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Comparative Odontometric Scaling in Two South American Tamarin Species: *Saguinus oedipus oedipus* and *Saguinus fuscicollis illigeri* (Callitrichinae, Cebidae)

Theodore M. Cole III
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To the Graduate Council:

I am submitting herewith a thesis written by Theodore M. Cole III entitled "Comparative Odontometric Scaling in Two South American Tamarin Species: *Saguinus oedipus oedipus* and *Saguinus fuscicollis illigeri* (Callitrichinae, Cebidae)." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Arts, with a major in Anthropology.

Fred H. Smith, Major Professor

We have read this thesis and recommend its acceptance:

R.L. Jantz, Margaret C. Wheeler, William M. Bass

Accepted for the Council:
Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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COMPARATIVE ODONTOMETRIC SCALING IN TWO SOUTH AMERICAN TAMARIN SPECIES: *SAGUINUS OEDIPUS OEDIPUS* AND *SAGUINUS FUSCICOLLIS ILLIGERI* (CALLITRICHINAE, CEBIDAE)

A Thesis
Presented for the
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Degree
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Theodore M. Cole, III

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ABSTRACT

Tamarins (Genus Saguinus) are small-bodied, arboreal monkeys found in the jungles and rain forests of South America. They belong to the subfamily Callitrichinae, and differ morphologically from other South American monkeys (belonging to the subfamily Cebinae) in a number of respects. The phylogenetic status of the Callitrichinae, relative to the Cebinae, has been the subject of much recent debate.

Previous research involving tamarins has involved a number of a priori assumptions and generalizations. There is a tendency to regard the tamarins as morphologically, behaviorally, and ecologically homogenous. A recent increase in the frequency and quality of studies involving tamarins has led to a questioning of many of these assumptions.

The purpose of this study was to document size and shape variation in the dentitions of two tamarin species: Saguinus oedipus oedipus and Saguinus fuscicollis illigeri. The sample included 62 illigeri (30 males and 32 females) and 61 oedipus (32 males and 29 females). In the course of the analysis, two null hypotheses were tested. The first was that neither species would show any sexual dimorphism in tooth size, as evinced by the maximum diameters of the teeth. Sex comparisons of tooth size variation were also examined

by observing the logged-value variances of the maximum tooth diameters. It was concluded that very little sexual dimorphism exists in the dentitions of the two species. The sexes of both species were therefore pooled in the subsequent species comparisons.

The second null hypothesis was that the dentitions of the species would show the same patterns of size-related proportional (allometric) variation. Interspecific studies of dental allometry frequently compare tooth size to an independent measure of body size, such as body mass. Body mass data were available for the sample, but few significant correlations between tooth size and body mass were found. As an alternative, intraspecific patterns of "internal" scaling variation were compared. Two methods of comparison were used: reduced major axis (RMA) regression and principal components analysis. It was found that individual tooth shape variation appears to be fairly independent of tooth size in both species. When tooth areas were examined, however, relative tooth areas and tooth size were found to be more strongly correlated. Within morphogenetic fields, comparisons of tooth areas conformed to the null hypothesis. When summed tooth areas were examined, the null hypothesis was rejected. The most striking species differences occurred in the relationships between the relative sizes of the

premolars and molars, in which geometric dissociations were found.

The underlying causes of intraspecific dental scaling variation are still unknown and it is uncertain whether these patterns of variation serve any functional purpose. An alternative explanation of intraspecific variation might involve individual variation in the onset, rate, and duration of dental development. In any case, the phenomenon of intraspecific, "internal" dental scaling is recognized as a potentially valuable subject for further study.

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CHAPTER I

INTRODUCTION

Tamarins are small-bodied, arboreal monkeys found in the jungles and rain forests of South America. The tamarins (Genus Saguinus) belong to the subfamily Callitrichinae (Family Cebidae) along with marmosets (Callithrix), pygmy marmosets (Cebuella), lion tamarins (Leontopithecus), and, possibly, Goeldi's monkey (Callimico) (Rosenberger 1979, 1983). These taxa are distinguished from the other South American cebids (subfamily Cebinae) by the possession of a suite of unique, derived morphological features. These include small body size, tritubercular upper molars and the absence of third molars (except Callimico), claws on all the digits except the hallux, the tendency to give birth to chimerous, dizygotic twins (except Callimico), and relatively unconvoluted brain morphology (relative to the Cebinae) (Ford 1980; Rosenberger 1983; Sussman and Kinzey 1984). These traits have been the object of considerable debate, with the arguments centering on whether these characters are primitive retentions (Hershkovitz 1977) or unique derivations (Rosenberger 1977; Maier 1978; Ford 1980a, 1980b; Leutenegger 1980) with respect to the callitrichine/ cebine divergence.

This debate will be discussed in more detail in the next chapter.

Why study tamarins? Of all the major taxonomic categories of primates, the New World monkeys (Infraorder Platyrrhini) have been studied the least when compared to the Old World monkeys, apes, and humans (Infraorder Catarrhini) and the prosimians (Infraorders Lemuriformes, Lorisiformes, and Tarsiiformes). Compared to these others, relatively little is known about platyrrhine ecology, behavior, or evolution. There are a numbers of reasons for this lack of knowledge. Attempts to study ecology and behavior in the wild are obviously impeded by the restrictions that remote localities, dense vegitation, and small, arboreal subjects can place on field methods.

Studies of platyrrhine evolution are mainly restricted to comparative studies of extant taxa, as the available fossil record in South America, while having grown considerably in recent years, is still inadequate for the satisfactory reconstruction of phylogenetic relationships between fossil and extant taxa.

There are also limitations on the study of comparitive anatomy in extant taxa, particularly the callitrichines. A lack of large study collections has forced researchers rely on small samples, while also forcing studies of animals such as tamarins to be made

on the generic level, without considering potentially significant interspecific variations in morphology.

Fortunately, researchers have begun to take increasing interest in the callitrichines. This interest has, in addition to making contributions to the understanding of callitrichine-cebine relationships, led to the discovery that the marmosets and tamarins are not as morphologically, ecologically, or behaviorally homogeneous as has previously been assumed.

The reasons for studying tamarins are numerous. First, detailed knowledge of their anatomy is essential to understanding the nature of their relationships to other South American primates.

Second, studies of their behavior and ecological adaptations can be used in conjunction with morphological data to give a better picture of how they have adapted to their specific niches in the neotropical ecosystem.

Third, many of the small South American primates are endangered and facing extinction, due mostly to the expansion of civilization and the destruction of their habitats. It is clear that we need to study them as completely as possible now, because the future of many species becomes more tenuous with each passing year. Fortunately, considerable interest is being generated in the protection of these endangered taxa, which is

helping to increase the population sizes of these animals.

Finally, as Cronin and Sarich (1978:18) have stated, the callitrichines are "one of the most recent and successful experiments in primate evolution." In studying them, we can contribute to a body of theory which can help to explain how and why tamarins (as well as other organisms) adapt and evolve. In other words, while the tamarins are interesting in and of themselves, the goal of biological science is the synthesis of empirical observations into postulates which help to explain what goes on the the natural world, with broad-ranging theories being borne of specifics. This study's purpose is to document intraspecific and interspecific proportional variability in two tamarin species and to make a contribution to the growing body of knowledge involving platyrrhine evolution.

Why study teeth? The most obvious function of teeth in mammals is the acquisition and processing of food. What is sometimes less obvious to persons who do not study teeth is why they should be intensively studied at all, given that their functional role is fairly straightforward. To briefly outline the reasons that the teeth are important:

1) Teeth are durable. This is an especially important consideration for paleontologists, because many taxa, such as the South American primates Micodon and Branisella, are known solely from their dentitions and jaw fragments.

2) Teeth are evolutionarily conservative and their features are most frequently of taxonomic relevance. Teeth are not subject to as many non-genetic plastic changes as are the skull and post-cranial skeleton. This is because teeth are generally thought to have more stringent genetic components governing their morphology and size (although the exact nature and magnitude of this genetic component is currently unresolved).

3) Teeth reflect adaptation. Tooth morphology is strongly related to diet in mammals and other organisms. Tooth size is also very important because it is related to both the diet type and the metabolic demands of the organism. These factors are both related to how teeth are adaptive in the masticatory sense. Teeth are also used for a variety of other, non-masticatory purposes, such as grooming (a suspected function of the procumbant "dental combs" of some prosimian taxa),

defense and intraspecific display and aggression (with the best examples being the baboons), and nonmasticatory use in both extant (Eskimos and Australian Aborigines) and fossil (Eurasian Neandertals) human groups.

Problems with previous research. While interest in the marmosets and tamarins has certainly increased, there have been a number of persistent problems in previous studies. The first and most obvious is a lack of sufficiently large samples which may be used in research. There are few skeletal collections large enough to produce samples of more than a handful of individuals, which raises the question of how representative the samples used in many studies are. Small sample sizes are particularly problematic where morphometric studies are concerned.

A related and perhaps more important problem is the tendency for some researchers to make sweeping statements in regard to the Callitrichinae in general, based on a limited sample of taxa. This disregards the potential presence of significant interspecific, and even intraspecific, variability in morphology, behavior, or ecology. The sample used in this study comes from the Oak Ridge Associated Universities Marmoset Research Center. The skeletal collection from ORAU, which is housed in the University of Tennessee Anthropology

Department, is currently the largest callitrichine collection in the United States or Canada (Albrecht 1982). Since the UT Collection was established, much emphasis has been placed on the examination of both interspecific and intraspecific variability (Glassman 1982, 1983; Schmidt 1984; Paxton 1985; Falsetti 1986). This thesis is meant to contribute to this series, with a realization of how harmful generalizations can be and how valuable descriptions of variability within lower taxonomic levels can be.

Statement of purpose. The object of this study is to examine patterns of variation in the dentitions of two tamarin species: Saguinus fuscicollis illigeri and Saguinus oedipus oedipus. The primary focus is the relationship between size and shape variation and how these factors combine together to reflect the phylogenetic histories of the species and their adaptive roles in their respective ecosystems. Most importantly, the effects of differences in body size on the odontometrics of closely-related species will be examined. Allometric, or "size and scaling", studies have become increasingly popular, to the point where allometry (to use the word in its popular sense) is no longer regarded as a mere excercise in statistical methods, but as a legitimate theoretical orientation within the life sciences.

In addition to providing the first extensive account of interspecific and intraspecific size and shape variability in the tamarin dentition, this study will test the common assumptions that callitrichids are morphologically homogenous, except in superficial characters (Hershkovitz 1977) and that tamarins exhibit little or no sexual dimorphism (Napier and Napier 1967; Hershkovitz 1977). The null hypotheses tested in this study are as follows:

1) There is no sexual dimorphism in the dental measurements of either Saguinus species.

2) The within-species patterns of odontometric scaling are identical. The means of testing these hypotheses will be extensively discussed later in the text.

CHAPTER II

A LITERATURE REVIEW OF TAMARIN BIOLOGY

This chapter presents a brief introduction to the biology of tamarins, a discussion which will provide a necessary foundation for later analyses and discussions. Previous studies of tamarins have examined geographic distribution, phylogenetic history, diet and foraging behavior, locomotor and postural behavior, and social behavior. Of these, only the first three will be discussed in any explicit detail, as these have the most important implications for this study. Detailed discussions of locomotor, postural, and social behavior may be found elsewhere (Sussman and Kinzey 1984).

Geographical Distribution

S. f. illigeri. According to Hershkovitz, S. fuscicollis has the widest geographic distribution of all tamarin species. The distribution covers:

> [the] Upper Amazonian region from the west bank of the Rio Madeira south of the Rio Amazonas in Brazil, and the south (right) bank of the Japurá-Río Caqueta-Caguán north of the Amazonas in Brazil and Colombia, west to the eastern base of the Cordillera Oriental in Colombia, Ecuador, Peru, and Bolivia (Hershkovitz 1977:636).

More specifically, the illigeri subspecies is found in the western central portion of the S. fuscicollis range. The illigeri are surrounded by the lagonotus,

leucogenys, and nigrifrons subspecies, all of which are separated by river boundaries. Hershkovitz precisely defines the illigeri range as follows (see Figure 1):

> In Loreto, eastern Peru, between the lower Ríos Huallaga and Ucayali, from the south bank of the Marañon south to the Río Caxiabatay and, possibly, to the Pisquí (Hershkovitz 1977:649).

S.o.oedipus. The S. oedipus group is separated from the other tamarin species by a large geographic gap. As Hershkovitz says, the absence of any connecting tamarin forms between the S. oedipus group and other groups "requires explanation" (1977:749). The group contains species of S. leucopus, S. geoffroyi, and S. oedipus and is found in the following range:

> Tropical forested zones of Colombia, Panamá, and Costa Rica, from the west bank of the lower Río Magdelena-Cauca, northwestern Colombia, west to the Pacific Coast, north in to Panamá and bordering parts of eastern Costa Rica (Hershkovitz 1977:753).

More specifically, the range of S. oedipus is defined as follows (see Figure 2):

> Northwestern Colombia between the Río Atrato and the lower Río Cauca-Madalena in the departments of Atlántico, Bolívar, Córdoba, northwestern Antioquia, and northeastern Chocó east of the Río Atrato; altitudinal range from near sea level to nearly 1,500 meters above (Hershkovitz 1977:765).

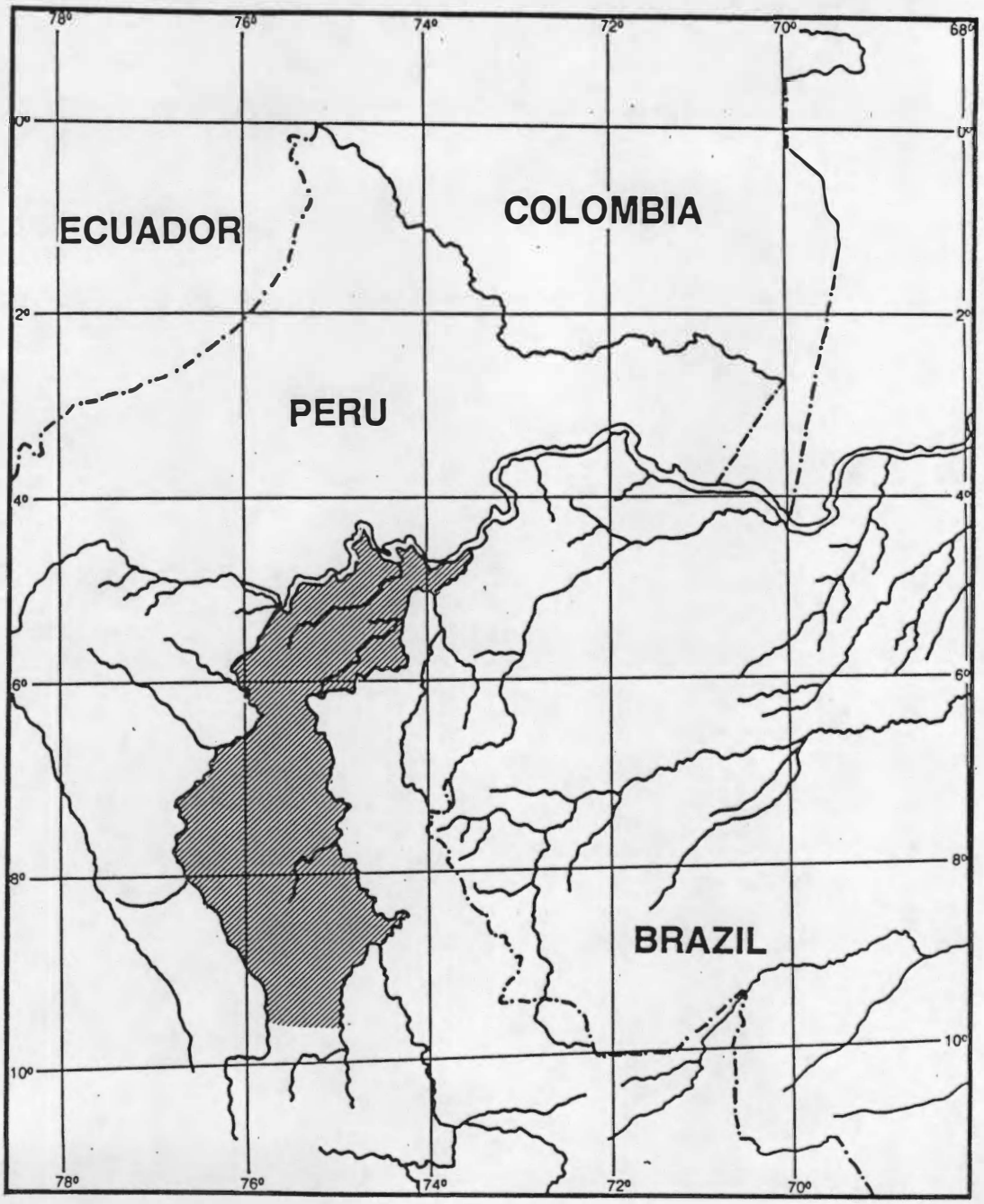

Figure 1. Geographical distribution (shaded area) of Saguinus fuscicollis illigeri.

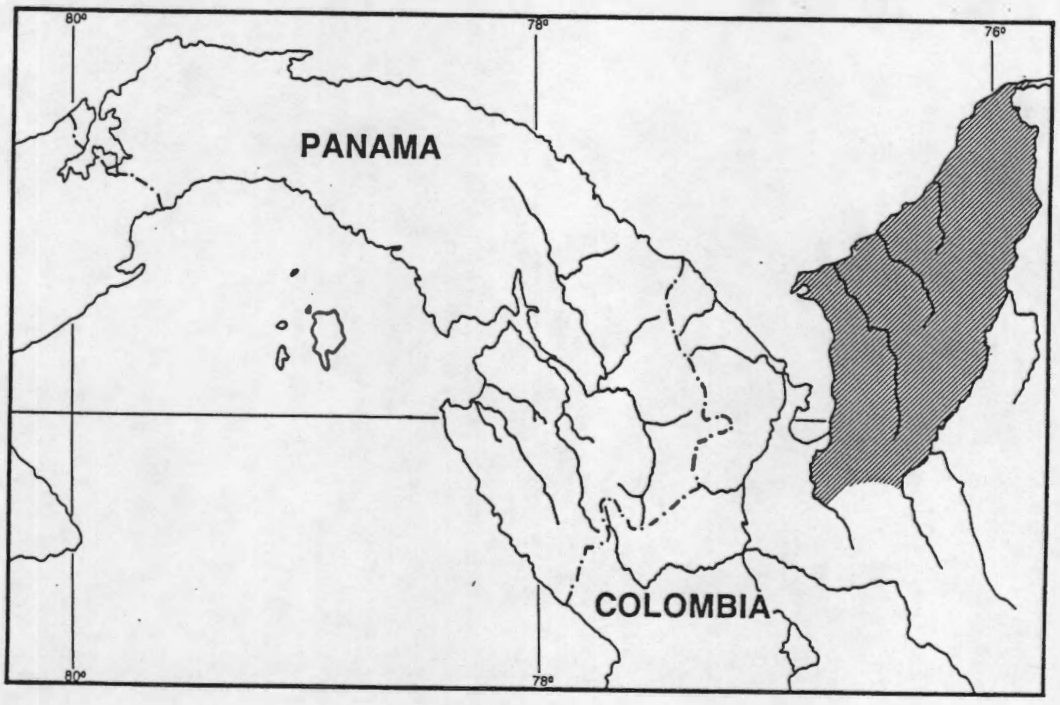

Figure 2. Geographical distribution (shaded area) of Saguinus oedipus oedipus.

Phylogenetic History

As mentioned in the Introduction, callitrichines differ from other platyrrhines in that they posses a number of unique features. These are small body size, claw-like tegulae on all the digits except the hallux, tritubercular upper molars and a loss of the third molars (except Callimico), relatively unconvoluted brain morphology (compared to other platyrrhines), and the tendency to give birth to chimeric, dizygotic twins (except Callimico). This suite of features led Hershkovitz (1977) to regard the Callitrichinae as being primitive with respect to the Cebinae. In fact, with the exception of third molar absence and some degree of lower incisor and canine specialization, the tamarins and marmosets are quite similar to the smaller, hypothetical platyrrhine ancestor that Hershkovitz (1977:406) presents.

Recent studies have promoted the seemingly more plausible theory that these characteristics are autapomorphic (uniquely derived) with respect to the callitrichine-cebine divergence (Rosenberger 1977, 1983; Cronin and Sarich 1978; Maier 1978; Ford 1980a, 1980b; Leutenegger 1980). Rather than respresenting a primitive condition, many researchers feel that at least some of the derived characters of the callitrichines

arose in conjunction with ecological specializations, especially exudate feeding and insectivory.

Biomolecular studies (Baba, et al. 1975; Cronin and Sarich 1978) lend support to the morphological studies which view the Callitrichinae as a specialized, rather than primitive, phylogenetic group. Cronin and Sarich state their perspective as follows:

> We see the marmosets [and tamarins] as a very compact evolutionary unit of relatively recent origin, with all extant lineages still sharing a common ancestral lineage on the order of 7-10 million years ago. This implies that the marmoset grade of evolution cannot reasonably be seen as a retention of features primitive for the New World monkeys as a whole, but should be seen as a derived state developing along the common lineage subsequent to the basic New World monkey radiation and finally resulting in the adaptive radiation from which the modern lines all stem. . . .
>
> To continue to view the marmosets as primitive within the cladistic context provided by the molecular evidence would require that their features be those of the most recent common ancestor of all extant New World monkeys, thus negating the reality of the cebid clade and grade of organization. This appears to us to make unrealistic demands upon the relatively rare contributions of parallel and convergent evolution. It seems far easier to view that most common recent common ancestor as a cebid, to see the cebid grade as the primitive one, to view many of the so-called `primitive' marmoset features as simply results of their small size, and to accept the marmosets as one of the most recent and successful experiments in primate evolution (1978:17-18).

Micodon and the Callitrichine-Cebine divergence.

Until recently, there were no fossil remains thought to be closely related to extant callitrichines. The fossil

record for platyrrhines is poor in general. In 1984, dental remains resembling a modern callitrichine were recovered, and an isolated left upper first molar was used as the type specimen for a new taxon, Genus Micodon (Setoguchi and Rosenberger 1985, Rosenberger and Setoguchi 1986). The molar falls within the size range of modern callitrichine molars and, with the exception of the presence of a hypocone, is quite similar in morphology to modern forms. The type specimen has also been assigned a species name: kiotensis. Two other teeth, a right central incisor and a left fourth premolar, also bear striking resemblances to their counterparts in modern callitrichines. These teeth, which are also isolated, are assigned to indeterminate genera, as they cannot be definitely associated with the type molar.

Micodon kiotensis poses some interesting problems for platyrrhine systematics. First, it comes from a geological formation associated with fauna from the Friasian Land Mammal Age of the South American Miocene (Hirschfeld and Marshall 1976). This formation has been K-Ar dated to between 14.0 and 15.4 million years BP (Marshall et al. 1977) and paleomagnetically dated to between 13.6 and 15.2 million years ago (Hayashida 1984). This predates the 7-10 million years BP divergence date obtained by Cronin and Sarich (1978) by a large margin. This does not mean that the calli-

trichines' unique features cannot be regarded as derived specializations. It does, however, suggest that the date of divergence may be earlier than most researchers of an "anti-primitive" stance may have thought.

