.19
LP4BL	13.54	0.6	12.48	14.27	13	4.43	13.22
LM1MD	15.61	0.6	14.84	16.58	13	3.84	11.15
LM1BLMES	12.66	0.73	11.67	14.05	13	5.77	18.80
LM1BLDIS	13.12	0.59	12.06	14.1	13	4.50	15.55
LM2MD	17.09	0.82	15.19	17.95	13	4.80	16.15
LM2BLMES	14.26	1.08	12.14	16.44	13	7.57	30.15
LM2BLDIS	14.39	0.84	12.89	15.91	13	5.84	20.99
LM3MD	17.53	0.67	16.46	18.64	12	3.82	12.44
LM3BLMES	13.67	0.69	12.33	14.56	12	5.05	16.31
LM3BLDIS	13.21	0.61	12.36	14.2	12	4.62	13.93

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