Second, the above statement assumes that Micodon is, in fact, a callitrichine. The most interesting implication of the fossil is that it challenges the traditional, discrete characters which set callitrichines and cebines apart (Setoguchi and Rosenberger 1985). In describing the specialized features of callitrichines, Micodon introduces an interesting contradiction. Previous studies have defined callitrichines as having small body sizes and tritubercular upper molars. Until now, with only extant populations available, there were no exceptions to the rule (aside from Callimico). The discovery of Micodon represents a case of a possible intermediate form--an animal having a four-cusped upper molar and falling within the size range of modern marmosets and tamarins. This raises the question of whether the reduction in cusp number was a consequence of overall body size reduction, as proponents of the phyletic dwarfism hypothesis claim (see below for a detailed discussion of this argument) or whether the callitrichines represent a dwarfing lineage at all.

which help to elucidate the phylogenetic relationships between taxa are rare, especially those which attempt to demonstrate how congeneric species are related. While the placement of marmosets (Callithrix) and tamarins (Saguinus) in separate genera is nearly universal (but see Rosenberger (1983) for a discussion of the biological reality of this division), the placements of the pygmy marmoset (Cebuella), the lion tamarin (Leontopithecus or Leontideus), and Goeldi's monkey (Callimico) remain unresolved. The division of callitrichids into "long-tusked" and "short-tusked" groups is a potential source of confusion. Sussman and Kinzey (1984:421) state that these terms "are especially useful in distinguishing two adaptively different groups, but not necessarily two phylogenetic clades."

The "long-tusked" group consists of tamarins (Saguinus) and lion tamarins (Leontopithecus), which are charcterized by lower canines which project prominently above the occlusal level of the lower incisors, the "typically anthropoid" condition, according to Sussman and Kinzey (1984:420). It should be clearly stated that the sharing of the "long-tusked" canine and incisor relationship does not necessarily imply that Saguinus and Leontopithecus share a monotypic divergence from the "short-tusked" group. The dental similarities shared between the two tamarin types may alternatively be

viewed as evolutionary parallelisms or as the shared retention of a primitive feature.

The "short-tusked" callitrichine group includes the marmoset genera Callithrix and Cebuella. In this group, "the lower incisors are narrow, elongate, and reach the occlusal level of the canine" (Sussman and Kinzey 1984:420). Contrary to what the name implies, the "short-tusked" complex probably arose from a lengthening of the incisors and not a reduction in the canine (Rosenberger 1983). The marmoset lower incisors are also characterized by a thickening of the labial enamel and an absence of lingual enamel (Rosenberger 1979; Sussman and Kinzey 1984). This is most likely a morphological correlate to the ecological specialization of exudate feeding, which involves the cutting, gouging, and scraping of tree bark.

Rosenberger (1979) places the pygmy marmosets in the genus Callithrix, while Cronin and Sarich report a very close immunological affinity between Callithrix jacchus and Cebuella. They consider this evidence sufficient for placing the generic status of Cebuella "in serious jeopardy" (Cronin and Sarich 1978:17).

The genus Leontopithecus is probably best considered as taxonomically separate from other tamarins, although possibly not to the extent that Hershkovitz (1977) removes it:

> Leontopithecus has no near relatives within the Callitrichidae. It needs no comparison with Cebuella and Callithrix, and its greater resemblances to Saguinus appear to be parallelisms associated to the size class to which both belong. . . . (Hershkovitz 1977:809).

There are a number of competing hypotheses regarding the phyogenetic reconstruction of the callitrichine family tree (DeBoer 1974; Hershkovitz 1977; Cronin and Sarich 1978; Ford 1980a, 1980b; Byrd 1981), but the phylogeny preferred by the present author is presented by Rosenberger (1981) and is illustrated in Figure 3. This organization seems to make the most sense when the adaptive morphological patterns exhibited by each genus are considered. In this scheme, Callimico is contained within the Callitrichinae in a separate tribe (Callimiconini) from the other callitrichines (Tribe Callitrichini). The Saguinus branch separates after that of Callimico, making Callithrix and Leontopithecus more closely related to each other than either is to Saguinus. Thus, it is proposed that the "primitive" features seen in Callithrix and Cebuella by Hershkovitz (1977) are actually derived specializations and that some of the "advanced" features seen in Saguinus may really be retentions of characteristics seen in the cebine ancestor of the Callitrichinae.

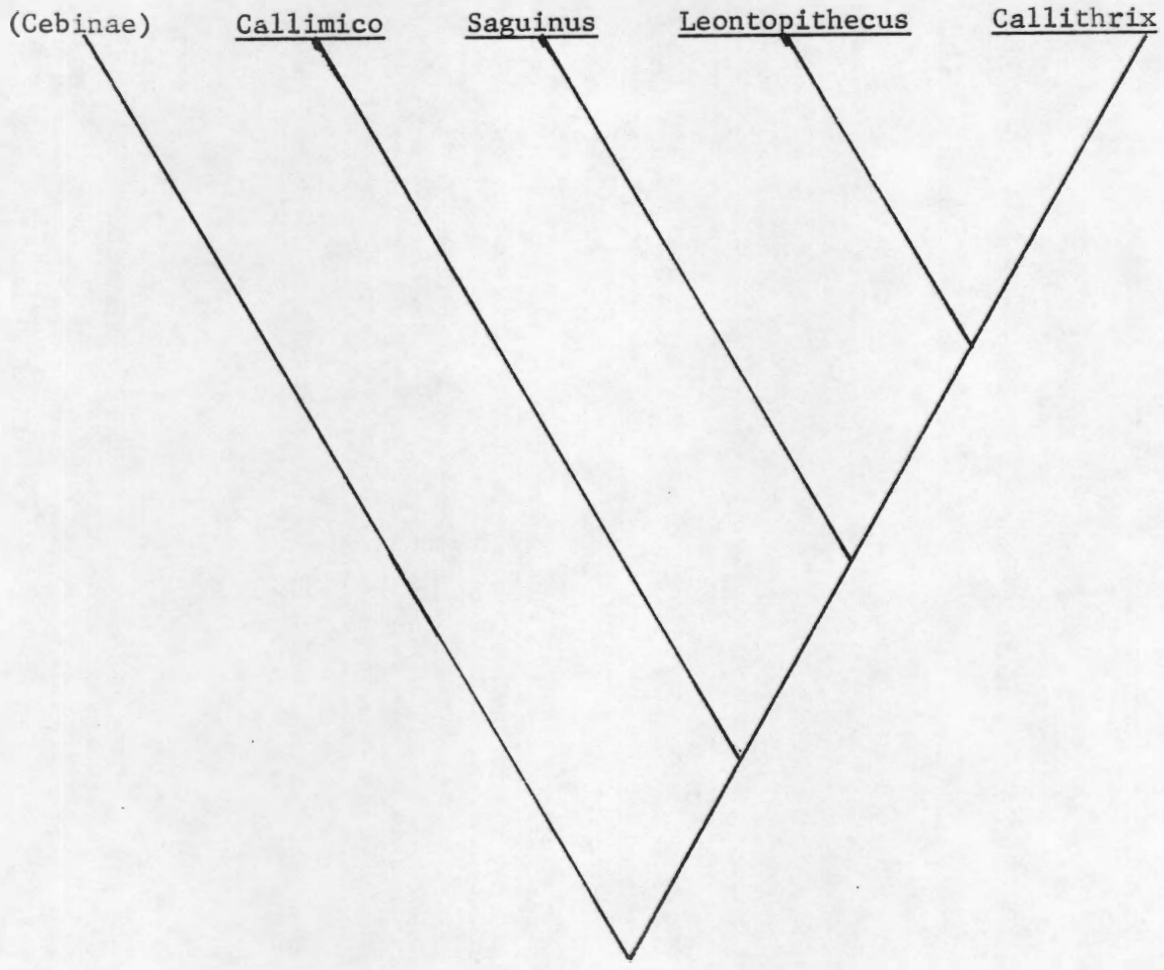

Figure 3. Rosenberger's (1981) reconstruction of callitrichine phylogeny.

There is little information which elucidates the phylogenetic relationships among Saguinus species. Hershkovitz (1968, 1970, 1977) has attempted to reconstruct species phylogenies through the use of metachromism, which involves directional evolution in the coloration of the pelage. He feels that Saguinus fuscicollis and Saguinus oedipus both evolved in the hairy-face tamarin group of which fuscicollis is a member. The outlying groups in the tamarin geographic range (S. oedipus and S. midas) then became isolated and more specialized (Hershkovitz 1977:606).

The only other study which examines the relationships between tamarin species in any detail is Cronin and Sarich (1978). They used biomolecular data and suggest that oedipus was an early offshoot of the hairy-face group, separating before the extant hairly-face taxa differentiated.

Later in this study, S. oedipus and S. fuscicollis will be examined in a context (that of geometric similarity) in which, for the purposes of description only, they will be assigned the roles of ancestor and descendant. It must be made clear at this point that both species may have evolved and differentiated considerably in the time since they shared a common ancestor. Neither of the taxa can justifiably be

claimed to resemble their last common ancestor more closely than the other.

The Question of Phyletic Dwarfism. Most researchers now reject Hershkovitz' (1977) contention that callitrichines are primitive with respect to the cebines (Ford 1980a, 1980b; Ford and Corruccini 1985; Leutenegger 1973, 1980; Maier 1978; Rosenberger 1977, 1978, 1983; Cronin and Sarich 1978; Sussman and Kinzey 1984). Of these, Ford (1980a, 1980b), Ford and Corruccini (1985), Leutenegger (1973, 1980), and Maier (1978) regard the callitrichines as members of a "dwarfing" or "nanistic" lineage. Phyletic dwarfism is a condition in which successive members of an evolutionary sequence exhibit a continuing decrease in overall body size. This is in opposition to Cope's Law, which states that body size tends to increase as a lineage evolves (Marshall and Corruccini 1978).

Phyletic dwarfism is frequently seen in island populations which, after separating from mainland parent populations, experience a decrease in body size. Marshall and Corruccini (1978:102) cite Elephas falconeri, a fossil elephant from Sicily and Malta which stood only three feet high at the shoulder, as a "classic example" of a dwarfed taxon.

Phyletic dwarfism tends to be episodic (Kurtén 1959) and is sometimes concurrent with large-scale

faunal extinctions (Marshall and Corruccini 1978). An example would be the reduction in size from the North American bison species of the Pleistocene (Bison antiquus) to the extant species (Bison bison) (Schultz et al. 1972; Edwards 1967). The size reduction of the bison was accompanied by a widespread extinction of other Pleistocene megafauna.

The cause of dwarfism in mammals is unclear. Some proposed hypotheses include the maximizing breeding population size within a given area and resource base, selection for smaller individuals, avoidance of predators, increased physiological efficiency in a given climate, selective pressures to fit an ecological niche vacant of smaller animals, or an interaction of some or all of the above Ford (1980b).

While several studies had previously considered callitrichines to be phyletic dwarfs (for example, Leutenegger (1973) and Maier (1978)), Ford (1980b) has produced the best-known argument for dwarfism. She presents a suite of features that she believes are either the direct consequence of or are closely correlated with dwarfism. The complex includes: a) reproductive twinning, b) absence of third molars, c) tritubercular third molars, d) claws (actually claw-like nails), and e) small body size. Callimico, which exhibits claw-like tegulae and small body size, but is

otherwise characterized by cebine features, is termed an "incipient dwarf platyrrhine" by Ford (1980b:31).

Sussman and Kinzey (1984) have taken exception, at least in part, to Ford's dwarfing "complex." The reason that they object is the contention that all of the above-mentioned features "are the result of the monkey's reduction in size through time" (Ford 1980b:40).

> Whether all of these factors are the result of small body size is still an open question, since one of the major features of dwarfing, relative increase in brain size, is not found in callitrichids (Bauchot and Stephan 1969; Clutton-Brock and Harvey 1980). More importantly, most features that are claimed to be associated with dwarfing can be equally well be explained without reference to a dwarfing hypothesis (see Rosenberger 1979, 1984) (Sussman and Kinzey 1984:443; emphasis theirs).

Sussman and Kinzey (1984) do not argue as strongly against Leutenegger's (1973) interesting suggestion that phyletic dwarfing is a causal factor of chimerous twinning in callitrichines. They say that it "may be an allometric correlate of body size" (Sussman and Kinzey 1984:443), which essentially means that it may, in fact, be a direct consequence of body size reduction. It must be noted here that Leutenegger's data which were used in his 1973 paper may contain some unnatural biases and are currently being reevaluated (Tardif, personal communication).

Another interesting question involves the possible mechanisms which would be effective in bringing phyletic dwarfism about in callitrichines. Levitch (1986) has compared allometric ontogenies of callitrichine and cebine taxa and suggested that the callitrichines dwarfed through temporal abbreviations (time hypomorphoses) of ancestral cebine growth patterns. The present author, in considering Rosenberger's (1977) sinking of the highly specialized taxa Cebuella into genus Callithrix, is entertaining the possibility that a great part of Cebuella's adaptation (a large relative intake of plant exudates with a corresponding decrease in body size) occurred through either time or rate hypomorphosis of the Callithrix ontogenetic pattern.

The problem with hypotheses concerning the causes and consequences of phyletic dwarfism is that none are truly testable in light of the relative absence of a callitrichine fossil record (Ford 1980b), with Micodon being the only probable fossil callitrichine (Setoguchi and Rosenberger 1985). As with all other studies (including the present one), hypotheses are built around and tested with comparisons of extant animals. At this point, researchers can only speculate as to what sequence the elements of the dwarfing complex occurred. Ford (1980b:39) believed that all of the elements arose in the same "dwarfing event", but the discovery of

Micodon suggests that small body size may have occurred before loss of the upper first molar hypocone (Setoguchi and Rosenberger 1985).

Tamarin Diet

Callitrichines are characterized by a specialized form of omnivorous diet, including a mixture of fruits, insects, plant exudates, and, in some cases, flowers, nectar, small vertebrates, and bird eggs (Napier and Napier 1967; Coimbra-Filho and Mittermeier 1977; Hershkovitz 1977; Neyman 1977; Rosenberger 1978; Terborgh 1983; Sussman and Kinzey 1984; Garber and Sussman 1986). Some of the unique derived features found in the callitrichines (small body size, tritubercular upper molars, and claw-like tegulae) are thought to be specializations which arose as adaptations to the exploitation of this ecological niche (Rosenberger 1977, 1983; Sussman and Kinzey 1984; Setoguchi and Rosenberger 1985). Some callitrichines (Callithrix and Cebuella) show the additional specialization of modified lower incisors, which are used for tree-gouging and exudate feeding (Coimbra-Filho and Mittermeier 1977; Rosenberger 1977, 1978).

Detailed accounts of specific foods utilized by tamarins in the wild are rare. Also rare are descriptions of the relative proportions of the types of foods (fruits, insects, etc.) used by specific taxa.

Neyman (1977) gives a detailed list of plant foods used by Saguinus oedipus oedipus, but gives little information about the types of insects eaten or the relative proportions of food types. There is also the question of whether oedipus feeds on plant exudates. Neyman's study is the most complete description of the oedipus diet to date. Saguinus geoffroyi, which is considered a subspecies of Saguinus oedipus (Saguinus oedipus geoffroyi) by Hershkovitz (1977), has been the subject of detailed dietary studies (Hladik and Hladik 1969; Dawson 1976, 1979; Garber 1980, 1984; Garber and Sussman 1984). Whatever its phylogenetic status, S. geoffroyi may not be a suitable analog for S. oedipus oedipus because of the distinct behavioral patterns which distinguish them (Tardif, personal communication).

More precise data are available for Saguinus fuscicollis in Terborgh (1983), a comparative ecological study of sympatric Amazonian primate species. The subspecies discussed by Terborgh is Saguinus fuscicollis weddelli, which is geographically separated from illigeri by S. f. leucogenys and S. f. nigrifrons. The fuscicollis subspecies are thought to be fairly homogenous behaviorally and ecologically (Hershkovitz 1977). There is even some feeling that Hershkovitz (1977) has "oversplit" the genus Saguinus into

subspecies with little reproductive isolation (Rosenberger 1983).

Weddelli, like the larger tamarin species (S. imperator) it is frequently found with, has a dietary make-up of roughly 42% fruits and seeds and 58% animal prey (Terborgh 1983:151). There is, however, a difference in the types of prey exploited. Weddelli and imperator apparently exploit plant resources in the same manner, but differ in their consumption of animal prey. The prey composition of weddelli consists of 73% insects and 13% vertebrates (the remaining 13% falling into a miscellaneous category) (Terborgh 1983:106). In contrast, imperator has a prey composition of 96% insects and 2% vertebrates, with a 2% miscellaneous category (including galls and millipedes). This difference in prey preference is correlated with a spatial separation. The smaller weddelli forages on tree trunks and thick branches, often searching knotholes for prey, while the larger imperator forages higher in the canopy and on the terminal branches. In this way, the species may exploit the same trees and minimize interspecific conflict at the same time (Terborgh 1983). Such separations of sympatric animals are also seen between S. geoffroyi and Sciurus, a tropical squirrel, although the exploited resources are not the same (Garber and Sussman 1984). Glassman (1983)

has suggested that differences in the postcranial skeletons of illigeri and oedipus are reflective of locomotor differences (also noted by Terborgh (1983)) and that oedipus is suited to habitual locomotion in terminal branches, moving by acrobatic leaps and bounds. If this is so, then oedipus might also show a different pattern of food exploitation than fuscicollis (Garber and Sussman 1984). Unfortunately, as mentioned earlier, there is no currently available, detailed description of the diet of wild oedipus. The closest possible analog is Saguinus geoffroyi. Hladik et al. (1971) describe a dietary composition of 10% leaves and shoots, 60% fruit, and 30% animal prey. This makes geoffroyi a "less insectivorous" arboreal omnivore than fuscicollis. While Terborgh (1983), in his summary of plant exploitation in fuscicollis and imperator states that "they share a single pool of fruit resources which they use in apparently identical fashion" (1983:200), there is a difference in the way that they exploit other plant resources. There appears to be a higher incidence of gumivory, or exudate feeding, among fuscicollis (Terborgh 1983:161). This may be a correlate of the preference of fuscicollis for foraging for prey on the main trunks of trees; exudates may just be in easier reach for fuscicollis. Terborgh (1983) mentions

instances in which pygmy marmosets (Cebuella) were chased away from their feeding sites by fuscicollis.

While it cannot be said with certainty that the diets of oedipus and fuscicollis are significantly different in composition, it seems as though the fuscicollis are the specialists within the tamarin group, with their increased concentration on insects, vertebrates, and exudates. It seems likely that, given its locomotor pattern and spatial use of tree canopies, oedipus is more in fitting with the rest of the tamarin species.

CHAPTER III

ALLOMETRIC METHOD AND THEORY

What is perhaps the best-known definition of allometry is presented by Gould (1966b:587): "Allometry then is the study of size and its consequences." Allometric equations are mathematical models for the changes or differences in proportion which occur as organisms grow or vary in size.

There are three basic types of allometry: ontogenetic, static, and evolutionary. Ontogenetic allometry describes the proportional changes which occur during the growth of an organism. A good example of ontogenetic allometry involves the proportional changes seen in growing human infants and children (Medawar 1945). If stature (or recumbent body length) is used as a measure of overall body size, then the sizes of various body parts may be expressed in terms relative to body size at a given developmental stage. For instance, newborns and infants have head heights that are larger, relative to body size, than those of older children. As a child grows, the proportion of head height to stature will decrease. The limbs exhibit an opposite trend. A newborn will have arms and legs that are relatively short in comparison to stature, but which will become relatively larger with the growth of the child.

Anthropological studies of ontogenetic allometry are usually concerned with the development of the cranium and the postcranial skeleton (see Jungers (1984) for an extensive review).

Studies of static allometry describe the proportional variation in the adult organisms of a single species or of a smaller intraspecific subdivision, such as a subspecies or a population. Studies of static allometry which involve only single taxa or populations and which make no interspecific or interpopulation comparisons are rare. Examples of studies involving the adults of a single taxa are Jolicoeur (1963a), Lauer (1975), Wolpoff (1985), and Cole (1986). Static allometry is much more common when incorporated into examinations of evolutionary allometry (see below).

Evolutionary studies of allometry are perhaps the most popular in anthropology, or for that matter, in the biological sciences. Evolutionary allometry involves comparisons of different taxa or different intraspecific populations, using either ontogenetic or static data. Such comparisons can either be made between the extant "endpoints" of phylogenetic branches, such as interspecific "shrew-to-elephant" studies (Alexander et al. 1979) (or, in the case of primates, "Microcebus-to-Gorilla" studies (Jungers (1984)), or within

evolutionary lineages. Intralineage comparisons may involve different fossil taxa (Pilbeam and Gould 1974; Wood and Stack 1980), fossil taxa and their presumed extant descendants (Marshall and Corruccini 1978), or a documented temporal series of intraspecific populations (Jantz and Owsley 1984; Cole 1986).

Evolutionary allometric studies of animals have been applied to an astounding range of topics including the brain (Pilbeam and Gould (1974) and Lande (1979), among many dozens), the dentition (Gould 1975; Marshall and Corruccini 1978; Gingerich and Smith 1985), the cranium (Giles 1956; Shea 1981, 1983a, 1983b, 1983c, 1983d, 1985a, 1985b; Cheverud 1982; Cochard 1985), the postcranial skeleton (Jungers and Sussman 1984; Aiello 1981), skeletal muscles (Alexander et al 1981; Preuschoft and Demes 1985), the internal organs (Larson 1978, 1982, 1984a, 1984b), sexual dimorphism (Leutenegger and Cheverud 1985), reproductive strategy (Leutenegger 1973; Clutton-Brock 1985), diet (Fleagle 1985; Milton and May 1976), metabolic rate (Martin 1981), and even life expectancy (Gunther and Guerra 1955; Lindstedt and Calder 1981). In each case, variations in these elements' relationship to some measure of body size are discussed.

Huxley's Allometry Equation

Allometric relationships are most commonly described by the power function

$$y = axb$$

where y is the dependent variable, x is the independent "size" variable, a is a scaling factor, and b is the allometric scaling coefficient. This method of describing variation in relative size was first used by Snell (1891), but it was given its widespread popularity in allometric studies by Huxley (1932), who supported the model with extensive empirical observations.

Recently, the power function has been questioned in regard to its suitability for serving as a model for allometric variation (Gould 1975a). This is especially true when the common practice of logarithmically transforming the equation into linear form is the topic of discussion (Smith 1980). By log-transforming the power function, the following equation is obtained:

$$\log (y) = \log(a) + b(\log(x)).$$

The biological validity of the log-transformation of the power function has recently been established in quantitative genetic studies by Lande (1979, 1985) and in studies of cellular biology (Katz 1980). The

log-transformation of the power function into linear form will be used throughout this study.

The scaling coefficient (b) is the most important component of the allometry equation. When the power function is log-transformed, the scaling coefficient represents the slope of the linear equation. It describes the change of the dependent variable relative to change in the independent variable. If measures of the same dimension (length, area, or volume) are being compared, then a value of b=1.0 indicates that the variables are varying at the same relative rate. For instance, if two lengths are being compared, an increase of 10% in one length will be accompanied by an increase of 10% in the other length. The result is the preservation of shape at different sizes. This phenomenon is known as isometry. It can be extended from simple, bivariate comparisons to multidimensional data, but the concept of constancy of shape throughout a given size range is the same. It is important to remember that the allometric scaling coefficient describes relative changes in proportions, rather than changes in absolute size.

If the allometric scaling coefficient is significantly different from 1.0, then a state of allometry (sensu stricto) is said to exist. If the slope is greater than 1.0, then there is a state of

positive allometry. When a body part is positively allometric when scaled against body size, the larger members of a population will have relatively larger parts than will smaller members. With negative allometry, the opposite is true. Larger individuals will have relatively smaller parts than will smaller members.

The Concept of Functional Equivalence

A central theme in allometric studies is functional equivalence. In fact, Fleagle's (1985) discussion of allometry is based on this concept, which describes the changes in proportions or morphology which occur in animals of different sizes in order for these animals may perform the same functions. A popular example (Gould 1975b) is the relationship between tooth size and body size in closely-related animals of different body sizes. Summed postcanine area is a frequently used estimation of the functional size of the dentition (Wolpoff 1971a; Gould 1975b). Postcanine area scales to the two-thirds power of body mass (b=0.67) because an area is being scaled against a volume. Basal metabolic rate, however, scales to the three-fourths power of body mass (b=0.75) (Keibler 1932). When the variables are adjusted to one dimension (by taking the square root of tooth area are the cube root of body mass), tooth area might be expected to scale isometrically with body

mass. This is not the case in reality, because metabolism then scales as positively allometric to tooth size. Although larger animals must process relatively less food in order to maintain their metabolism, their teeth must theoretically scale positively.

The major problem in studying functional equivalence involves the actual isolation and recognition of the phenomenon. A classic example involves the robust australopithecine taxon Australopithecus robustus (Pilbeam and Gould 1974; Wolpoff 1980; Wood and Stack 1980). This taxon is characterized by a massive masticatory apparatus and posterior teeth which are greatly expanded relative to cranial size in comparison to the other South African taxon, A. africanus. The expanded dentition is a frequently cited example of a dietary specialization, in which coarse plant foods such as roots, tubers, seeds, and grasses were exploited. This hypothesis is supported by the robust masticatory apparatus (Grine 1981; Shea 1985b). But the robust australopithecines also differ from the gracile forms in terms of overall body size (as evinced by cranial size). Because of this size increase, the following question arises: When looking only at the dentition, how much of the observed occlusal expansion is simply the result of increased body size (an allometric attempt

to preserve function at a larger size) and how much can be attributed to the results of selection for an adaptive specialization?

Many attempts have been made to separate functional equivalence from adaptive specialization. These studies attempt to "correct for" body size, so that only the effects of adaptive specialization remain. A well-known example from the anthropological allometry literature involves "Microcebus-to-Gorilla" baseline studies of the postcranial skeleton (Jungers 1984). In such studies, an interspecific regression line is sometimes drawn throughtout the total range of size variation. Taxa falling on or near the baseline are then interpreted as being functionally equivalent, while outliers (usually gibbons, orangutans, indrids, or spider monkeys) are interpreted as specializations. This approach is commonly known as the "criterion of subtraction" method. Its use is based on a fallacy that has plagued a number of studies in the past (Smith 1980), because an allometric "baseline" extending over a large size range does not necessarily reflect equivalent function. It is also important not to confuse isometric scaling with equivalence in function. Similar proportions may be suited to different locomotor patterns in primates of differing body mass (Alexander et al. 1981; Jungers 1984).

In comparing the dental scaling of primate taxa, one means of attempting to isolate functional equivalence might be to examine how proportions vary throughout a size range of animals of different diet. Kay (1975) separated a large range of primate taxa into three dietary categories: insectivores, folivores, and frugivores. He found that tooth size and body size scaled isometrically within dietary groups. This finding runs counter to the theoretical expectations of positive allometry in such cases.

Another approach involves Smith's (1980, 1985) concept of "narrow allometry." In a study using this concept, functional equivalence and specialization could be separated by reducing the effects of differing body size. This would be accomplished by comparing the scaling patterns in animals of similar size and differing adaptative patterns. This approach has recently been applied to a comparison of the dental scaling of insectivores and small-bodied primate taxa (Gingerich and Smith 1985).

Geometric Similarity

As stated previously, the null hypothesis throughout this study is that the dentition of the larger tamarin species (S. o. oedipus) is, on the average, a large-scale, "blown-up" version of the dentition of the smaller species (S. f. illigeri). In

other words, if the size of the illigeri dentition were increased to that of oedipus, with shape being preserved, then the two dentitions would be identical.

When discussing size and shape variation in a single group, the term isometry is used to denote a constancy in shape over the entire size range. This isometric state (with the regression slope equal to 1.0) is indicative of a type of geometric similarity (Gould 1971) throughout the size range. When two groups are plotted on the same set of bivariate axes, isometry throughout the entire sample becomes a special case in which the null hypothesis of a continuum of interspecific constancy is not rejected. The occurrence of superimposed lines is rare when the slopes depart strongly from isometry. This is because the preservation of geometric similarity among different groups with identical slopes and intercepts does not necessarily denote a preservation of functional equivalence. Geometric similarity frequently involves differences in intercepts (with identical slopes), which is more common than concomitant within- and between-species isometry in cases of allometric (non-isometric) scaling.

A concept which is helpful in describing the relationships between slopes and intercepts of regression lines is heterochrony. Heterochrony is defined as "the

phenomenon of changes through time in appearance or rate of development of ancestral characters" (McNamara 1986:4). In the strictest sense, heterochrony describes how descendant species differ from their ancestors in the onset, rate, and duration of growth. The data used in this study do not exactly conform to this definition for two reasons. First, because they are measurements of permanent teeth, they are static data, rather than an ontogenetic series. Thus, this study compares the end products of growth, rather than patterns of the growth processes themselves. Second, the phylogenetic relationship between the two tamarin species is not an ancestor-descendant relationship. Instead, the species represent closely-related, extant "endpoints" within the tamarin radiation. As such, the comparison of the dentitions of the tamarins is technically not a heterochronic problem. Because of this, the present examination and comparisons of regressions will be termed in investigation of geometric similarity, rather than heterochrony.

Althought this is not an actual heterochronic analysis, heterochrony is being discussed here because of its utility in describing and comparing patterns of static allometric variation. An excellent review of heterochronic terminology has recently been provided by McNamara (1986). Other helpful references include Gould

(1971) and Alberch et al. (1979). McNamara (1986: Figure 1) has organized heterochronic phenomena into a "hierarchy of heterochrony," which is reproduced here in Figure 4.

Paedomorphosis describes the state in which the adults of a descendant species resemble the subadults of the ancestral species in form, although not necessarily in size. There are three types of paedomorphosis: progenesis, neoteny, and post-displacement. Progenesis is a case in which the descendant species follows the same growth trajectory as the ancestor, but matures at an earlier developmental age. The early cessation of growth produces descendant adults which resemble ancestral subadults in both size and shape. Neoteny is a condition in which members of the descendant species resemble juveniles of the ancestral species in form, although the descendant adults are larger in size. Neoteny arises as a result of a slowing of the rate of morphological development relative to the growth period. Post-displacement involves a delay in the onset of growth in the descendant species (relative to the ancestral species). In this case, the trajectory and rate of growth are similar, but the descendant species grows for less time. The result is a descendant species which is equal in size to the ancestor, but retains some

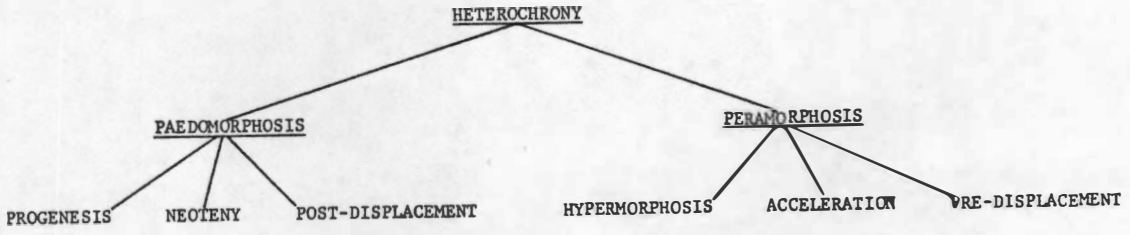

Figure 4. The "hierarchy of heterochrony," after McNamara (1986:Figure 1).

of the morphological characteristics of ancestral juveniles (McNamara 1986).

Peramorphosis describes cases of heterochrony in which the descendant growth trajectory extends "beyond" the ancestral adult stage (McNamara 1986). As with paedomorphosis, peramorphosis is divided into three types: hypermorphosis, acceleration, and pre-displacement. Hypermorphosis results when the descendant species grows along the ancestral growth trajectory, but for a longer period of time. The descendant species then resembles an "overgrown" adult ancestor. Acceleration is a fairly straightforward concept. The descendant species grows at a faster rate than the ancestor, with the descendant adults being smaller than the ancestral adults in many cases. In other words, acceleration produces an advancement in form, but not necessarily an advancement in size. Pre-displacement is the direct opposite of post-displacement. It involves an earlier onset of growth in the descendant than in the ancestor. The result is a descendant which is more developed (or "overgrown") in form, but is equal in size to the ancestor (McNamara 1986).

While these terms are designed to be applied to the comparison of ontogenies in ancestors and descendants, they are also quite useful in describing the

relationships between patterns of static scaling. In this study, there are no ancestors and descendants, but heterochronic terminology may still be successfully utilized. Instead of describing ancestor-descendant relationships, heterochronic terminology will be used in the description of size-correlated variation in shape. In each comparison, the smaller species (S. f. illigeri) will be placed in the ancestor role, with the larger species (S. o. oedipus) being place in the descendant role.

Figure 5 shows idealized plots of how each of the heterochronic phenomena would appear when applied to the data in this study.

Progenesis does not occur in this study because there are no cases in which the mean values for the ancestral (oedipus) species are less than those for the descendant species (see Chapter V).

Hypermorphosis. In a case of hypermorphosis, the regression lines for illigeri and oedipus would have both identical slopes and identical intercepts. In other words, the variation in oedipus would be an "extension" of the variation in illigeri, with oedipus being comparable to an "overgrown" illigeri. This is a special case of geometric similarity in which the regression line may be isometric, negatively allometric,

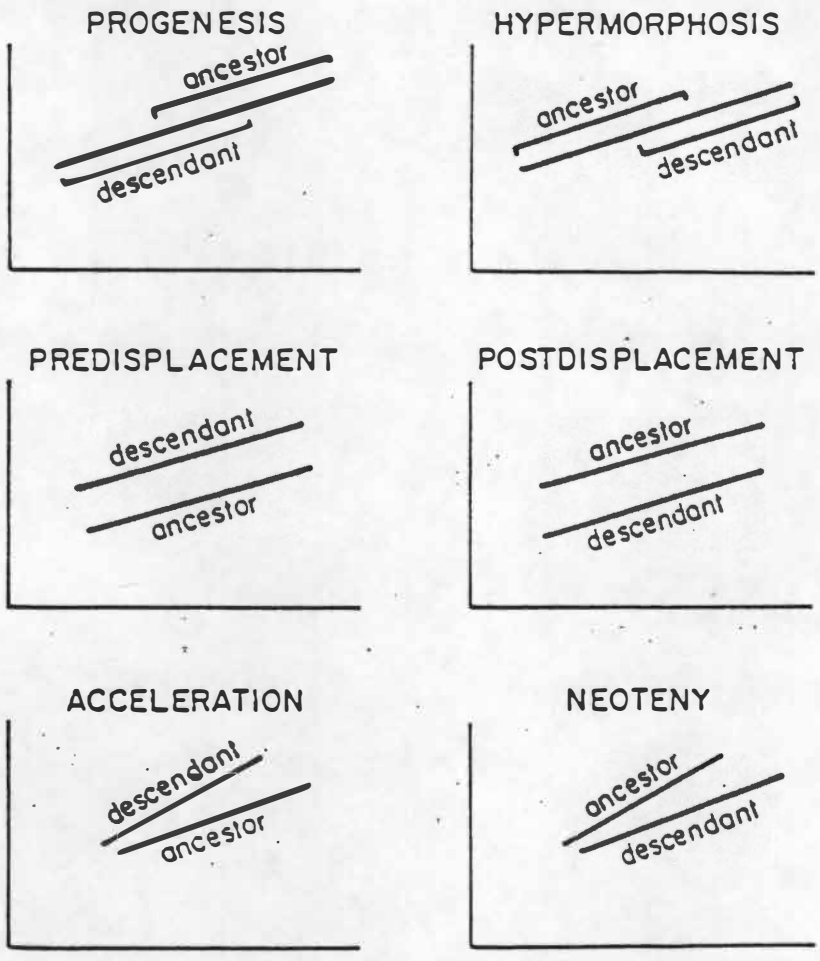

Figure 5. Idealized plots illustrating the types of heterochronic relationships (A=ancestor, D=descendant). This figure is reproduced from McKinney (1986; in press) and is used with the permission of the author.

or positively allometric. Once again, it is vital to remember that these are comparisons of static patterns of allometric variation and are not comparisons of ontogenetic trajectories.

Pre-displacement. This is a case where the slopes for illigeri and oedipus would be identical and would tend to be negatively allometric. The intercepts would be significantly different, with that of oedipus being the greater (more positive). This shift in intercepts, called a transposition (Meunier 1959; Gould 1971; Kurten 1954), is necessary to preserve function if the regression lines are strongly allometric. As Gould (1971:117) notes, allometric scaling coefficients which are strongly different from isometry "are almost always size limiting (Gould 1966a, 1966b) because extrapolation to a much- widened size range produces such drastic and rapid changes in shape." In other words, if oedipus were an "overgrown" illigeri with a very negatively allometric slope, then it would not be able to retain the same function. A transposition of the oedipus intercept is then a size-related adjustment made to retain the same function at a significantly larger size.

Post-displacement. This case is similar to that of pre-displacement. The slopes are parallel and the intercepts significantly different. The difference is that this transposition occurs in cases of strong

positive allometry. Because of the steep slopes, the intercept of the larger species (oedipus) is placed below that of the smaller species (illigeri). The reason for this transposition is the same: a simple "overgrowth" of the smaller species in a case of strong positive allometry would adversely affect the functional structure of the larger species. An excellent example of this phenomenon is found in Kurtén's (1955) study of the dentitions of fossil and extant European bears. This example is briefly and lucidly summarized by Gould (1971:125-126). Kurtén regressed paracone height for the first upper molar on the crown length for the same tooth for samples of the modern brown bear (Ursus arctos) and the Pleistocene cave bear (Ursus spelaeus). The results were two strongly allometric (b=1.47) parallel lines, with that of the larger species (U. spelaeus) transposed below that of the smaller species (U. arctos). Kurtén's explanation for this transposition was that it was an attempt to preserve function at a larger size:

> Imagine the allometric pattern of U. arctos projected into the larger size of U. spelaeus. The result would be a very hypsodont tooth. . . . The first molar would then jut out of the tooth row and probably inconveniance its bearer (Kurtén 1955:114).

Like hypermorphosis, pre- and post-displacement are varieties of geometric similarity. It should be made

clear that geometric similarity and isometry are not necessarily the same thing. Gould (1971) emphasizes that geometric similarity does not mean that all of the individuals in two or more regressions have the same shape, but that their size-related patterns of shape variation are the same. Isometry, then, is a description of of shape constancy or, in other words, a term describing intraspecific geometric similarity.

Acceleration and Neoteny. In discussing the static data used in this study, care must be taken not to misunderstand or abuse the terms "acceleration" and "neoteny." These terms were originally intended for use in comparative studies of ontogenetic patterning. Here, they are used to describe the linear dissociation of static scaling patterns. Like the definitions for geometric similarity., these terms will be used to describe the patterning of the larger species (oedipus) relative to that of the smaller species (illigeri). Acceleration describes instances in which a regression line for oedipus is more positively allometric (steeper) than that of illigeri. Neoteny will be used to describe instances in which the regression line for oedipus is more negatively allometric (less steep). The comparisons of intercepts in these cases are relatively unimportant.

In summary, the terms hypermorphosis, pre-displacement, and post-displacement are descriptive of instances in which the allometric patterning is consistent from species to species. Shifts in intercepts are size-related dissociations of allometric patterning. These are sometimes necessary for preserving functional equivalence over a wide size range. Acceleration and neoteny involve dissociations of slopes. These changes may either be related to different expressions of intraspecific functional equivalence, to adaptive differences which are unrelated to size, or to a combination of the two.

Measures of Body Size

Previous studies of primate dental allometry have attempted to scale tooth size (either lengths, breadths, or areas) against either body size (mass) or a size "surrogate" derived from skeletal measurements. Examples of such measurements are skull length, basion-prosthion distance, skull volume, maximum lengths of long bones, long bone volumes, mandibular measurements, skeletal weight, and, in studies of humans, stature.

Ideally, dental scaling is best expressed by relating tooth size to body mass. Theoretically, tooth size and body size should be positively correlated, as there is a functional relationship between them. The

larger-sized members of a population are required to consume and metabolize more food than smaller members, requiring a corresponding increase in absolute functional tooth size.

To date, only two primate studies have related tooth size to body mass of the intraspecific level, both of them involving human populations (Anderson et al. 1977; Wolpoff 1985). No such studies have been performed using non-human primates (Wolpoff 1985). This research was originally intended to be the first such study, but few significant relationships were found between tooth size and body mass. During the spring and summer of 1985, available live-weight data were collected for individuals which had lived in the ORAU Marmoset Research Center and whose remains are now housed in the Department of Anthropology at the University of Tennessee, Knoxville.

The methodology of body weight use was established as follows: The ORAU Marmoset Research Center has live-weight data from previously conducted serology studies. A sample of blood was taken at irregular intervals from each animal. At the same time, its weight was recorded to the nearest gram. When examining the records, the author found that the body weight of many individuals tended to fluctuate widely from month to month. For instance, an adult male oedipus might

weigh 450 grams one month, weigh 520 grams the next, and then drop to 470 the next. Such seemingly drastic rises and falls were found to be quite common within the sample. Lauer (1975) has also reported problems with the substantial, non-genetic variations in weight which may occur during the adult lives of Macaca mulatta.

In an effort to control the fluctuations seen in many individuals, the maximum value of the recorded weights of each animal was used as the body weight for this study. Exceptions were made in cases of obvious outliers. For example, if an individual averaged 450 grams over six weighing periods, increased to 520 grams for one period, returned to 450 grams the next month and remained in that range, the 520 gram figure was deleted and the maximum value within the "normal" range was recorded.

An alternative method would have been to average all of the available weights in the "normal" range for each individual. This was not done because of the possibility of combining adult figures for an individual with lower weights recorded before growth had ceased. All of the individuals in the sample were "dental" adults, with both the upper and lower second molars having erupted, but there is no way of being certain that each individual was otherwise mature.

In recording weights from the medical records, care was taken to exclude data for pregnant or lactating females or for any individual with documented medical problems. There may have been a tendency to underestimate the weights of some wild-caught individuals whose records included only one or two entries taken soon after their receipt by the colony. It is quite possible that these individuals were somewhat emaciated, as their weights tend to be below the average of the captive-born animals or those wild-born individuals which had been housed in the colony for some time.

When correlations between tooth measurements (see Table A-1 of the Appendix for measurement definitions and Appendix B for measurement and body weight correlations) and body weights were calculated (using the PROC CORR procedure of SAS (1982a)), they were either very low (below 0.10) or nearly non-existant (between 0.00 and 0.01), with almost none being significantly different from zero at the 0.05 level. The measurements of tooth size were maximum buccolingual diameters, maximum mesiodistal diameters, individual tooth areas (excepting the incisors), summed postcanine areas (upper and lower), and summed molar area (upper and lower). These measures were also scaled against body weight using least-squares linear regression (the GLM procedure

of SAS 1982b). When the sample was divided into four groups (by both species and sex), very few of the slopes were found to be significantly different from zero. The slopes that were significant were confined to the sample of female oedipus. Similarly, there were few significantly different slopes when the sexes were pooled and the species kept separate. A number of significant slopes were obtained when the entire sample was pooled, but the results are most probably the result of the significant species differences in absolute sizes of both the teeth and body weight. A plot of this phenomenon would consist of two unpatterned clusters or "clouds" of points, the means of which would be different enough on both the x- and y-axes to produce a significant interspecific regression line. Because of the lack of significant relationships between tooth sizes and body weight within the sample, the use of body weight as an independent measure of body size is impossible in this study.

The fact that there is a lack of significant correlation between tooth size and body weight is significant in itself. One possible explanation may be that the intraspecific range of variation in either tooth size or body weight (or both) may not be large enough to produce significant statistical relationships (Thorndike 1978; Smith 1981a). Another possibility is

that tooth size and body weight are naturally weakly-correlated in tamarins, implying a low-level genetic relationship between the two. Yet another possibility may be that a captive environment and a provisioned diet may exaggerate the effects of the environmental component of body weight, decreasing the relative influence of the genetic component. Finally, these factors may be acting in combination with one another.

While the environmental influence on body weight in captivity may be exaggerated in comparison to populations of wild animals, a recent study by Harrill (1986) has shown that the weights are not entirely unrealistic when compared to skeletal measures. She found numerous significant correlations, particularly in illigeri, between long bone dimensions and body weights. Her study used the same sample of animals as the present study, with the same weight data and postcranial data from Falsetti (1986). Thus the lack of significant correlations between tooth size and body size cannot not be attributed solely to the use of captive weights.

Body Size Surrogates

Since the use of body weights is inappropriate in this study, another measure of body size must be used. A common practice in studies of dental allometry is the

use of skeletal measures as "surrogates" of body mass. Smith (1981b) has discussed the problems that arise when choosing skeletal measures of size. For instance, the relationship between tooth size and maximum femur length in a species may not be equivalent to the relationship between tooth size and cranial length. This leaves the researcher with the decision of which measure is the most appropriate measure of body mass. The use of different size estimators by different researchers also produces incomparability between studies (Smith 1981b).

Practicality places limits on the potential estimators of body size that can be used with the UT Collection. Postcranial estimators (such as femur length) are impractical because many of the individuals used in this study are represented by only the cranium and dentition. For this same reason, the use of skeletal weight cannot be used as a measure of body size. To use a postcranial measure would severely reduce the available sample size. Also, a recent comparison of these taxa (Glassman 1983) has suggested that differences in locomotor behavior between illigeri and oedipus are reflected by postcranial morphometrics. Thus, there is a strong possibility that the relationships between tooth size and postcranial measures of body size may exhibit significant species differences and may therefore be incomparable.

The use of cranial metrics are also limited. Many of the crania have been heavily damaged by removal of the brain at the time of autopsy. This limits size estimators such as cranial volume (Albrecht 1978), cranial capacity, and cranial mass. Possible size measures which are present on all the the available crania are glabello-occipital length (Howells 1973:170-171), basion-prosthion length (Howells 1973:174; see Gould (1975b) for an application of this measure to dental scaling), and basion-nasion height (Howells 1973:171-172). Skeletal estimators of body size will not be used in this study for several reasons. First, measures such as basion-prosthion distance and bicondylar breadth are highly interrelated with the dimensions of the dental arcade (by virtue of following roughly the same geometric growth gradients), thus introducing problems of circularity with their use. Also, measures such as glabello-occipital length and basion-nasion height may be affected by differences in vault shape between species (author's observations), leading to problems of incomparability similar to those involving postcranial measures.

Second, any dental scaling study which uses skeletal measures as surrogates for body weight makes a necessary assumption of a perfect (r=1.00), isometric (b=1.00) relationship between the surrogate and body

weight (Smith 1981b). This relationship is assumed in both intraspecific and interspecific studies.

Finally, there is the unrealistic assumption of functional equivalence in which the functional relationship between tooth size and body weight is inferred through a surrogate measure. As a hypothetical example, there might be identical functional and statistical relationships between tooth size and body weight in two taxa. However, the relationships between femur length (the chosen surrogate) and body weight (unavailable in most skeletal collections) may be quite different, perhaps as a result of differring modes of locomotion. The subsequent scaling of tooth size against femur length might produce significant differences between taxa and lead to functional interpretations with no basis in biological reality. The author therefore agrees with Smith (1980,1981b) and Gingerich and Smith (1985), who state that body weight has no substitute when functional relationships between tooth size and body weight are being sought.

Internal Measures of Size

Because functional relationships between tooth size and body weight may not be described due to low correlations and because they may not be satisfactorily inferred through skeletal surrogates, other means of examining dental scaling phenomena must be sought. This

approach will be used throughout the analysis of the tamarin dentition and will be performed using two methods: reduced major axis linear regression (using the concepts of geometric similarity) and principal components analysis. Both of these methods will be used to describe "internal" allometric variation within the dentition. In both cases, the measure of "size" is derived from the teeth themselves. The species may then be compared and the null hypothesis of interspecific geometric similarity tested.

Regression Line-fitting Techniques

When describing bivariate allometric relationships, there are two basic methods for producing a linear regression equation. The first method, called Model I by some authors (Sokal and Rohlf 1981; Wolpoff 1985), is the familiar least-squares linear regression. The least-squares method fits a regression line for a plot of points so that the summed squared error is as small as possible and the sum of the residuals is equal to zero. The summed squared error consists of the summed differences between the expected and observed values for the dependent (y-axis) variable. This method is best used when a dependent variable is actually being predicted from an independent variable. It may also be used to describe the behavior of the dependent variable in relation to the independent variable. Thus,

an a priori assignment of dependence and independence must be made when examining the relationship between two variables. In addition, least-squares regression requires the assumption that the independent (x-axis) variable has no measurement error, with all of the error contained in the dependent (y-axis) variable residuals. In allometric studies which use least-squares regression, the independent variable is the measure of size (for example, body weight) and the dependent variable is the size of the part of which the relative proportion is being measured.

The second method (Model II) involves either the major axis, reduced major axis, or Bartlett's methods. Of these, the most popular for bivariate allometry is reduced major axis (RMA). RMA assumes no independent-dependent relationship between variables. It also recognizes that, in biological data sets, there will be few, if any, instances in which one of the variables may be considered error-free (Sokal and Rohlf 1981). RMA is best suited to looking for structural relationships between variable pairs. In other words, it allows the examination of linear relationships without the arbitrary assumptions of dependence and freedom from error.

There has been a great deal of debate over which is the better method for bivariate allometric analyses

(Wolpoff 1985). The problem with many of these discussions is that they tend to be generalized promotions of one technique over the other for use in all applications. The proper question should be which technique is the more appropriate choice for a particular data set and for answering the questions posed in the research.

Because this study deals with comparisons between dental measurements, the RMA technique for line-fitting will be used. With RMA regression, "size" is determined by both of the variables being compared and is measured along the regression line. When examining the allometric relationships between, for example, summed upper premolar area and summed upper molar area, there is no a priori criterion for assigning dependency. In this respect, the data are better suited to RMA than to least-squares. Also, the aim of the analysis is not to predict one dimension from another, but to examine the functional relationships between variables.

The slope of an RMA regression line (b) is derived by dividing the standard deviation of log-transformed y-axis variable by the standard deviation of the log-transformed x-axis variable (Sokal and Rohlf 1981):

$$b_{RMA} = S_Y / S_X .$$

As with least-squares linear regression, the variables on both axes are first logarithmically transformed, in keeping with the transformation of Huxley's (1932) power function. The intercept (a) of the RMA regression line is derived in the following equation:

$$\log(a) = \bar{Y} - b(\log\bar{X}).$$

In the equation above, $\bar{Y}$ is the mean of the log-transformed y-axis variable, $\bar{X}$ is the mean of the log-transformed x-axis variable, and b is the RMA slope.

The slopes of RMA regressions are systematically higher that those produced from the same variables by least-squares regression. The RMA slope may be derived from the least-squares slope as follows:

$$b_{RMA} = b_{LS} / r_{XY} .$$

In the equation above, b_{LS} is the least-squares slope and r_{XY} is the Pearson product-moment correlation coefficient for the x- and y-axis variables. It is evident from the equation that the two slopes will be more alike as r_{XY} approaches 1.0. Thus, while the slopes are similarly interpreted as allometric scaling coefficients, low between-variable correlations can lead to differing interpretations. This is a particularly important problem if inferences about differences between metabolic and geometric scaling are made

(Gingerich and Smith 1985). Such interpretive problems do not occur in this study, as only structural patterning is being examined.

While RMA is sometimes the most appropriate method of fitting regression lines, it is subject to a variety of problems.

> Simply put, the main objections are two. First, because the slope is the ratio of the standard deviations, it responds to the separate variabilities but not to the covariation of the dependent and independent variables. For instance, if the dependent variable is by its nature the more variable of the two, the regression slope will be greater than 1.0 regardless of the actual relation if the variables. Second, at very low correlations the regression has no meaning; the ratio of the standard deviations can be quite high in this case while the least mean square slope, which is this ratio multiplied by the correlation, may not be significantly different from 0.0. In such a case, the reduced major axis slope is obviously a poor reflection of the biological relationship (Wolpoff 1985:294).

While these problems may exist, the RMA method is still the most appropriate for a study of this nature. This is especially true with a data set like the one used here. Low correlations may occur in instances where a narrow range of variation is sampled. In this study, the problem of low correlations (and consequently meaningless regressions) was lessened by only performing RMA regressions on variable pairs in which the correlation coefficient was significantly different from zero (see Chapter VI).

Comparison of Regression Lines

A frequent concern in allometric studies is the comparison of regression lines for different groups. The biological reasons for testing differences in slopes and intercepts were enumerated earlier in the discussion of geometric similarity. With least-squares linear regression, the comparison of slopes and intercepts is fairly straightforward and precise. For examples of how these processes are carried out step-by-step, see Neter et al. (1985) and Sokal and Rohlf (1981). The comparisons made are particularly easy if a statistical package such as the GLM procedure of SAS (1982b) is available.

With RMA regression, the methods are not so easy and precise. The significance of the slope differences is not as precisely stated as with the analysis-of-variance approach used in PROC GLM (SAS 1982b). The same is true for intercept differences (even more so than with slopes). RMA slopes are compared with a z-statistic given by Sokal and Rohlf (1981). The equation is as follows:

$$z = \frac{b_1 - b_2}{(S_1^2 + S_2^2)^{1/2}}$$

in which b_1 and b_2 are the RMA slopes for the groups being compared and S_1^2 and S_2^2 are the squared regression

standard errors for the same groups. The standard error for each group is calculated as follows:

$$S_i = \frac{S_Y}{S_X}\sqrt{\frac{1 - r^2}{N}}$$

in which S_Y and S_X are the standard deviations for y and x, respectively, r^2 is the squared Pearson product-moment correlation coefficient, and N is the group sample size (Sokal and Rohlf 1981; Ford and Corruccini 1985). The z-statistic is an expression of the probability that the RMA slopes for both groups "were sampled from the same statistical universe" (Ford and Corruccini 1985:407).

Significant differences in intercepts for lines with the same slope are much more difficult to assess. One method of estimating how regression intercepts differ is through a qualitative assessment of the regression plots (McKinney, personal communication). This study will use this approach, as the author is unaware of a reliable test for RMA intercept differences.

Principal Components Analysis

Principal components analysis (PCA) is a very popular method in morphometric studies, particularly if allometric phenomena are the primary focus. The aim of principal components analysis is to reduce a large

number of original variables into a fewer number of interpretable components, thus illustrating how the original variables interact to produce the variation seen in the sample. Each principal component is a multiple, linear combination of the original variables. The first component (PC I) is oriented in the multivariate data space so that it "accounts for" as much of the sample variation as possible. The second component is orthogonal to the first and accounts for as much of the remaining, unexplained variation as possible. Successive components account for increasingly smaller percentages of the total sample variation until all of it has been accounted for or explained. There are as many principal components as there were original variables and each component axis is orthogonal (statistically independent) to each of the other component axes. Because each component accounts for as much unexplained variation as possible, a few of the larger components may be used to adequately explain most of the variation resulting from a much larger number of original variables. This is because many of the smaller components may be regarded as relatively insignificant when compared to the larger components.

PCA was first applied to allometric problems by Jolicoeur (1963a, 1963b) in his "multivariate generalization" of allometry. According to Jolicoeur's theory,

the loading of each variable (also known as the eigenvector or direction cosine) on the first principal component (PC I) can be interpreted in the same manner as the bivariate allometric scaling coefficient (b) in Huxley's (1932) power formula. The reasoning behind this equivalence is that, in many cases, the differentiation of individuals along the first axis will be due to differences in absolute size, as this is usually the major source of metric variation in a sample. Thus, the first component loadings for each variable are measures of how those variables are correlated with a statistically generated, "internal" measure of size. This is especially useful in studies of this type where other measures of size are either unavailable or inappropriate.

The first component loadings are interpreted in the same manner as allometric scaling coefficients produced by bivariate, linear regression. In each case, the value for isometry is represented by the inverse of the square root of the number of original variables. This is because all of the variables should be weighted equally in an isometric sample and because the sum of the squared loadings should equal one. As an example, if four original variables are included in a PCA, then the hypothetical "isometry vector" should be represented as:

$$u_i = (.5 \quad .5 \quad .5 \quad .5),$$

where

$$(.5)^2 + (.5)^2 + (.5)^2 + (.5)^2 = 1.$$

While the use of a multivariate generalization of allometry has been the subject of much debate (Jungers and German 1981; Hills 1982; Corruccini 1983), most researchers agree that the allometric scaling coefficients derived from this method should not automatically be considered equivalent to least-squares or RMA coefficients where body parts are scaled against weight. This equivalence may only be assumed when the results of a PCA where body weight is <u>included</u> show the resulting coefficients for each method to be compatible (Corruccini 1983; Shea 1985a). As with other size measures, there are important assumptions which must be made when using any surrogate measure of size in place of body weight, even if the size estimator is internal.

The use of PCA for allometric analyses has been criticized on several points. First, when examining the first component loading for a variable, the loading was not produced by variation in that variable alone, but by every other variable used in the analysis, as well (Jungers and German 1981). If one variable has an unusually strong allometric loading (positive or negative), it can bias the other variable loadings

because of the requirements that the summed PC I loadings must be equal to zero.

Second, there is a requirement that the first component must account for a substantial amount of the total variation, although the exact percentage which it must account for is an arbitrary decision. If the first component variation is relatively small, then the axis will be describing "shape" instead of "size." The terms are placed in quotations because the first axis contains both size and shape components which cannot be adequately separated, although attempts have been made (Shea 1985a). To attempt to make such a separation in an allometric study would defeat the purpose of the research, which is an examination of the relationship between size and shape.

Third, Corruccini (1983:452) has stated that, in order to produce valid results, the PCA method

> requires high and uniform intercorrelation among included variables. There must be no large residual axes responsible for much of the variance of a character that is not colinear with axis one.

While RMA regression and principal components analysis are both suitable for expressing allometric variation, both are being included in this analysis. RMA offers the advantage of comparing intraspecific scaling patterns in terms of geometric similarity. The disadvantage of RMA is that size is defined in very

fine-grained terms by only two variables at any one time. PCA offers the advantage of including a large number of variables, giving a better picture of overall size-related phenomena. The main disadvantage of PCA, as far as this study is concerned, is that comparisons in terms of geometric similarity are extremely difficult, if not impossible. Because neither type of analysis is wholly adequate for this study, both will be used to provide the most complete description of scaling phenomema possible.

CHAPTER IV

SAMPLING AND MEASUREMENT TECHNIQUES

The Sample

The sample consists of 123 tamarins from two congeneric species: *Saguinus oedipus oedipus* Linnaeus (the cotton-top tamarin) and *Saguinus fuscicollis illigeri* Pucheran (Illiger's saddle-back tamarin). The *illigeri* sample contains 62 individuals (30 males and 32 females). The *oedipus* sample contains 61 individuals (32 males and 29 females).

The sample was taken from the *Saguinus* skeletal collection housed at the University of Tennessee, Knoxville. The animals were donated upon death to the UT Collection by the Marmoset Research Center of Oak Ridge Associated Universities, Oak Ridge, Tennessee. Roughly half of the animals used were born in the Oak Ridge colony, with the remainder being wild-caught. For detailed descriptions of the Oak Ridge colony and the UT Collection, see Glassman (1983), Schmidt (1984), and Falsetti (1986).

To be included in the sample, individuals were required to meet a number of criteria. First, the sex and species of each individual must have been fully and accurately documented. The great majority of the animals in the UT Collection are so documented. Second,

all of the included individuals are "dental adults", meaning that all 32 permanent teeth had erupted at the time of death. Third, there must not have been any grossly obvious dental pathologies or anomalies (very small supernumerary teeth excluded) in any of the included individuals.

In performing this study, it is assumed that there are no significant differences between captive-born and wild-caught individuals in regard to tooth development. In other words, it is assumed that the effects that environment has on the dental phenotype are negligible.

The Choice of Measurements

Odontometric studies have traditionally been dominated by the use of two measures: maximum mesiodistal diameter (the maximum length of the tooth measured along the tooth row) and maximum buccolingual diameter (the maximum breadth of the tooth measured perpendicular to the tooth row). This has been the case for studies of both humans (see Goose (1963) and Wolpoff (1971b) for reviews) and non-human primates (see, for example, Swindler (1976)). Recently, Corruccini (1983) has described the shortcomings of these tried-and-true measures, suggesting that their utility has been long exhausted. He promotes, instead, the use of detailed multivariate descriptions of crown morphology. His analysis of hominoid third molars provides an

interesting, effective description of how fossil hominoids (both hominids and pongids) relate to extant humans and pongids in terms of the metrics of crown features.

Kay (1975), in a well-known study of crown morphology, compared anatomical features of the lower second molars of a variety of primate taxa. His study was especially interesting in that he described the allometric relationships which arose when crown features were scaled against maximum tooth length.

With regard to the tamarin teeth, such technically sophisticated techniques fall outside the specified purpose of this study. This study is meant to provide a detailed, but not so fine-grained, picture of generic variablility in size and scaling.

The major shortcomcoming of the use of simple lengths and breadths involves the calculations of tooth areas. When length and breadth are multiplied to get an estimate of tooth area, there will nearly always be a consistent overestimation of actual occlusal area. This is especially true of tooth crowns (such as the lower second premolar in tamarins) which are triangular, rather than rectangular or rhomboidal in cross-section. In the incisors, as Goose (1963) noted, there is no actual occusal area in unworn teeth which may be estimated by the multiplication of lengths and

breadths. Despite the problems inherent in its use, "tooth area" will be used in this study as an indicator of overall tooth size. Use of tooth area is perfectly adequate given the stated goal of this comparison, which is to describe size-related variation in tooth proportions. This standpoint is probably best summarized and defended by Gould (1975), who looked at allometric variation in the dentitions of closely-related herbivore taxa.

> But I preferred, in this preliminary study, to survey a wide range of groups with a rapid, accurate and admittedly imperfect measure, than to concentrate on a few species in a single group with a slow, less accurate (for me) and better measure. I am trying to establish (or rather suggest) the most general trend of dental scaling (where no data now exist), not to measure precisely the specific parameters within any particular group (Gould 1975:353).

Measurement Definitions and Nomenclature

Moorrees (1957:78) defines the "mesiodistal crown diameter" (called the maximum mesiodistal diameter in this study) as "the greatest mesiodistal dimension of the tooth crown, measured parallel to the occlusal and labial surfaces." He then defines the "labiolingual crown diameter" (here, the maximum buccolingual diameter) as "the greatest distance between the labial [buccal] and lingual surfaces of the tooth crown in a plane perpendicular to that in which the mesiodistal diameter was measured" (1957:80). In Moorrees' study,

as in most other odontometric analyses, the buccolingual measurement is defined of the basis of the mesiodistal measurement (Wolpoff 1971b). Because the landmarks necessary for the proper orientation of tamarin teeth are much easier to use with precision when taking mesiodistal measurements, the same practice is adopted in this study. To maximize accuracy and replicability, mesiodistal measurements are defined on the basis of crown morphology and are the subsequent basis for the buccolingual measurements.

Due to the asymmetrical nature of many of the crowns in the tamarin dentition, simple descriptions of mesiodistal and buccolingual diameters (see Moorrees (1957), cited above) are not sufficiently detailed for the purposes of this study. As a result, while the terms "mesiodistal" and "buccolingual" will be used, the measurements have, in the cases of certain teeth, been adjusted and refined by the author. Detailed definitions of the measurements taken are found in Appendix A.

For the purpose of brevity, the measurements described in the following section have been assigned abbreviated variable names. The first letter in each name is either a "U" or an "L", signifying whether the tooth is part of the upper or lower dentition, respectively. The second letter identifies the tooth as

an incisor, canine, premolar, or molar ("I", "C", "P", or "M", respectively). Following the first two letters, a number identifies the position of an individual tooth in a sequence of incisors (1 or 2), premolars (2, 3, or 4), or molars (1 or 2). As there is only one canine, no number is necessary in that case. All teeth are numbered in the traditional mesiodistal (front-to-back) order.

Finally, each variable has two letters which identify the measurement being taken. Maximum buccolingual diameter is represented by "BL". Maximum mesiodistal diameter is represented by "MD". As an example, the maximum buccolingual diameter of the upper first molar is represented by the variable "UM1BL".

Measurement Techniques

Tooth crown measurements were taken with a vernier micrometer calibrated to 0.001 mm. All measurements were rounded to the nearest 0.01 mm. To facilitate measurement taking, the micrometer was fastened to a tabletop with a small, vacuum-base vise, leaving both of the observer's hands free for measuring. The tooth being measured was held in the left hand while the right hand rotated the barrel of the micrometer. Rotation was stopped when resistence was first felt, with the observer taking care to avoid distorting measurements or damaging teeth with the application of too much

pressure. The observer looked at the occlusal surface to assure that the measurement was being taken correctly and, if necessary, adjustments were made and measurements were retaken.

In some cases, a digital sliding caliper (calibrated to 0.005 mm) was used in measuring. These measrements were also rounded to the nearest 0.01 mm. The sliding caliper was used in cases where accurate measurement with the micrometer was impossible. Examples would be the dimensions of molars which could not be extracted from the jaws. Before measurement of the sample began, the micrometer and sliding caliper were tested against each other (using metal standards). Results of this comparison suggest that the two instruments do not produce significantly different results.

Prediction of Missing Values

Multivariate statistical analyses such as principal components analysis require that no individuals have missing data. Otherwise, these individuals will be omitted. Similarly, the comparisons of standard deviations which estimate the reduced major axis regression slopes require that there be no missing observations in the variables being compared.

To avoid rejecting many individuals, missing values were estimated using ESTIMATE, a SAS version of the

FORTRAN program written by Key (1983). This program estimates missing values on the basis of within-group covariance matrices. For the tamarin data, these groups consisted of the illigeri males, the illigeri females, the oedipus males, and the oedipus females. To ensure the accuracy of these estimates (to the greatest possible degree), individuals missing more than four of the 32 variables (12.5%) were removed from the sample.

CHAPTER V

DESCRIPTIVE STATISTICS

Means, standard deviations, variances, maximum and minimum values, and coefficients of variation for illigeri and oedipus are shown in Tables 1 and 2, respectively. Descriptive statistics for illigeri males, illigeri females, oedipus males, and oedipus females are shown in Tables 3, 4, 5, and 6, respectively. T-tests for each dimension were performed between species means using the PROC MEANS procedure (SAS 1982a). The null hypothesis in each case was that the species means were equal. The degrees of freedom for each test were dependent on the significance of the folded test statistic (F'), which tests the equality of sample variances (SAS 1982b:218-219). The alpha-level for rejection of the null hypothesis for equal variances (where F' = 1.00) was 0.05 in each case. The tests for equality of variances were performed with data that had been (natural) log-transformed. The object of the transformation was to reduce the possibility that variances might be significantly different by simple virtue of a significant difference in sample means. In other words, this transformation was done to prevent differences in variance which might result from simple size differences.

Table 1. Descriptive statistics for Saguinus fuscicollis illigeri (N=62).

VARIABLE	N	MEAN	STANDARD DEVIATION	MINIMUM VALUE	MAXIMUM VALUE	VARIANCE	CV
UI1BL	62	1.570	0.092	1.410	1.820	0.008	5.831
UI1MD	62	2.160	0.116	1.900	2.460	0.013	5.360
UI2BL	62	1.502	0.113	1.210	1.690	0.013	7.548
UI2MD	62	1.826	0.103	1.610	2.050	0.011	5.628
UCBL	62	2.035	0.089	1.880	2.310	0.008	4.387
UCMD	62	2.516	0.109	2.310	2.750	0.012	4.327
UP2BL	62	2.189	0.104	1.930	2.410	0.011	4.732
UP2MD	62	1.878	0.097	1.610	2.130	0.009	5.177
UP3BL	62	2.533	0.133	2.230	2.840	0.018	5.244
UP3MD	62	1.612	0.069	1.450	1.880	0.005	4.251
UP4BL	62	2.723	0.125	2.460	3.020	0.016	4.595
UP4MD	62	1.623	0.063	1.480	1.750	0.004	3.904
UM1BL	62	2.766	0.123	2.480	3.110	0.015	4.458
UM1MD	62	2.222	0.102	2.010	2.460	0.010	4.601
UM2BL	62	2.336	0.143	1.890	2.650	0.020	6.114
UM2MD	62	1.489	0.133	1.220	1.860	0.018	8.935
LI1BL	62	1.598	0.093	1.440	1.810	0.009	5.800
LI1MD	62	1.480	0.069	1.330	1.660	0.005	4.689
LI2BL	62	1.761	0.089	1.580	1.980	0.008	5.054
LI2MD	62	1.348	0.065	1.200	1.500	0.004	4.840
LCBL	62	2.417	0.108	2.160	2.660	0.012	4.454
LCMD	62	2.292	0.118	2.030	2.600	0.014	5.132
LP2BL	62	1.977	0.110	1.750	2.260	0.012	5.542
LP2MD	62	2.102	0.130	1.760	2.380	0.017	6.202
LP3BL	62	1.855	0.103	1.590	2.070	0.011	5.566
LP3MD	62	1.769	0.089	1.560	1.920	0.008	5.012
LP4BL	62	1.920	0.100	1.730	2.150	0.010	5.205
LP4MD	62	1.807	0.076	1.660	1.980	0.006	4.217
LM1BL	62	1.971	0.088	1.750	2.150	0.008	4.467
LM1MD	62	2.249	0.102	2.040	2.470	0.010	4.549
LM2BL	62	1.652	0.094	1.450	1.890	0.009	5.671
LM2MD	62	2.028	0.109	1.760	2.280	0.012	5.370

Table 2. Descriptive statistics for *Saguinus oedipus oedipus* (N=61).

VARIABLE	N	MEAN	STANDARD DEVIATION	MINIMUM VALUE	MAXIMUM VALUE	VARIANCE	CV
UI1BL	61	1.805	0.077	1.630	2.000	0.006	4.241
UI1MD	61	2.217	0.101	1.990	2.410	0.010	4.575
UI2BL	61	1.594	0.078	1.400	1.830	0.006	4.924
UI2MD	61	1.988	0.112	1.680	2.240	0.012	5.623
UCBL	61	2.431	0.119	2.160	2.710	0.014	4.887
UCMD	61	2.859	0.118	2.640	3.270	0.014	4.124
UP2BL	61	2.721	0.138	2.350	2.980	0.019	5.079
UP2MD	61	2.258	0.104	1.960	2.550	0.011	4.618
UP3BL	61	3.077	0.127	2.800	3.390	0.016	4.126
UP3MD	61	2.028	0.104	1.780	2.360	0.011	5.144
UP4BL	61	3.201	0.123	2.990	3.550	0.015	3.829
UP4MD	61	1.855	0.077	1.680	2.010	0.006	4.125
UM1BL	61	3.204	0.101	2.960	3.450	0.010	3.150
UM1MD	61	2.583	0.098	2.430	2.900	0.010	3.796
UM2BL	61	2.570	0.109	2.240	2.790	0.012	4.246
UM2MD	61	1.567	0.073	1.420	1.770	0.005	4.672
LI1BL	61	1.767	0.075	1.560	1.940	0.006	4.227
LI1MD	61	1.583	0.055	1.450	1.710	0.003	3.503
LI2BL	61	1.880	0.087	1.710	2.110	0.008	4.627
LI2MD	61	1.389	0.072	1.160	1.590	0.005	5.196
LCBL	61	2.740	0.105	2.440	2.920	0.011	3.828
LCMD	61	2.541	0.130	2.100	2.790	0.017	5.110
LP2BL	61	2.231	0.116	1.980	2.480	0.013	5.181
LP2MD	61	2.635	0.105	2.410	2.840	0.011	3.977
LP3BL	61	2.205	0.109	1.940	2.430	0.012	4.934
LP3MD	61	2.222	0.101	1.950	2.430	0.010	4.529
LP4BL	61	2.309	0.111	2.100	2.510	0.012	4.796
LP4MD	61	2.146	0.100	1.930	2.350	0.010	4.646
LM1BL	61	2.172	0.085	1.960	2.410	0.007	3.890
LM1MD	61	2.704	0.090	2.500	2.900	0.008	3.316
LM2BL	61	1.795	0.064	1.660	1.960	0.004	3.551
LM2MD	61	2.102	0.099	1.840	2.320	0.010	4.707

Table 3. Descriptive statistics for Saguinus fuscicollis illigeri males (N=30).

VARIABLE	N	MEAN	STANDARD DEVIATION	MINIMUM VALUE	MAXIMUM VALUE	VARIANCE	CV
UI1BL	30	1.559	0.094	1.410	1.820	0.009	6.002
UI1MD	30	2.158	0.130	1.900	2.460	0.017	6.045
UI2BL	30	1.470	0.119	1.220	1.690	0.014	8.063
UI2MD	30	1.823	0.105	1.610	2.050	0.011	5.776
UCBL	30	2.050	0.105	1.880	2.310	0.011	5.118
UCMD	30	2.523	0.123	2.310	2.740	0.015	4.885
UP2BL	30	2.187	0.120	1.930	2.410	0.014	5.470
UP2MD	30	1.867	0.109	1.630	2.130	0.012	5.832
UP3BL	30	2.516	0.144	2.230	2.840	0.021	5.709
UP3MD	30	1.596	0.077	1.450	1.880	0.006	4.811
UP4BL	30	2.717	0.140	2.460	3.020	0.020	5.149
UP4MD	30	1.613	0.069	1.480	1.750	0.005	4.290
UM1BL	30	2.749	0.146	2.480	3.110	0.021	5.317
UM1MD	30	2.207	0.097	2.010	2.440	0.009	4.400
UM2BL	30	2.333	0.156	1.980	2.650	0.024	6.678
UM2MD	30	1.473	0.126	1.220	1.700	0.016	8.528
LI1BL	30	1.587	0.100	1.440	1.810	0.010	6.304
LI1MD	30	1.484	0.072	1.340	1.660	0.005	4.836
LI2BL	30	1.760	0.093	1.630	1.960	0.009	5.294
LI2MD	30	1.353	0.063	1.220	1.500	0.004	4.687
LCBL	30	2.425	0.120	2.220	2.660	0.014	4.962
LCMD	30	2.289	0.127	2.060	2.600	0.016	5.540
LP2BL	30	1.976	0.120	1.770	2.260	0.014	6.087
LP2MD	30	2.119	0.127	1.830	2.380	0.016	6.008
LP3BL	30	1.841	0.116	1.590	2.040	0.013	6.311
LP3MD	30	1.742	0.091	1.560	1.920	0.008	5.201
LP4BL	30	1.918	0.111	1.730	2.150	0.012	5.779
LP4MD	30	1.812	0.074	1.670	1.930	0.006	4.093
LM1BL	30	1.952	0.083	1.830	2.120	0.007	4.236
LM1MD	30	2.220	0.096	2.070	2.420	0.009	4.317
LM2BL	30	1.668	0.101	1.450	1.890	0.010	6.050
LM2MD	30	2.023	0.112	1.810	2.230	0.013	5.536

Table 4. Descriptive statistics for Saguinus fuscicollis illigeri females (N=32).

VARIABLE	N	MEAN	STANDARD DEVIATION	MINIMUM VALUE	MAXIMUM VALUE	VARIANCE	CV
UI1BL	32	1.579	0.090	1.450	1.800	0.008	5.693
UI1MD	32	2.162	0.102	1.960	2.410	0.010	4.728
UI2BL	32	1.532	0.101	1.210	1.670	0.010	6.592
UI2MD	32	1.828	0.102	1.650	2.050	0.010	5.575
UCBL	32	2.020	0.070	1.880	2.170	0.005	3.471
UCMD	32	2.509	0.095	2.330	2.750	0.009	3.781
UP2BL	32	2.191	0.088	2.010	2.380	0.008	4.010
UP2MD	32	1.889	0.085	1.610	2.030	0.007	4.513
UP3BL	32	2.550	0.122	2.340	2.780	0.015	4.779
UP3MD	32	1.627	0.057	1.510	1.740	0.003	3.491
UP4BL	32	2.728	0.111	2.500	2.930	0.012	4.086
UP4MD	32	1.632	0.057	1.530	1.750	0.003	3.492
UM1BL	32	2.782	0.097	2.540	2.920	0.009	3.487
UM1MD	32	2.235	0.107	2.080	2.460	0.011	4.768
UM2BL	32	2.339	0.132	1.890	2.530	0.017	5.642
UM2MD	32	1.505	0.140	1.300	1.860	0.020	9.300
LI1BL	32	1.607	0.086	1.460	1.800	0.007	5.326
LI1MD	32	1.477	0.068	1.330	1.640	0.005	4.611
LI2BL	32	1.762	0.086	1.580	1.980	0.007	4.903
LI2MD	32	1.344	0.068	1.200	1.470	0.005	5.035
LCBL	32	2.409	0.096	2.160	2.550	0.009	3.965
LCMD	32	2.296	0.110	2.030	2.530	0.012	4.806
LP2BL	32	1.977	0.100	1.750	2.170	0.010	5.078
LP2MD	32	2.086	0.133	1.760	2.330	0.018	6.387
LP3BL	32	1.868	0.089	1.690	2.070	0.008	4.780
LP3MD	32	1.794	0.080	1.610	1.910	0.006	4.477
LP4BL	32	1.923	0.090	1.730	2.100	0.008	4.697
LP4MD	32	1.802	0.079	1.660	1.980	0.006	4.378
LM1BL	32	1.989	0.090	1.750	2.150	0.008	4.547
LM1MD	32	2.277	0.102	2.040	2.470	0.010	4.469
LM2BL	32	1.636	0.085	1.460	1.850	0.007	5.195
LM2MD	32	2.034	0.107	1.760	2.280	0.012	5.285

Table 5. Descriptive statistics for Saguinus oedipus oedipus males (N=32).

VARIABLE	N	MEAN	STANDARD DEVIATION	MINIMUM VALUE	MAXIMUM VALUE	VARIANCE	CV
UI1BL	32	1.837	0.066	1.680	2.000	0.004	3.568
UI1MD	32	2.214	0.106	1.990	2.410	0.011	4.792
UI2BL	32	1.612	0.064	1.490	1.730	0.004	3.994
UI2MD	32	1.987	0.106	1.710	2.150	0.011	5.330
UCBL	32	2.488	0.090	2.270	2.710	0.008	3.627
UCMD	32	2.857	0.087	2.650	3.140	0.008	3.044
UP2BL	32	2.726	0.112	2.490	2.940	0.012	4.097
UP2MD	32	2.274	0.106	2.090	2.550	0.011	4.682
UP3BL	32	3.072	0.118	2.880	3.380	0.014	3.849
UP3MD	32	2.036	0.103	1.870	2.360	0.011	5.076
UP4BL	32	3.191	0.116	3.010	3.500	0.013	3.628
UP4MD	32	1.838	0.074	1.680	1.960	0.006	4.045
UM1BL	32	3.213	0.108	2.960	3.450	0.012	3.355
UM1MD	32	2.583	0.106	2.430	2.900	0.011	4.089
UM2BL	32	2.567	0.109	2.390	2.790	0.012	4.237
UM2MD	32	1.562	0.060	1.430	1.680	0.004	3.815
LI1BL	32	1.776	0.063	1.600	1.880	0.004	3.570
LI1MD	32	1.568	0.061	1.450	1.710	0.004	3.921
LI2BL	32	1.894	0.076	1.720	2.040	0.006	4.011
LI2MD	32	1.388	0.061	1.260	1.500	0.004	4.429
LCBL	32	2.760	0.093	2.540	2.920	0.009	3.370
LCMD	32	2.539	0.115	2.330	2.740	0.013	4.543
LP2BL	32	2.267	0.108	2.030	2.480	0.012	4.746
LP2MD	32	2.664	0.096	2.420	2.840	0.009	3.603
LP3BL	32	2.217	0.122	1.940	2.430	0.015	5.510
LP3MD	32	2.246	0.080	2.080	2.390	0.006	3.569
LP4BL	32	2.307	0.121	2.100	2.510	0.015	5.241
LP4MD	32	2.161	0.098	1.930	2.350	0.010	4.538
LM1BL	32	2.163	0.088	1.960	2.360	0.008	4.047
LM1MD	32	2.706	0.096	2.500	2.900	0.009	3.554
LM2BL	32	1.804	0.057	1.670	1.890	0.003	3.179
LM2MD	32	2.117	0.078	1.940	2.320	0.006	3.666

Table 6. Descriptive statistics for Saguinus oedipus oedipus females (N=29).

VARIABLE	N	MEAN	STANDARD DEVIATION	MINIMUM VALUE	MAXIMUM VALUE	VARIANCE	CV
UI1BL	29	1.769	0.073	1.630	1.910	0.005	4.131
UI1MD	29	2.220	0.098	2.040	2.380	0.010	4.407
UI2BL	29	1.574	0.088	1.400	1.830	0.008	5.623
UI2MD	29	1.989	0.120	1.680	2.240	0.014	6.025
UCBL	29	2.368	0.116	2.160	2.670	0.013	4.893
UCMD	29	2.862	0.146	2.640	3.270	0.021	5.112
UP2BL	29	2.717	0.165	2.350	2.980	0.027	6.059
UP2MD	29	2.240	0.101	1.960	2.400	0.010	4.491
UP3BL	29	3.083	0.138	2.800	3.390	0.019	4.470
UP3MD	29	2.018	0.106	1.780	2.180	0.011	5.270
UP4BL	29	3.213	0.131	2.990	3.550	0.017	4.070
UP4MD	29	1.874	0.076	1.730	2.010	0.006	4.038
UM1BL	29	3.193	0.094	2.960	3.400	0.009	2.931
UM1MD	29	2.582	0.091	2.470	2.770	0.008	3.515
UM2BL	29	2.574	0.111	2.240	2.760	0.012	4.327
UM2MD	29	1.572	0.087	1.420	1.770	0.007	5.504
LI1BL	29	1.757	0.085	1.560	1.940	0.007	4.865
LI1MD	29	1.600	0.043	1.480	1.660	0.002	2.699
LI2BL	29	1.863	0.096	1.710	2.110	0.009	5.174
LI2MD	29	1.390	0.083	1.160	1.590	0.007	6.007
LCBL	29	2.718	0.114	2.440	2.920	0.013	4.196
LCMD	29	2.543	0.146	2.100	2.790	0.021	5.751
LP2BL	29	2.190	0.112	1.980	2.440	0.013	5.112
LP2MD	29	2.602	0.106	2.410	2.830	0.011	4.074
LP3BL	29	2.191	0.092	1.970	2.400	0.008	4.198
LP3MD	29	2.195	0.115	1.950	2.430	0.013	5.230
LP4BL	29	2.312	0.100	2.100	2.490	0.010	4.346
LP4MD	29	2.128	0.100	1.930	2.320	0.010	4.712
LM1BL	29	2.183	0.081	2.020	2.410	0.007	3.722
LM1MD	29	2.702	0.084	2.540	2.840	0.007	3.094
LM2BL	29	1.786	0.070	1.660	1.960	0.005	3.914
LM2MD	29	2.087	0.118	1.840	2.310	0.014	5.635

The confidence interval for tests of species means was 0.0016. This figure was derived by dividing the desired alpha-level for a single t-test (0.05) by the total number of tests (32 -- one for each variable). In this way, the alpha-level in each of the 32 comparisons of means is equivalent to a 0.05 level in a single test.

The size ranges for illigeri and oedipus overlap in the case of every variable. There are, however, significant differences in species means in every case, with oedipus consistently having the greater mean value (see Table 7). These results show that, on the average, the dentition of oedipus is significantly larger than that of illigeri. This is in fitting with the overall significant size difference between the species. Body mass is often used as an overall indicator of size and the author found that there was a significant difference in the means of body weights taken from the medical records of the ORAU Marmoset Research Center (see Chapter III). A sample of illigeri (N=53) averaged 363 grams while a sample of oedipus (N=26) averaged 465 grams. These means were significantly different at the 0.05 level (DF=77; t=-8.3755).

As Table 8 illustrates, there were significant species differences in the variances of the log-transformation of ten of the 32 variables (UI1BL,

Table 7. Tests of significance for differences in S. f. illigeri (N=62) and S. o. oedipus (N=61) means.

		Mean	Std	t	DF	P
UI1BL	Sfi	1.60	.0915	-15.4625	118.0*	.0001**
	Soo	1.80	.0765			
UI1MD	Sfi	2.16	.1158	-2.9132	121.0	.0043
	Sfi	2.22	.1014			
UI2BL	Sfi	1.50	.1134	-5.2025	108.7*	.0001**
	Soo	1.59	.0785			
UI2MD	Sfi	1.83	.1027	-8.3655	121.0	.0001**
	Soo	1.99	.1118			
UCBL	Sfi	2.03	.0893	-20.9300	121.0	.0001**
	Soo	2.43	.1188			
UCMD	Sfi	2.52	.1089	-16.7853	121.0	.0001**
	Soo	2.86	.1179			
UP2BL	Sfi	2.19	.1036	-24.1962	121.0	.0001**
	Soo	2.72	.1382			
UP2MD	Sfi	1.88	.0972	-20.8871	121.0	.0001**
	Soo	2.26	.1043			
UP3BL	Sfi	2.53	.1328	-23.2110	121.0	.0001**
	Soo	3.08	.1270			
UP3MD	Sfi	1.61	.0685	-26.1676	121.0	.0001**
	Soo	2.03	.1043			
UP4BL	Sfi	2.72	.1251	-21.2100	121.0	.0001**
	Soo	3.20	.1226			
UP4MD	Sfi	1.62	.0633	-18.3551	121.0	.0001**
	Soo	1.85	.0765			
UM1BL	Sfi	2.77	.1233	-21.5277	117.1*	.0001**
	Soo	3.20	.1226			
UM1MD	Sfi	2.22	.1022	-19.9938	121.0	.0001**
	Soo	2.58	.0980			
UM2BL	Sfi	2.34	.1428	-10.2206	114.1*	.0001**
	Soo	2.57	.1091			
UM2MD	Sfi	1.49	.1331	-4.0119	95.1*	.0001**
	Soo	1.57	.0732			
LI1BL	Sfi	1.60	.0923	-11.1329	116.5*	.0001**
	Soo	1.77	.0747			
LI1MD	Sfi	1.48	.0694	-9.1390	116.1*	.0001**
	Soo	1.58	.0555			
LI2BL	Sfi	1.76	.0890	-7.4802	121.0	.0001**
	Soo	1.88	.0870			
LI2MD	Sfi	1.35	.0635	-3.2628	121.0	.0001**
	Soo	1.39	.0722			
LCBL	Sfi	2.42	.1076	-16.8628	121.0	.0001**
	Soo	2.74	.1049			
LCMD	Sfi	2.29	.1177	-11.1292	121.0	.0001**
	Soo	2.54	.1298			

Table 7 (Continued)

		Mean	Std	t	DF	P
LP2BL	Sfi	1.98	.1095	-12.5137	121.0	.0001**
	Soo	2.23	.1156			
LP2MD	Sfi	2.10	.1304	-24.9972	116.4*	.0001**
	Soo	2.63	.1048			
LP3BL	Sfi	1.86	.1033	-18.2989	121.0	.0001**
	Soo	2.21	.1088			
LP3MD	Sfi	1.77	.0887	-26.4884	121.0	.0001**
	Soo	2.22	.1006			
LP4BL	Sfi	1.92	.1000	-20.4391	121.0	.0001**
	Soo	2.31	.1108			
LP4MD	Sfi	1.81	.0762	-21.1874	121.0	.0001**
	Soo	2.15	.0997			
LM1BL	Sfi	1.97	.0880	-12.9458	121.0	.0001**
	Soo	2.17	.0845			
LM1MD	Sfi	2.25	.1023	-26.2162	119.4*	.0001**
	Soo	2.70	.0897			
LM2BL	Sfi	1.65	.0937	-9.9335	107.7*	.0001**
	Soo	1.80	.0637			
LM2MD	Sfi	2.03	.1089	-3.9454	121.0	.0001**

* Variances are significantly different at 0.05.
** Means are significantly different at 0.05.

Table 8. Tests of significance for differences in S. f. illigeri (N=62, DF=61) and S. o. oedipus (N=61, DF=60) logged-value variances.

		Mean	Var	F'	P
UI1BL	Sfi	.4491	.0033	1.81	.0026*
	Soo	.5894	.0018		
UI1MD	Sfi	.7685	.0029	1.36	.2317
	Soo	.7951	.0021		
UI2BL	Sfi	.4040	.0061	2.52	.0005**
	Soo	.4648	.0024		
UI2MD	Sfi	.6004	.0032	1.03	.9222
	Soo	.6853	.0032		
UCBL	Sfi	.7094	.0019	1.28	.3357
	Soo	.8870	.0024		
UCMD	Sfi	.9217	.0019	1.11	.6753
	Soo	1.0497	.0017		
UP2BL	Sfi	.7824	.0023	1.17	.5423
	Soo	.9999	.0026		
UP2MD	Sfi	.6290	.0027	1.28	.3402
	Soo	.8134	.0021		
UP3BL	Sfi	.9281	.0027	1.63	.0593
	Soo	1.1232	.0017		
UP3MD	Sfi	.4766	.0018	1.49	.1228
	Soo	.7056	.0026		
UP4BL	Sfi	1.0007	.0021	1.48	.1307
	Soo	1.1629	.0014		
UP4MD	Sfi	.4833	.0015	1.12	.6704
	Soo	.6170	.0017		
UM1BL	Sfi	1.0163	.0020	2.01	.0074*
	Soo	1.1683	.0010		
UM1MD	Sfi	.7972	.0021	1.49	.1232
	Soo	.9482	.0014		
UM2BL	Sfi	.8467	.0040	2.16	.0032*
	Soo	.9431	.0018		
UM2MD	Sfi	.3945	.0078	3.62	.0001**
	Soo	.4480	.0022		
LI1BL	Sfi	.4670	.0033	1.79	.0259*
	Soo	.5681	.0018		
LI1MD	Sfi	.3910	.0022	1.76	.0297*
	Soo	.4590	.0012		
LI2BL	Sfi	.5646	.0025	1.20	.4867
	Soo	.6301	.0021		
LI2MD	Sfi	.2977	.0024	1.15	.5782
	Soo	.3271	.0028		
LCBL	Sfi	.8815	.0020	1.32	.2894
	Soo	1.0072	.0015		
LCMD	Sfi	.8283	.0026	1.03	.8940
	Soo	.9312	.0027		

Table 8 (Continued)

		Mean	Var	F'	P
LP2BL	Sfi	.6799	.0031	1.15	.5903
	Soo	.8010	.0027		
LP2MD	Sfi	.7409	.0040	2.47	.0006**
	Soo	.9679	.0016		
LP3BL	Sfi	.6164	.0031	1.27	.3628
	Soo	.7869	.0025		
LP3MD	Sfi	.5692	.0026	1.23	.4267
	Soo	.7973	.0021		
LP4BL	Sfi	.6513	.0027	1.16	.5719
	Soo	.8358	.0023		
LP4MD	Sfi	.5908	.0018	1.22	.4405
	Soo	.7623	.0022		
LM1BL	Sfi	.6775	.0020	1.32	.2782
	Soo	.7751	.0015		
LM1MD	Sfi	.8096	.0021	1.86	.0170*
	Soo	.9942	.0011		
LM2BL	Sfi	.5003	.0032	2.53	.0004**
	Soo	.5844	.0013		
LM2MD	Sfi	.7058	.0029	1.28	.3330
	Soo	.7420	.0022		

* Variances are significantly different at 0.05.
** Variances are significantly different at 0.05 for 32 comparisons.

UI2BL, UM1BL, UM2BL, UM2MD, LI1BL, LI1MD, LP2MD, LM1MD, and LM2BL). Note that in Table 8, there are two levels of significance specified: 0.05 and 0.0015. These are actually equivalent with regard to their applications. The 0.05 alpha-level is used in determining the degrees of freedom and t-statistics for the comparison of means (a single variable case). The 0.0015 level is the same as the one used to compare means (0.05 divided by the number of variables (32)). It is used when examining the number of significant differences in variances between two samples.

The species samples were divided by sex and tests for differences in male and female means were performed. F'-statistics for the comparisons of the log-transformed variable variances were also examined. The alpha-levels used were the same as the species comparison. The results for the illigeri sample is shown in Table 9. The illigeri sample shows no significant differences in sex means. In the oedipus sample (Table 10), there were significant sex differences for two variables: UI1BL and UCBL. In both cases, the male means were greater.

In the sex comparison of variances for the log-transformed variables for the illigeri sample (Table 11), there were no significant differences between males and females at the 32 variable level of significance

Table 9. Tests of significance for differences in male (N=30) and female (N=32) means for S. f. illigeri.

	Sex	Mean	Std	t	DF	P
UI1BL	M	1.56	.0936	-.8744	60.0	.3854
	F	1.58	.0899			
UI1MD	M	2.16	.1304	-.1314	60.0	.8959
	F	2.16	.1022			
UI2BL	M	1.47	.1185	-2.2392	60.0	.0289
	F	1.53	.1010			
UI2MD	M	1.82	.1053	-.1702	60.0	.8654
	F	1.83	.1019			
UCBL	M	2.05	.1049	1.3294	50.1*	.1897
	F	2.02	.0701			
UCMD	M	2.52	.1233	.5240	60.0	.6022
	F	2.51	.0949			
UP2BL	M	2.19	.1197	-.1358	60.0	.8924
	F	2.19	.0879			
UP2MD	M	1.87	.1089	-.9050	60.0	.3691
	F	1.89	.0852			
UP3BL	M	2.52	.1436	-1.0079	60.0	.3175
	F	2.55	.1219			
UP3MD	M	1.60	.0768	-1.8456	60.0	.0699
	F	1.63	.0568			
UP4BL	M	2.72	.1399	-.3467	60.0	.7300
	F	2.73	.1115			
UP4MD	M	1.61	.0692	-1.1562	60.0	.2522
	F	1.63	.0570			
UM1BL	M	2.75	.1462	-1.0266	49.9*	.3095
	F	2.78	.0970			
UM1MD	M	2.21	.0971	-1.0662	60.0	.2906
	F	2.24	.1066			
UM2BL	M	2.33	.1558	-.1566	60.0	.8761
	F	2.34	.1320			
UM2MD	M	1.47	.1256	-.9361	60.0	.3530
	F	1.50	.1399			
LI1BL	M	1.59	.1001	-.8544	60.0	.3963
	F	1.61	.0856			
LI1MD	M	1.48	.0718	.4000	60.0	.6906
	F	1.48	.0681			
LI2BL	M	1.76	.0932	-.0822	60.0	.9347
	F	1.76	.0864			
LI2MD	M	1.35	.0634	.5357	60.0	.5942
	F	1.34	.0677			
LCBL	M	2.43	.1203	.5794	60.0	.5645
	F	2.41	.0955			

Table 9 (Continued)

	Sex	Mean	Std	t	DF	P
LCMD	M	2.29	.1268	-.2198	60.0	.8267
	F	2.30	.1103			
LP2BL	M	1.98	.1202	-.0654	60.0	.9481
	F	1.98	.1004			
LP2MD	M	2.12	.1273	.9782	60.0	.3319
	F	2.09	.1332			
LP3BL	M	1.84	.1162	-1.0464	60.0	.2296
	F	1.87	.0893			
LP3MD	M	1.74	.0906	-2.3821	60.0	.0204
	F	1.79	.0803			
LP4BL	M	1.92	.1108	-.2132	60.0	.8319
	F	1.92	.0903			
LP4MD	M	1.81	.0742	.5370	60.0	.5933
	F	1.80	.0789			
LM1BL	M	1.95	.0827	-1.6664	60.0	.1008
	F	1.99	.0904			
LM1MD	M	2.22	.0958	-2.2877	60.0	.0257
	F	2.28	.1018			
LM2BL	M	1.67	.1009	1.3569	60.0	.1799
	F	1.64	.0850			
LM2MD	M	2.02	.1120	-.3976	60.0	.6923
	F	2.03	.1075			

* Variances are significantly different at 0.05.

Table 10. Tests of significance for differences in male (N=32) and female (N=29) means for S. o. oedipus.

	Sex	Mean	Std	t	Df	P
UI1BL	M	1.84	.0655	3.7894	59.0	.0004*
	F	1.77	.0731			
UI1MD	M	2.21	.1061	-.2014	59.0	.8411
	F	2.22	.0978			
UI2BL	M	1.61	.0644	1.1910	59.0	.0598
	F	1.57	.0885			
UI2MD	M	1.99	.1059	-.0712	59.0	.9435
	F	1.99	.1199			
UCBL	M	2.49	.0902	4.5314	59.0	.0001*
	F	2.37	.1159			
UCMD	M	2.86	.0869	-.1764	44.7*	.8608
	F	2.86	.1463			
UP2BL	M	2.73	.1117	.2580	48.6*	.7975
	F	2.72	.1646			
UP2MD	M	2.27	.1065	1.2809	59.0	.2053
	F	2.24	.1006			
UP3BL	M	3.07	.1183	-.3424	59.0	.7333
	F	3.08	.1378			
UP3MD	M	2.04	.1034	.6690	59.0	.5061
	F	2.02	.1064			
UP4BL	M	3.19	.1158	-.6913	59.0	.4921
	F	3.21	.1078			
UP4MD	M	1.84	.0743	-1.8719	59.0	.0662
	F	1.87	.0757			
UM1BL	M	3.21	.1078	.7456	59.0	.4589
	F	3.19	.0936			
UM1MD	M	2.58	.1056	.0540	59.0	.9571
	F	2.58	.0908			
UM2BL	M	2.57	.1088	-.2342	59.0	.8157
	F	2.57	.1114			
UM2MD	M	1.56	.0596	-.5484	49.1*	.5859
	F	1.57	.0865			
LI1BL	M	1.78	.0634	.9962	59.0	.3232
	F	1.76	.0855			
LI1MD	M	1.57	.0615	-2.2973	59.0	.0252
	F	1.60	.0432			
LI2BL	M	1.89	.0760	1.3980	59.0	.1673
	F	1.86	.0964			
LI2MD	M	1.39	.0615	-.1173	59.0	.9070
	F	1.39	.0835			
LCBL	M	2.76	.0930	1.6096	59.0	.1128
	F	2.72	.1140			

Table 10 (Continued)

	Sex	Mean	Std	t	DF	P
LCMD	M	2.54	.1154	-.1008	59.0	.9201
	F	2.54	.1462			
LP2BL	M	2.27	.1076	2.7555	59.0	.0078
	F	2.19	.1120			
LP2MD	M	2.66	.0960	2.3973	59.0	.0197
	F	2.60	.1060			
LP3BL	M	2.22	.1222	.9355	59.0	.3533
	F	2.19	.0920			
LP3MD	M	2.25	.0802	1.9830	49.5*	.0529
	F	2.20	.1148			
LP4BL	M	2.31	.1209	-.1694	59.0	.8661
	F	2.31	.1005			
LP4MD	M	2.16	.0981	1.2974	59.0	.1995
	F	2.13	.1003			
LM1BL	M	2.16	.0875	-.9355	59.0	.3533
	F	2.18	.0812			
LM1MD	M	2.71	.0961	.1534	59.0	.8786
	F	2.70	.0836			
LM2BL	M	1.80	.0573	1.1181	59.0	.2680
	F	1.79	.0699			
LM2MD	M	2.12	.0776	1.1760	47.8*	.2454
	F	2.09	.1176			

* Variances are significantly different at 0.05.

Table 11. Tests of significance for differences in male (N=30, DF=29) and female (N=32, DF=31) logged-value variances for S. f. illigeri.

	Sex	Mean	Var	F'	P
UI1BL	M	.4423	.0035	1.11	.7722
	F	.4555	.0031		
UI1MD	M	.7673	.0036	1.63	.1864
	F	.7697	.0022		
UI2BL	M	.3820	.0069	1.46	.3012
	F	.4247	.0047		
UI2MD	M	.5991	.0033	1.08	.8365
	F	.6016	.0031		
UCBL	M	.7168	.0026	2.11	.0437*
	F	.7025	.0012		
UCMD	M	.9244	.0024	1.67	.1648
	F	.9191	.0014		
UP2BL	M	.7812	.0030	1.85	.0964
	F	.7835	.0016		
UP2MD	M	.6225	.0034	1.56	.2263
	F	.6351	.0022		
UP3BL	M	.9210	.0032	1.42	.3421
	F	.9349	.0023		
UP3MD	M	.4662	.0022	1.77	.1227
	F	.4863	.0012		
UP4BL	M	.9984	.0026	1.57	.2202
	F	1.0029	.0017		
UP4MD	M	.4772	.0019	1.55	.2343
	F	.4890	.0012		
UM1BL	M	1.0099	.0028	2.27	.0272*
	F	1.0224	.0012		
UM1MD	M	.7909	.0019	1.16	.6965
	F	.8032	.0022		
UM2BL	M	.8451	.0046	1.34	.4224
	F	.8481	.0034		
UM2MD	M	.3873	.0074	1.11	.7802
	F	.4045	.0083		
LI1BL	M	.4602	.0038	1.33	.4315
	F	.4733	.0028		
LI1MD	M	.3934	.0023	1.09	.8215
	F	.3887	.0021		
LI2BL	M	.5640	.0027	1.12	.7482
	F	.5652	.0024		
LI2MD	M	.3013	.0022	1.19	.6436
	F	.2944	.0026		
LCBL	M	.8847	.0024	1.49	.2783
	F	.8784	.0016		

Table 11 (Continued)

	Sex	Mean	Var	F'	P
LCMD	M	.8267	.0030	1.29	.4834
	F	.8298	.0023		
LP2BL	M	.6791	.0037	1.38	.3819
	F	.6806	.0027		
LP2MD	M	.7490	.0037	1.14	.7190
	F	.7333	.0042		
LP3BL	M	.6084	.0040	1.81	.1080
	F	.6240	.0022		
LP3MD	M	.5539	.0027	1.30	.4700
	F	.5835	.0021		
LP4BL	M	.6495	.0033	1.49	.2743
	F	.6529	.0022		
LP4MD	M	.5938	.0017	1.13	.7385
	F	.5879	.0019		
LM1BL	M	.6680	.0018	1.10	.7944
	F	.6865	.0021		
LM1MD	M	.7965	.0018	1.12	.6147
	F	.8220	.0020		
LM2BL	M	.5101	.0036	1.33	.4372
	F	.4911	.0027		
LM2MD	M	.7029	.0030	1.08	.8356
	F	.7085	.0028		

* Variances are significantly different at 0.05.

(.0015). There were two cases (UCBL and UM1BL) in which the differences were significant at the single variable level (0.05). These differences are important only in determining the t-values and degrees of freedom for the tests of significance between sex means.

The comparison of male and female variances for oedipus is shown in Table 12. There were four cases in which the variances were different at the single-case significance level of 0.05 (UCMD, UP2BL, LP3MD, and LM2MD), but, again, these are only of importance in assigning the degrees of freedom for significance tests of sex means.

In summary, there appears to be little sexual dimorphism in the dentitions of illigeri and oedipus, as measured by the means and variances of tooth diameters. On the other hand, the species means are significantly different in 31 of 32 cases (with UI1MD being the exception), with significantly different variances in four of thirty-two cases (UI2BL, UM2MD, LP2MD, and LM2BL). Because the magnitudes of the intraspecific sex differences are negligible in comparison to the highly significant species differences, the sexes will be pooled in all future analyses.

Table 12. Tests of significance for differences in male (N=32, DF=31) and female (N=29, DF=28) logged-value variances for *S. o. oedipus*.

	Sex	Mean	Var	F'	P
UI1BL	M	.4423	.0035	1.11	.7722
	F	.4555	.0031		
UI1MD	M	.7673	.0036	1.63	.1864
	F	.7697	.0022		
UI2BL	M	.3820	.0069	1.46	.3012
	F	.4247	.0047		
UI2MD	M	.5991	.0033	1.08	.8365
	F	.6016	.0031		
UCBL	M	.7168	.0026	2.11	.0437*
	F	.7025	.0012		
UCMD	M	.9244	.0024	1.67	.1648
	F	.9191	.0014		
UP2BL	M	.7812	.0030	1.85	.0964
	F	.7835	.0016		
UP2MD	M	.6225	.0034	1.56	.2263
	F	.6351	.0022		
UP3BL	M	.9210	.0032	1.42	.3421
	F	.9349	.0023		
UP3MD	M	.4662	.0022	1.77	.1227
	F	.4863	.0012		
UP4BL	M	.9984	.0026	1.57	.2202
	F	1.0029	.0017		
UP4MD	M	.4772	.0019	1.55	.2343
	F	.4890	.0012		
UM1BL	M	1.0099	.0028	2.27	.0272*
	F	1.0224	.0017		
UM1MD	M	.7909	.0019	1.16	.6965
	F	.8032	.0022		
UM2BL	M	.8451	.0046	1.34	.4224
	F	.8481	.0034		
UM2MD	M	.3873	.0074	1.11	.7802
	F	.4045	.0083		
LI1BL	M	.4602	.0038	1.33	.4315
	F	.4733	.0028		
LI1MD	M	.3934	.0023	1.09	.8215
	F	.3887	.0021		
LI2BL	M	.5640	.0027	1.12	.7482
	F	.5652	.0024		
LI2MD	M	.3013	.0022	1.19	.6436
	F	.2944	.0026		
LCBL	M	.8847	.0024	1.49	.2783
	F	.8784	.0016		
LCMD	M	.8267	.0030	1.29	.4834
	F	.8298	.0023		

Table 12 (Continued)

	Sex	Mean	Var	F'	P
LP2BL	M	.6791	.0037	1.38	.3819
	F	.6806	.0027		
LP2MD	M	.7490	.0037	1.38	.3819
	F	.7333	.0042		
LP3BL	M	.6084	.0040	1.81	.1080
	F	.6240	.0022		
LP3MD	M	.5539	.0027	1.30	.4700
	F	.5835	.0021		
LP4BL	M	.6495	.0033	1.49	.2743
	F	.6529	.0022		
LP4MD	M	.5938	.0017	1.13	.7385
	F	.5879	.0019		
LM1BL	M	.6680	.0018	1.21	.6147
	F	.6865	.0021		
LM1MD	M	.7965	.0018	1.10	.7944
	F	.8220	.0020		
LM2BL	M	.5101	.0036	1.33	.4372
	F	.4911	.0027		
LM2MD	M	.7029	.0030	1.08	.8356
	F	.7085	.0028		

* Variances are significantly different at 0.05.

CHAPTER VI

ALLOMETRIC ANALYSIS

In examining scaling phenomena in the tamarin dentition, the analysis was carried out in a hierarchical fashion. First, the maximum mesiodistal and buccolingual diameters for each individual tooth were compared through correlation analysis and RMA regression. The correlation analysis was performed to reduce the possiblity of conducting RMA regressions which would be meaningless because of low correlations between variables. If the diameters being compared exhibited significant correlations for both species, then an RMA regression was performed to test the null hypothesis that oedipus teeth are simple, hypermorphic "blow-ups" of illigeri teeth.

Second, all of the buccolingual diameters for the upper jaw were subjected to intraspecific principal components analysis. The process was repeated for the upper mesiodistal diameters, the lower buccolingual diameters, and the lower mesiodistal diameters. The reason for separating the upper and lower teeth was to limit the number of variables involved in each analysis so that the interpretations would be made more straightforward. The buccolingual and mesiodistal diameters within the jaws were separated for the same reason and

because of evidence from previous multivariate studies suggesting a degree of genetic independence between tooth lengths and widths (Suarez and Bernor 1972; Suarez and Williams 1973; Lombardi 1975, 1978).

Third, individual tooth areas were examined by RMA regression, with species comparisons being done in terms of geometric similarity. These comparisons were done (by jaw) within Dahlberg's (1945) four morphogenetic fields: incisors, canines, premolars, and molars. The canine was actually excluded from this phase of the analysis, because of its morphogenetic field having only a single tooth. In each of the remaining types, one tooth in each field (the polar tooth) served as the x-axis variable against which the remaining area(s) was scaled. The polar teeth were (for both upper and lower jaws) the central incisor, the second premolar, and the first molar. As with the RMA analysis of individual areas, the correlations between x- and y-axis variables were tested for significance to ensure that the RMA regressions would be meaningful.

Fourth, the individual tooth areas were subjected (by jaw) to principal components analysis on the intra-specific level. The null hypothesis was that the patterns of intraspecific scaling would be similar.

Fifth, the tooth areas within each morphogenetic field were summed and species comparisons were performed

using RMA regressions. In each jaw, summed incisor area and canine area were both scaled against summed postcanine area. Species comparisons with the postcanine dentition were then made by scaling summed premolar areas against summed molar areas.

Finally, the summed areas for the morphogenetic fields (including the canine) were subjected to principal components analysis for each jaw. The null hypothesis was the same as in previous comparisons: the intraspecific pattern for oedipus should represent a hypermorphic extension of the illigeri pattern.

Individual Tooth Diameters -- RMA Analysis

The allometric variation in individual teeth was examined in both species by producing RMA regressions of the maximum mesiodistal diameter on the maximum buccolingual diameter. The choice of the y- and x-axis variables was made to reflect crown index (100 times MD/BL), a standard, univariate measure of tooth shape (Wolpoff 1971b:10).

Each slope was classified into one of three categories: 1) isometry, 2) positive allometry, and 3) negative allometry. The classification of a regression pattern depends upon whether the slope is significantly different from isometry. A slope was classified as signficantly different from isometry if the value for isometry (b=1.00) fell outside its 95% confidence

interval. The upper and lower limits for the confidence interval were determined by two standard errors on either side of the slope estimate. The significance of differences in slopes was determined by the z-statistic. This test is an expression of the probability that the slopes are the same.

Correlations between the mesiodistal and buccolingual diameters in individual teeth are shown in Table 13. The correlations were tested for significance using a t-statistic (Sokal and Rohlf 1981; SAS 1982a). In each case, the null hypothesis was that the correlation coefficient was not significantly different from zero. In Table 13, the null hypotheses were rejected if the t-statistic probabilities were less than 0.0031. This figure is the 16-case equivalent of a single-case 0.05 level of significance. As Table 13 shows, there were only three of sixteen cases in which both species had correlation coefficients which were significant (M^2, I_1, and M_2). There were three cases in which only the illigeri sample had significant correlations ($\bar{C}$, I_2, and $\underline{C}$). There were two cases in which only the oedipus sample had significant correlations (P^2 and P^3). The RMA regression equations for M^2, I_1, and M_2 are given in Table 14. The plots for these equations are shown in Figures 6, 7, and 8, respectively.

Table 13. Correlations between mesiodistal and buccolingual diameters for individual teeth. Also shown are t-statistic probabilities.

		Upper Teeth				Lower Teeth	
		r	P			r	P
I1	Sfi	.03868	.7654	I1	Sfi	.37113	.0030*
	Soo	.30933	.0153		Soo	.37388	.0030*
I2	Sfi	.12764	.3228	I2	Sfi	.53351	.0001*
	Soo	.12275	.3460		Soo	.27224	.0338
C	Sfi	.37965	.0025*	C	Sfi	.59781	.0001*
	Soo	.19219	.1378		Soo	.27801	.0301
P2	Sfi	.31588	.0124	P2	Sfi	.17156	.1825
	Soo	.37879	.0026*		Soo	.27088	.0347
P3	Sfi	.27978	.0276	P3	Sfi	.25204	.0481
	Soo	.46704	.0001*		Soo	-.15716	.2264
P4	Sfi	.21433	.0944	P4	Sfi	.24279	.0573
	Soo	.35214	.0054		Soo	.02740	.8340
M1	Sfi	.34433	.0061	M1	Sfi	.34705	.0057
	Soo	.16465	.2048		Soo	.15759	.2252
M2	Sfi	.51361	.0001*	M2	Sfi	.42114	.0007*
	Soo	.59518	.0001*		Soo	.39977	.0014*

* Correlation is significantly different from zero at the 0.05 level.

Table 14. RMA regression statistics for M2, I1, and M2. The slopes and intercepts are represented by b and a, respectively. Also shown are the 95% confidence intervals for the slope estimates and the z-statistic for testing differences in slopes.

		b	95% CI	zb	a
M2	Sfi	1.408	1.101 -- 1.714*	1.6793	-.797
	Soo	1.089	.865 -- 1.313		-.587
I1	Sfi	.818	.625 -- 1.011	-.4067	.009
	Soo	.824	.628 -- 1.020		-.009
M2	Sfi	.950	.731 -- 1.169	-2.0073**	.230
	Soo	1.333	1.177 -- 1.490*		-.037

* Slope is significantly different from isometry at the 0.05 level.

** Species slopes are significantly different from each other at the 0.05 level.

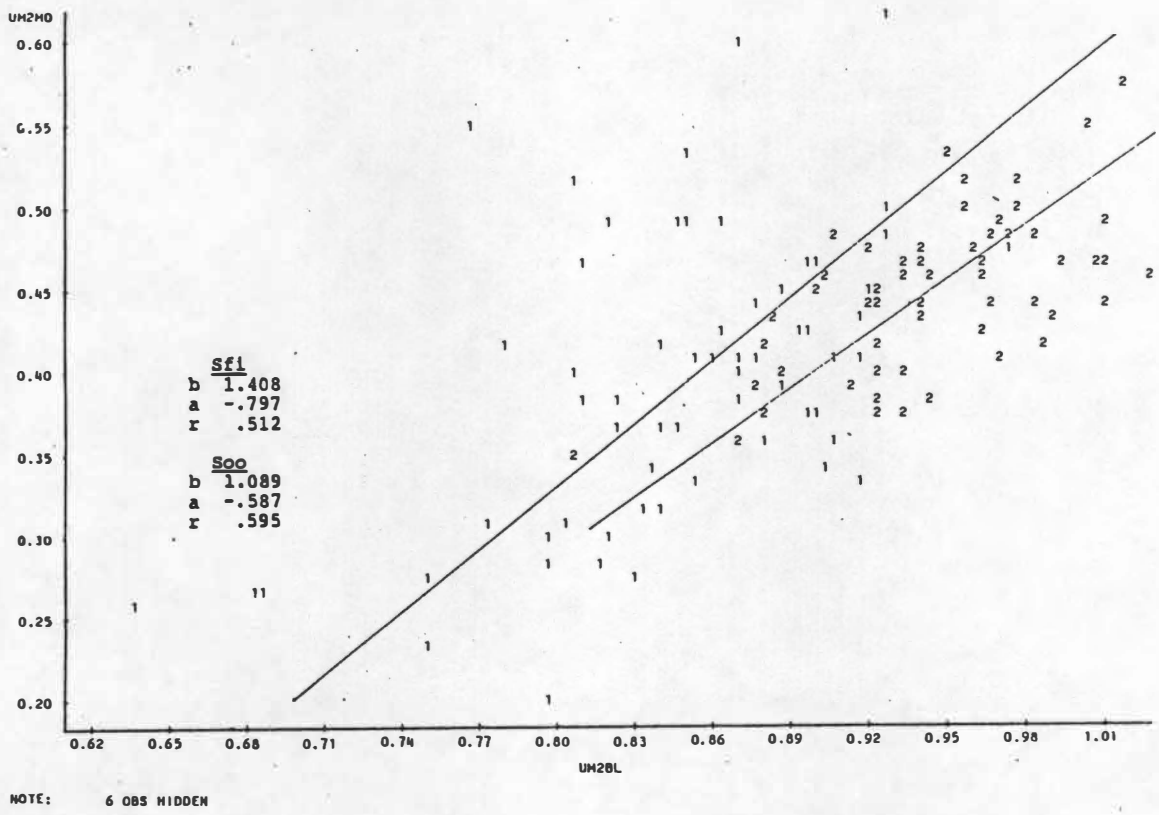

Figure 6. Plots of intraspecific RMA regressions of UM2MD on UM2BL for S. f. illigeri and S. o. oedipus. The log-transformed data are plotted on arithmetic axes in this and all subsequent plots. Also, in this and all subsequent regression plots, illigeri individuals are designated by "1" and oedipus individuals are designated by "2".

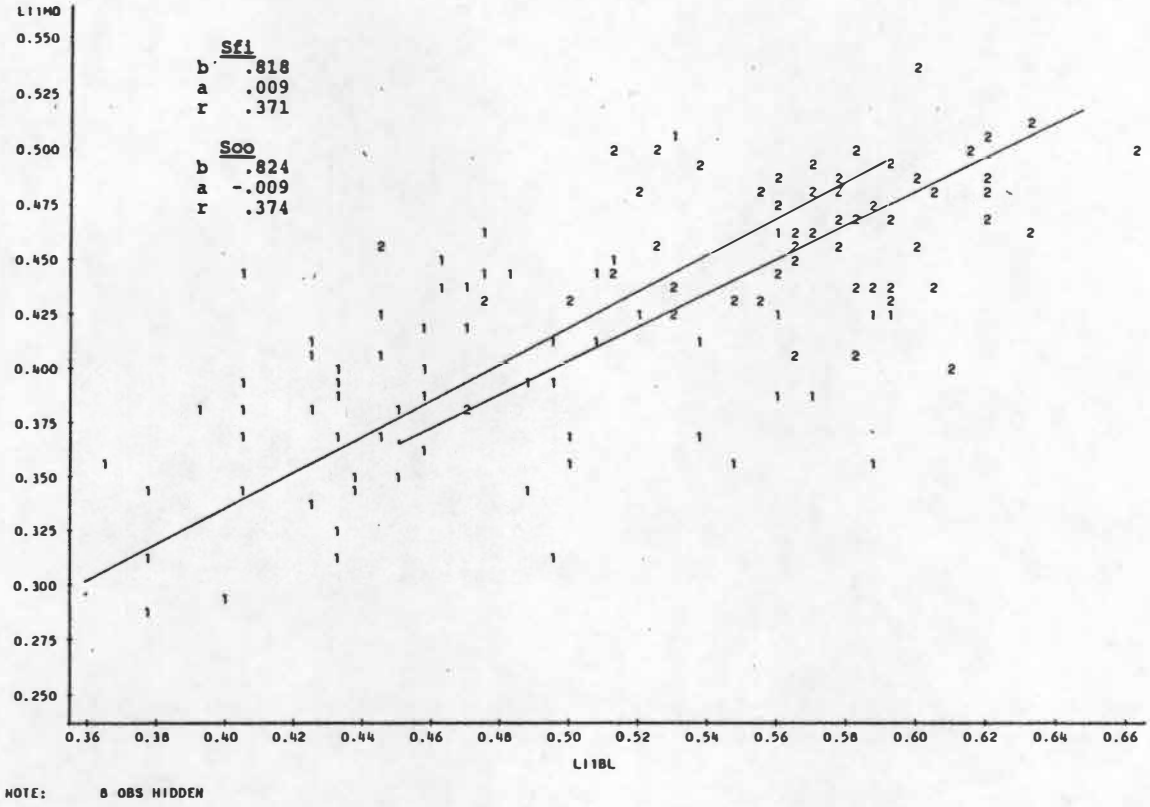

Figure 7. Plots of intraspecific RMA regressions of LI1BL on LI1MD for S. f. illigeri and S. o. oedipus.

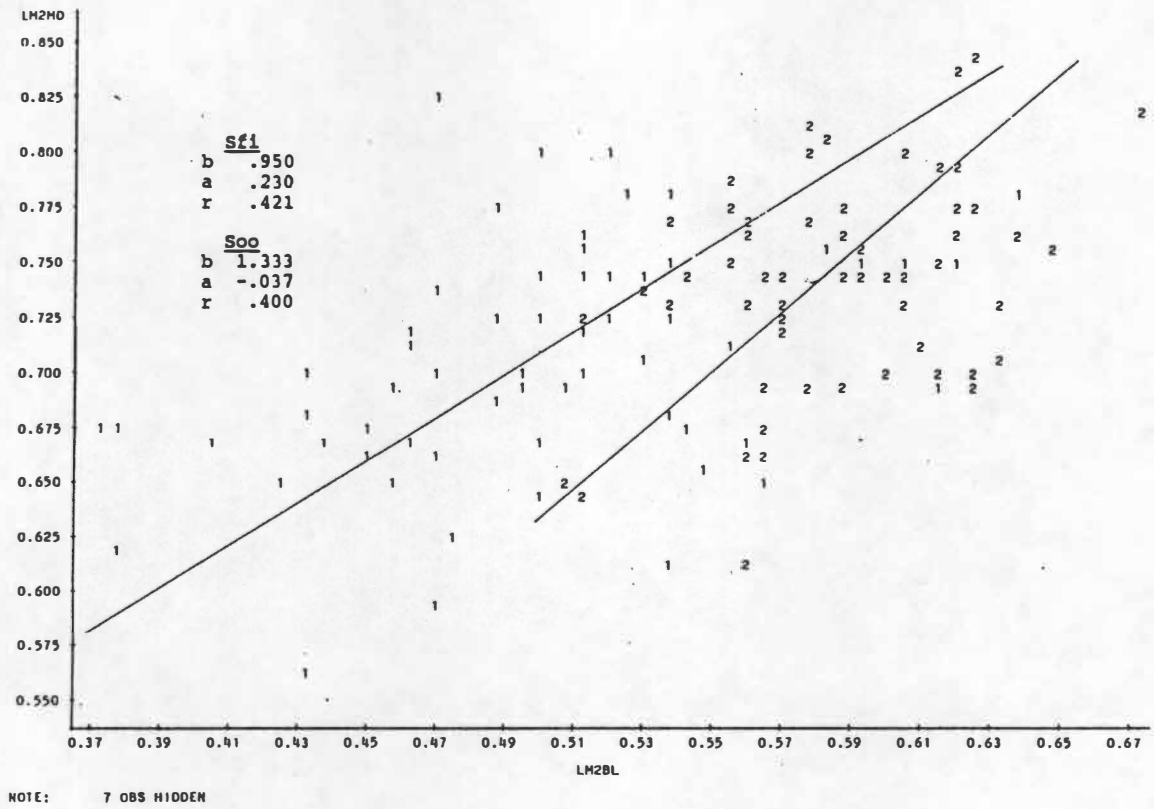

Figure 8. Plots of intraspecific RMA regressions of LM2MD on LM2BL for S. f. illigeri and S. o. oedipus.

Upper second molar. The slopes for illigeri and oedipus are 1.408 and 1.089, respectively. The illigeri slope is significantly different from isometry and is classified as positively allometric. The oedipus slope is not significantly different from isometry. The z-statistic shows that the species slopes are not significantly different from each other. The isometric oedipus pattern is interpreted as neotenous, relative to the illigeri pattern. An examination of the regression plot (Figure 6) shows that the mean of the oedipus lies below the illigeri regression line. This indicates that, on the average, the oedipus teeth are more mesio-distally expanded than would be the case with hyper-morphosis.

Lower central incisor. The RMA slopes for illigeri and oedipus are .818 and .824, respectively. Neither slope is significantly different from isometry. The z-statistic indicates that the species slopes are not significantly different from each other. The regression plot (Figure 7) shows that the illigeri and oedipus patterns are nearly superimposed. The oedipus pattern is therefore interpreted as a hypermorphic extension of the illigeri pattern, with both slopes being isometric.

Lower second molar. The RMA slopes for illigeri and oedipus are .950 and 1.333, respectively. The illigeri slope is not significantly different from

isometry. The oedipus slope is significantly different from isometry and is classified as positively allometric. The z-statistic indicates that the species slopes are significantly different from each other. The positively allometric oedipus pattern is therefore interpreted as accelerated, relative to the isometric illigeri pattern. The regression plot (Figure 8) shows that the oedipus mean lies below the illigeri regression line, indicates that the oedipus teeth, on the average, more mesiodistally expanded than would be the case with hypermorphosis.

In most cases, the shapes of individual teeth are not strongly correlated with size. This suggests that intraspecific tooth shape variation, as measured by the maximum diameters, is not an allometric phenomenon. In the three cases in which tooth shape was significantly correlated with size in both species, three different types of geometric relationships were seen. The lower central incisors of illigeri and oedipus exhibited geometrically similar patterns (isometric hypermorphosis), thus conforming to the null hypothesis. The upper and lower second molars exhibited patterns which were geometrically dissociated, indicating that the differences in shape between species cannot be explained in terms of extension of one pattern into a different size range.

Individual Tooth Diameters -- PCA Analysis

Upper buccolingual diameters. The upper buccolingual diameters for each tooth were log-transformed and used to construct intraspecific covariance matrices. The intraspecific matrices for illigeri and oedipus may be found in Appendix C. The matrices were subjected to principal components analysis (Jolicoeur 1963a, 1963b). In Jolicoeur's multivariate generalization, the first component eigenvectors have been standardized by dividing each by the value for isometry, so that the isometry value will be 1.00. The standardized coefficients were classified into one of three categories: 1) isometric (0.95 -- 1.05), 2) "near-isometric" (0.90 -- 0.94 and 1.06 -- 1.10), and 3) allometric (less than 0.90 and greater that 1.10). The near-isometric category is used to describe coefficients which are close to isometry, but probably do not indicate much size-related shape change, given the small ranges of species variation.

The results of the PCA on the upper buccolingual diameters are shown in Table 15. The first principal component (PC I) for the illigeri sample accounts for 39.8% of the total sample variance. While a proportionally larger first component might be more desirable, the 39.8% is probably sufficiently reflective of size-related shape patterning. The strongest allometric

Table 15. Principal components analysis of upper buccolingual diameters.

	Raw PC I Loadings		Standardized Coefficients	
	Sfi	Soo	Sfi	Soo
I1	.3455	.3797	.9771	1.0739
I2	.5683	.4663	1.6073	1.3082
C	.2192	.3690	.6200	1.0438
P2	.3268	.3999	.9243	1.1312
P3	.3291	.3392	.9309	.9594
P4	.2581	.3531	.7300	.9987
M1	.2660	.1732	.7524	.4898
M2	.3965	.2694	1.1214	.7620

Raw Isometry: .3536

PC I Variance (% of total): Sfi 39.8
Soo 40.5

Vector Correlation: .9520

Vector Angle: 17.82°

patterning is seen in the lateral incisor (positive -- 1.6073) and the canine (negative -- .6200). Allometric patterning is also seen in the fourth premolar and first molar (both negative -- .7300 and .7524, respectively) and in the second molar (positive -- 1.1214). The remaining teeth, the second and third premolars, exhibit negative near-isometry (.9243 and .9309, respectively).

In the oedipus sample, the pattern seen is somewhat different from that of the illigeri. In this case, the first component accounts for 40.5% of the total sample variation. The strongest allometric patterning occurs in the canine (positive -- 1.3082) and the first molar (negative -- .4898). Allometric patterning is also seen in the second premolar (positive -- 1.1312) and the second molar (negative -- .7620). One tooth, the central incisor, exhibits positive near-isometry (1.0739). The remaining teeth (canine, third premolar, and fourth premolar) show isometric scaling (1.0438, .9594, and .9987, respectively).

One method of comparing patterns of multivariate scaling which are derived from different covariance matrices is to calculate correlations and angles between first component vectors (Blackith et al. 1984). To calculate the correlation coefficient, the raw first component loading of a variable for one species is multiplied by the raw first component loading for the

same variable for the other species. These products are derived for each variable included in the PCA and suumed together to obtain the correlation coefficient. The differences between vectors may be expressed as an angle, with smaller angles indicating higher correlations. The angle is derived by taking the inverse cosine of the correlation coefficient.

The correlation coefficient for the upper buccolingual diameters indicates a high (though not perfect) correlation between the illigeri and oedipus patterns. This high correlation is also reflected by a fairly small angle (17.82°). Both species are characterized by having the most positively allometric coefficient belong to the lateral incisor. The largest differences are in the canine (positive near-isometry for oedipus and strongly negative allometry for illigeri) and in the second molar (positive allometry in illigeri and negative allometry in oedipus). The most similar loadings are seen in the third premolar (negative near-isometry in illigeri and isometry in oedipus). The central incisor also shows some similarity (isometry in illigeri and positive near-isometry in oedipus). The premolars show differing trends. The sequence of scaling classification for oedipus (from P2 to P4) is positive--isometric--isometric. For illigeri, the sequence is

negative--negative near-isometric--negative near-isometric.

Upper mesiodistal diameters. The results of the PCA on upper mesiodistal diameters is shown in Table 16. The pattern for illigeri is one of negative allometry for all of the teeth except the second molar, which exhibits an extremely high positive allometry coefficient (2.1532). The oedipus coefficients also show an unusual pattern: alternating strongly positive and negative coefficients with a very low negative coefficient for the second molar. Because the sum of the squared, raw PC I loadings for each species must be equal to 1.0, aberrantly high or low loadings on a single variable will, in effect, exert a bias on the loadings of the remaining variables.

To correct for this bias, the upper mesiodistal analysis was redone without the second molar. The results are shown in Table 17. An examination of the correlation coefficients and angles show great species similarity with the omission of the second molar (.9095 versus .6549 and 24.56° versus 49.09°). The percentage of the total variance for the first component also shows an increase in both species (45.1% versus 43.7% for illigeri and 43.8% versus 38.4% for oedipus). The species loadings appear to follow roughly similar patterns. The greatest differences appear in the canine

Table 16. Principal components analysis of upper mesiodistal diameters.

	Raw PC I Loadings		Standardized Coefficients	
	Sfi	Soo	Sfi	Soo
I1	.2382	.3770	.6736	1.0664
I2	.2525	.4757	.7142	1.3455
C	.1779	.2443	.5032	.6910
P2	.2548	.4221	.7206	1.1940
P3	.2503	.5210	.7080	1.4737
P4	.2618	.3255	.7403	.9207
M1	.2688	.1103	.7602	.3119
M2	.7613	.0640	2.1532	.1810

Raw Isometry: .3536

PC I Variance (% of total): Sfi 43.7
Soo 38.4

Vector Correlation: .6549

Vector Angle: 49.09°

Table 17. Principal components analysis of upper mesio-distal diameters, minus the second molar.

	Raw PC I Loadings		Standardized Coefficients	
	Sfi	Soo	Sfi	Soo
I1	.4367	.3801	1.1555	1.0058
I2	.4733	.4838	1.2522	1.2800
C	.3375	.2382	.8929	1.5182
P2	.4736	.4185	1.2531	1.1073
P3	.3403	.5213	.9002	1.3793
P4	.2765	.3255	.7613	.8612
M1	.2342	.1087	.6198	.2876

Raw Isometry: .3780

PC I Variance (% of total): Sfi 45.1
Soo 43.8

Vector Correlation: .9095

Vector Angle: 24.56°

(strongly positive allometry in oedipus and negative allometry in illigeri) and the third premolar (positive allometry in oedipus and negative near-isometry in illigeri). There is a difference in classification for the central incisor (positive allometry in illigeri and isometry in oedipus). Teeth with similar loadings are the lateral incisor (both species positively allometric), the second premolar (both species positively allometric), and the fourth premolar (both species negatively allometric). Both species exhibit negative allometry in the first molar, but oedipus is much more strongly allometric. To roughly summarize, the illigeri and oedipus coefficients appear to converge and diverge on alternating teeth.

Lower buccolingual diameters. The lower buccolingual PCA shows the greatest degree of species similarity (see Table 18). The correlation coefficient is .9905, with an angle of 7.90°. Coefficients which differ in classification are the central incisor (positive allometry in illigeri and positive near-isometry in oedipus), the third premolar (positive allometry in illigeri and positive near-isometry in oedipus), and the fourth premolar (positive allometry in illigeri and isometry in oedipus). The greatest differences come in teeth with the same classifications: the positively allometric premolar (1.1438 in illigeri

Table 18. Principal components analysis of lower bucco-lingual diameters.

	Raw PC I Loadings		Standardized Coefficients	
	Sfi	Soo	Sfi	Soo
I1	.4010	.3783	1.1343	1.0700
I2	.4067	.4040	1.1503	1.1427
C	.2273	.2679	.6428	.7576
P2	.4044	.4963	1.1438	1.4037
P3	.4033	.3831	1.1408	1.0833
P4	.3969	.3603	1.1226	1.0190
M1	.2243	.1450	.6345	.4100
M2	.2968	.2794	.8394	.7903

Raw Isometry: .3536

PC I Variance (% of total): Sfi 51.6
Soo 38.6

Vector Correlation: .9905

Vector Angle: 7.90°

and 1.4037 in oedipus) and the negatively allometric molar (.6345 in illigeri and .4100 in oedipus). Other interesting features include the nearly identical coefficients for the lateral incisor and second molar and the consistency of the premolar coefficients for illigeri.

Lower mesiodistal diameters. The lower mesiodistal variables show a fairly large degree of divergence in the patterning of the anterior teeth, with less difference in the coefficients of the posterior dentition (see Table 19). In illigeri, both incisors scale isometrically. In oedipus, the central incisor is negatively allometric while the lateral incisor is positively allometric. This suggests that there is a fairly constant relationship in the proportions of LI1MD and LI2MD in illigeri, while a strong allometric relationship between the incisors is seen in oedipus. In the canine, the oedipus pattern is positively allometric, while the illigeri pattern is negatively allometric. The second premolars are positively allometric in both (more so in illigeri). The third premolars are positively allometric in illigeri, compared to the isometric pattern seen in oedipus. The fourth premolar is negatively allometric in illigeri, compared to being isometric in oedipus. Both molars scale similarly (negatively allometric) in both

Table 19. Principal components analysis of lower mesiodistal diameters.

	Raw PC I Loadings		Standardized Coefficients	
	Sfi	Soo	Sfi	Soo
I1	.3418	.2285	.9669	.6462
I2	.3536	.4685	1.0003	1.3252
C	.2989	.4548	.8454	1.2862
P2	.5630	.4078	1.5925	1.1534
P3	.4178	.3450	1.1817	.9759
P4	.2594	.3360	.7337	.9504
M1	.1592	.2434	.4504	.6884
M2	.2908	.2530	.8225	.7155

Raw Isometry: .3536

PC I Variance (% of total): Sfi 34.0
Soo 37.0

Vector Correlation: .9529

Vector Angle: 17.66°

species. The implications of these similarities and differences will be adressed later in the discussion of the allometric analysis (Chapter VII).

Tooth Areas Within Morphogenetic Fields -- RMA Analysis

One point of interest in this study is the pattern of allometric relationships between teeth of the same morphogenetic category (and presumably the same genetic field). These relationships will be especially important in later discussions of species differences. In the cases of the incisors, premolars, and molars, a polar tooth was chosen (the central incisor, the second premolar, and the first molar). In the case of the incisors and molars, the area of the remaining tooth was regressed on the area of the polar tooth. In the case of the premolars, the third and fourth premolar areas were regressed, in turn, on the second premolar area. Separate analyses were conducted for each jaw. As with the RMA analysis of individual tooth diameters, the correlations between tooth areas were first analyzed. The results of this analysis are shown in Table 20. RMA regressions were possible for both species in all but one case because most of the correlations were significantly different from zero. The RMA regression statistics are summarized in Table 21.

Upper lateral incisor of upper central incisor.

The RMA slopes for illigeri and oedipus are 1.274 and

Table 20. Correlations between tooth areas, within morphogenetic fields. Also shown are t-statistic probabilities.

Upper Teeth		r	P	Lower Teeth		r	P
I2/I1	Sfi	.44333	.0003*	I2/I1	Sfi	.73897	.0001*
	Soo	.62107	.0001*		Soo	.70742	.0001*
P3/P2	Sfi	.69323	.0001*	P3/P2	Sfi	.61209	.0001*
	Soo	.68959	.0001*		Soo	.56325	.0001*
P4/P2	Sfi	.48918	.0001*	P4/P2	Sfi	.50630	.0001*
	Soo	.56113	.0001*		Soo	.41883	.0008*
M2/M1	Sfi	.51639	.0001*	M2/M1	Sfi	.43675	.0004*
	Soo	.15137	.2442		Soo	.46185	.0002*

* Correlation is significantly different from zero at 0.05 level.

Table 21. RMA regression statistics for tooth areas, within morphogenetic fields.

		b	95% CI	zb	a
I2/I1	Sfi	1.274	.984 -- 1.564	.8848	-.547
	Soo	1.112	.889 -- 1.336		-.390
P3/P2	Sfi	.934	.763 -- 1.105	-.3340	.087
	Soo	.975	.794 -- 1.156		.060
P4/P2	Sfi	.820	.638 -- 1.002	.1406	.327
	Soo	.803	.632 -- .973*		.325
I2/I1	Sfi	1.007	.834 -- 1.113	-1.4797	-.001
	Soo	1.213	.993 -- 1.433		-.289
P3/P2	Sfi	.926	.740 -- 1.113	.3070	-.131
	Soo	.840	.311 -- 1.370		.100
P4/P2	Sfi	.820	.617 -- 1.023	-.7542	.008
	Soo	.925	.734 -- 1.116		-.038
M2/M1	Sfi	1.225	.968 -- 1.542	-.0510	-.660
	Soo	1.265	.978 -- 1.553		-.912

* Significantly different from isometry.

1.112, respectively. Neither slope is significantly different from isometry. The z-statistic indicates that the slopes are not significantly different from each other. The regression plots (Figure 9) show that the regression lines are nearly superimposed. The oedipus pattern is therefore interpreted as an isometric, hypermorphic extension of the isometric illigeri pattern.

Upper third premolar on upper second premolar. The RMA slopes for illigeri and oedipus are .934 and .975, respectively. Neither slope is significantly different from isometry. The z-statistic indicates that the slopes are not significantly different from each other. The regression plots (Figure 10) show that the oedipus mean does not fall far from an extension of the illigeri regression line. The isometric oedipus pattern is therefore interpreted as a hypermorphic extension of the isometric illigeri pattern.

Upper fourth premolar on upper second premolar. The RMA slopes for illigeri and oedipus are .820 and .803, respectively. The illigeri slope is not significantly different from isometry, although the upper confidence limit (1.002) is very close. The oedipus slope is significantly different from isometry, making it negatively allometric. The regression plot (Figure 11) shows that the oedipus pattern is nearly

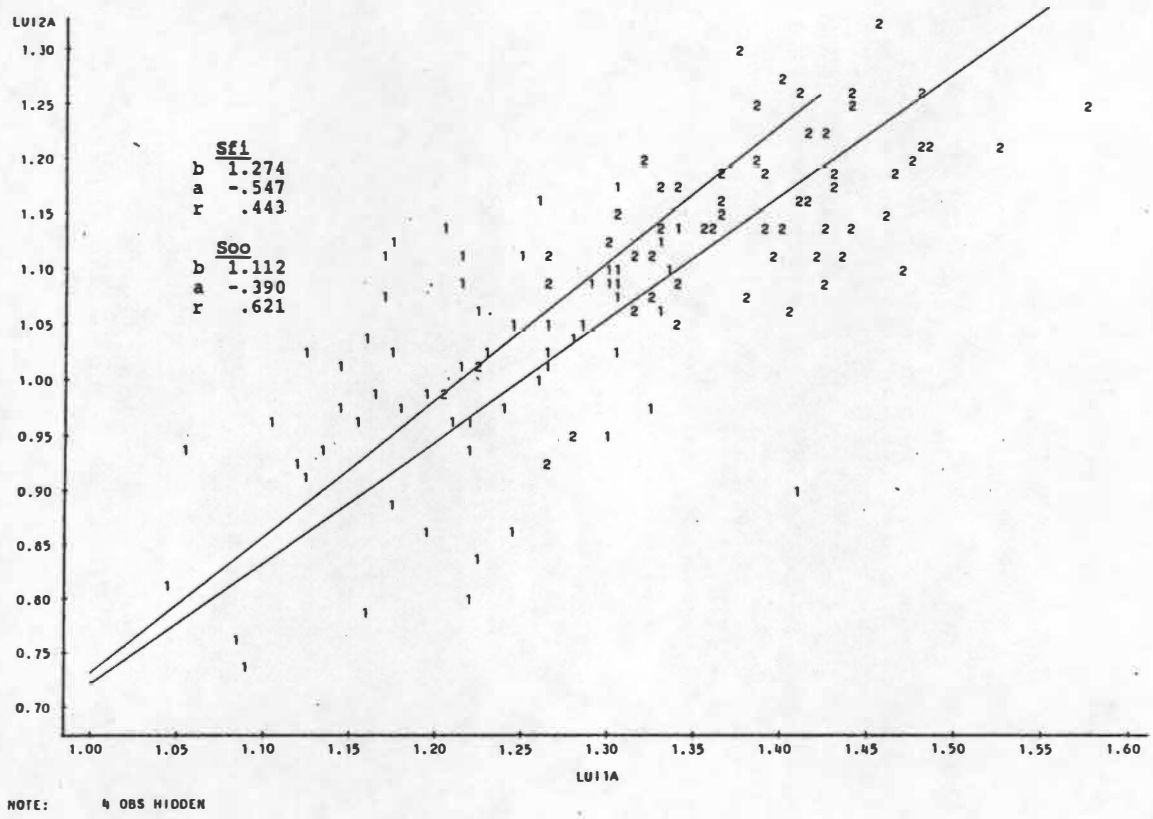

Figure 9. Plots of intraspecific RMA regressions of upper lateral incisor area on upper central incisor area for S. f. illigeri and S. o. oedipus.

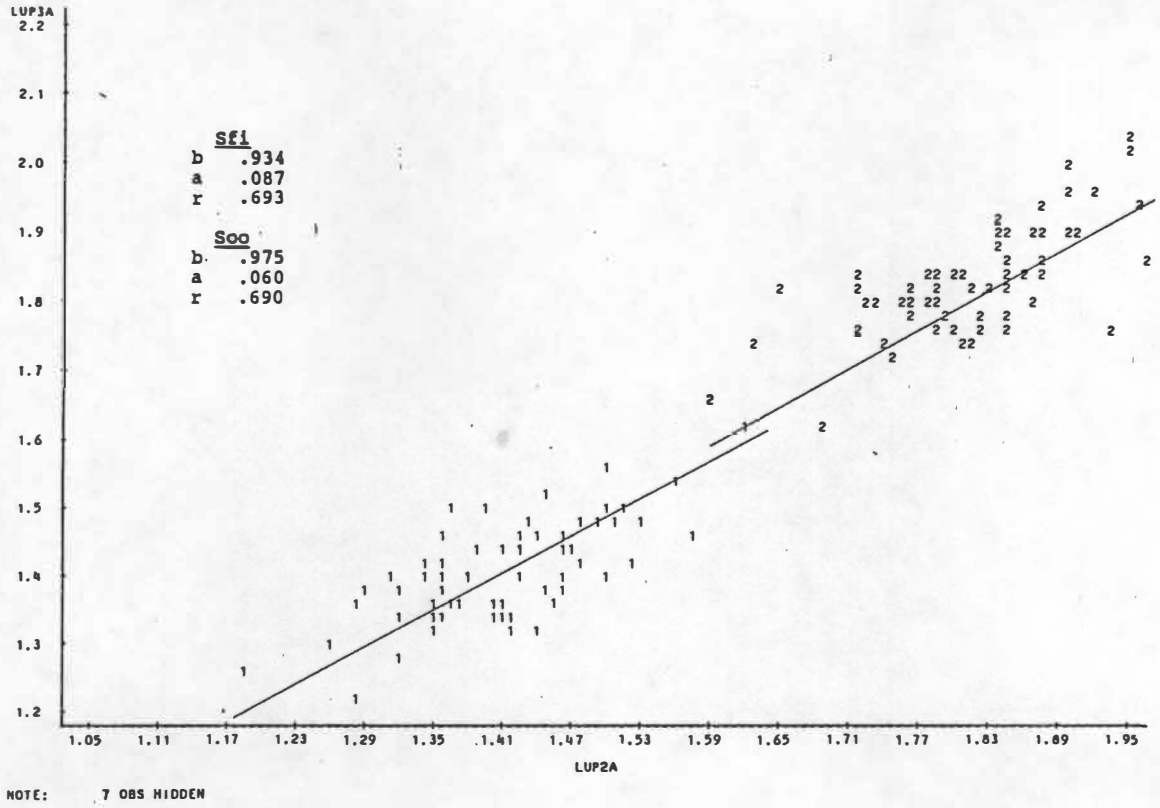

Figure 10. Plots of intraspecific RMA regressions of upper third premolar area on upper second premolar area for S. f. illigeri and S. o. oedipus.

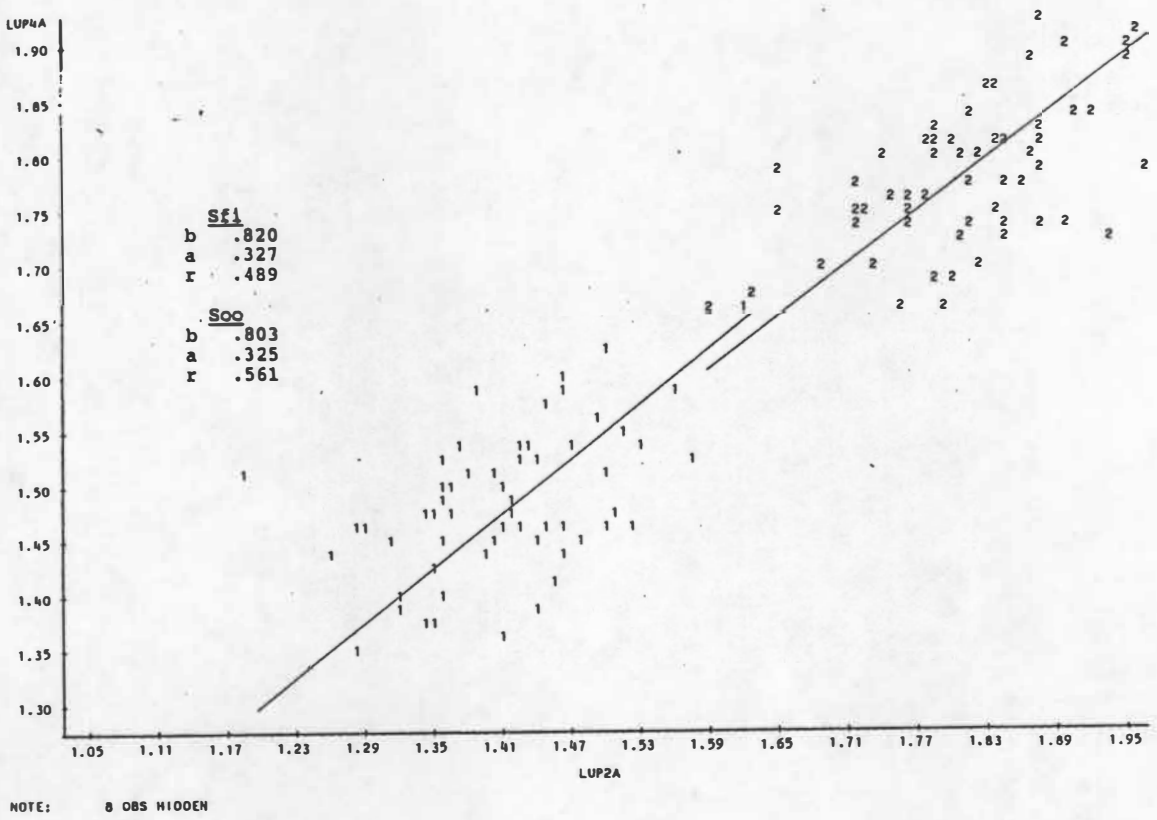

Figure 11. Plots of intraspecific RMA regressions of upper fourth premolar area on upper second premolar area for S. f. illigeri and S. o. oedipus.

superimposed on an extension of the illigeri regression line. The negatively allometric oedipus pattern is therefore interpreted as a hypermorphic extension of a negatively allometric illigeri pattern.

Upper second molar on upper first molar. The regression of second molar area on first molar area produces the only case of RMA regression of areas in which one of the species correlations is not significant. The illigeri correlation is significant (r=.51639), with the regression line having a positively allometric slope of b=1.782. The oedipus correlation, however, is not significantly different from zero (r=.15137). Therefore, the scaling of upper second molar area on first molar area cannot be discussed in comparative terms.

Lower lateral incisor on lower central incisor. The RMA slopes for illigeri and oedipus are 1.007 and 1.213, respectively. Neither slope is significantly different from isometry. The z-statistic indicates that the slopes are not significantly different from each other. The regression plot (Figure 12) shows that there is an apparent difference in slopes, but since they are not significantly different, they cannot be considered dissociated. The isometric oedipus pattern is therefore considered a hypermorphic extension of the isometric illigeri pattern.

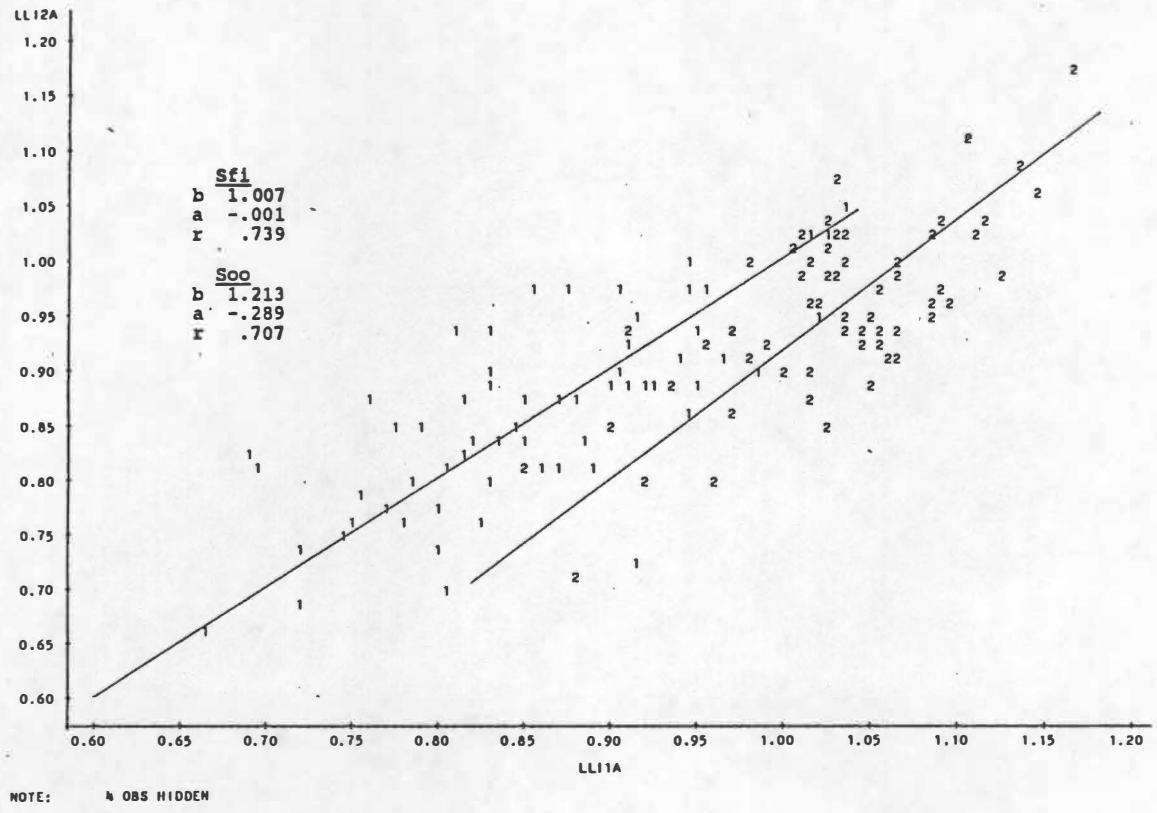

Figure 12. Plots of intraspecific RMA regressions of lower lateral incisor area on lower central incisor area for S. f. illigeri and S. o. oedipus.

Lower third premolar on lower second premolar. The RMA slopes for illigeri and oedipus are .926 and .804, respectively. Neither slope is significantly different from isometry. The z-statistic shows that the slopes are not significantly different from each other. The regression plot (Figure 13) shows that the oedipus mean falls very close to an extension of the illigeri pattern. The isometric oedipus plot is therefore interpreted as a hypermorphic extension of the isometric illigeri pattern.

Lower fourth premolar on lower second premolar. The RMA slopes for illigeri and oedipus are .820 and .925, respectively. Neither slope is signifiacntly different from isometry. THe z-statistic indicates that the slopes are not significantly different from each other. The regression plot (Figure 14) shows that the oedipus mean falls very close to an extension of the illigeri regression line. The isometric oedipus pattern is therefore interpreted as as a hypermorphic extension of the isometric illigeri pattern.

Lower second molar on lower first molar. The RMA slopes for illigeri and oedipus are 1.255 and 1.265, respectively. Neither slope is significantly different from isometry, although the lower confidence limits for both species are very close to 1.00. The z-statistic indicates that the slopes are not significantly

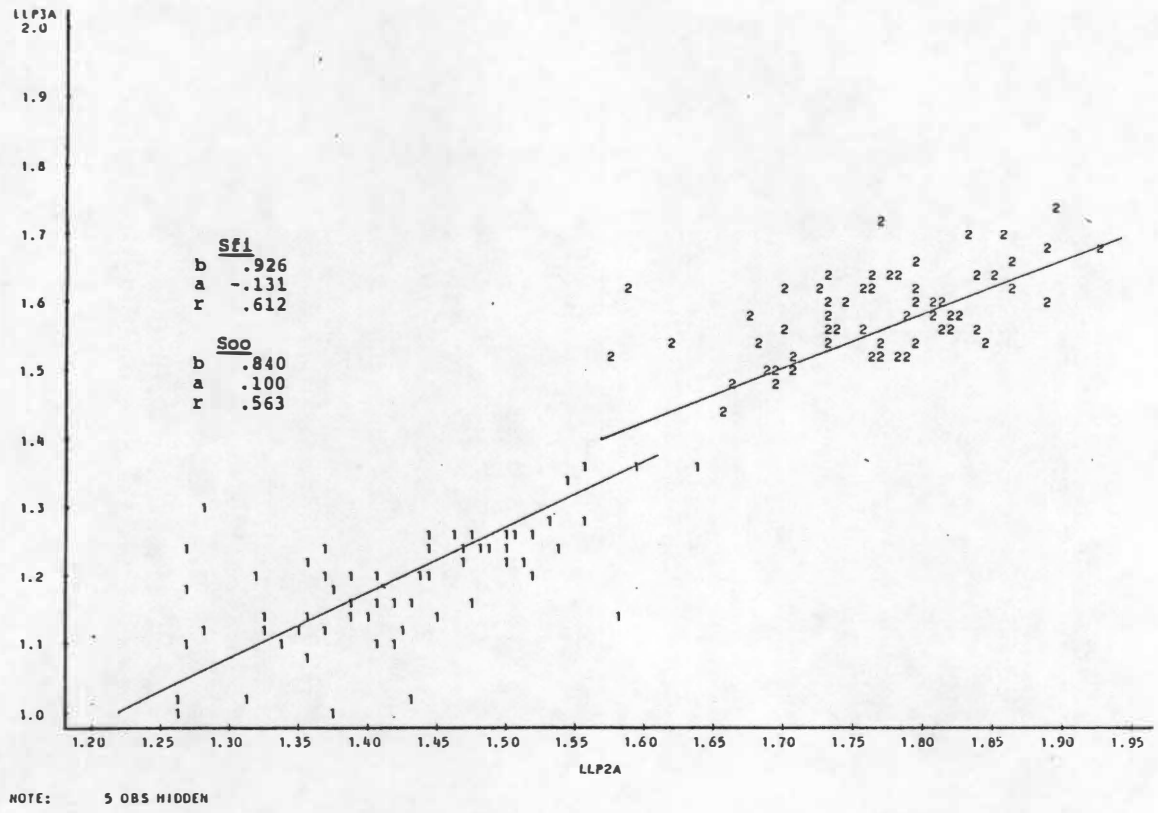

Figure 13. Plots of intraspecific RMA regressions of lower third premolar area on lower second premolar area for S. f. illigeri and S. o. oedipus.

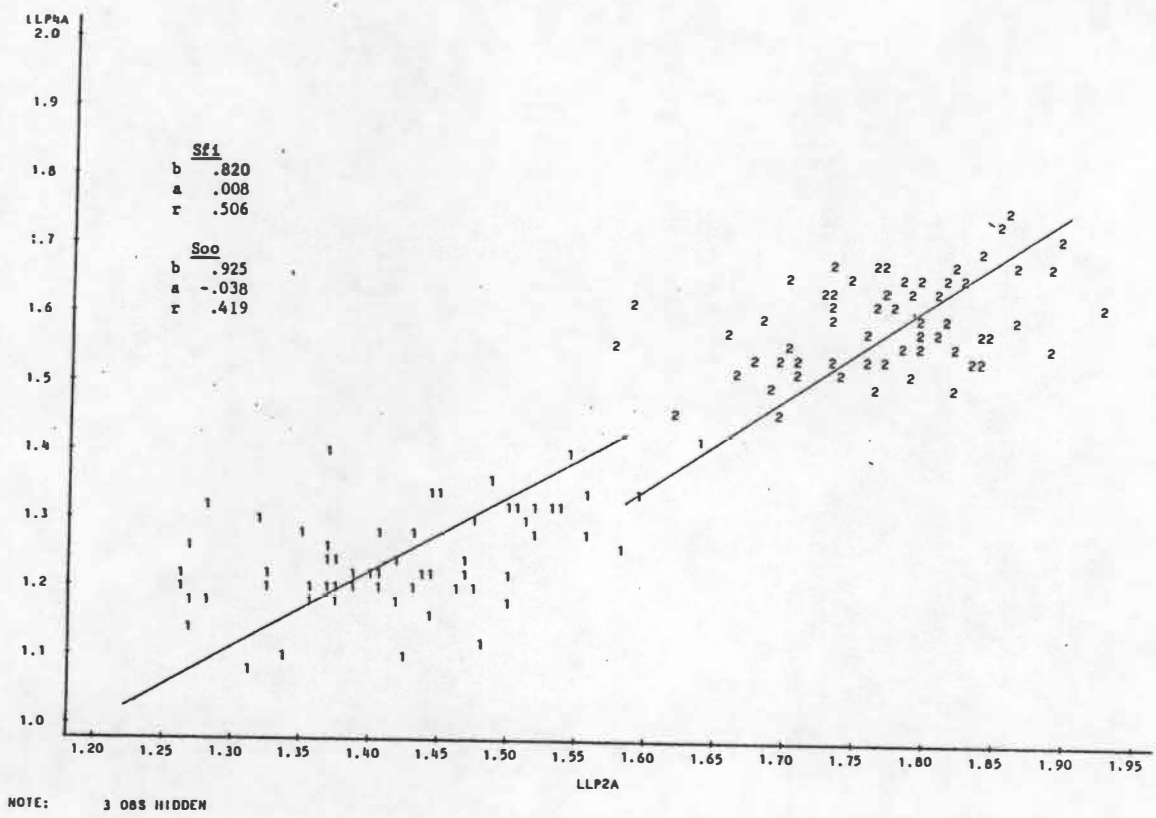

Figure 14. Plots of intraspecific RMA regressions of lower fourth premolar area on lower second premolar area for S. f. illigeri and S. o. oedipus.

different from each other. The regression plot (Figure 15) shows that the oedipus pattern is transposed below the illigeri plot. The isometric oedipus pattern is therefore interpreted as a post-displacement of the isometric illigeri pattern. The intraspecific scaling paterns are similar, but the oedipus second molars are, on the average, less expanded, relative to the first molars, than would be the case with hypermorphosis.

Individual Tooth Areas -- PCA Analysis

In order to observe and compare the scaling interactions throughout the upper and lower dental arcades, intraspecific principal components analyses were performed with individual tooth areas. Separate analyses were done for the upper and lower dentition.

Upper tooth areas. The results of the PCA on the upper teeth are shown in Table 22. The first component for the illigeri sample accounts for 49.4% of the total illigeri variance. The oedipus first component accounts for 49.0% of the total oedipus sample variance. The vector correlation is .9079 and the vector angle is 24.78°. As with the PCA of upper mesiodistal diameters, there appear to be some extreme loadings which may potentially produce biases in other loadings. In the illgeri sample, the standardized coefficient for the upper second molar is strongly positive (1.6388), while

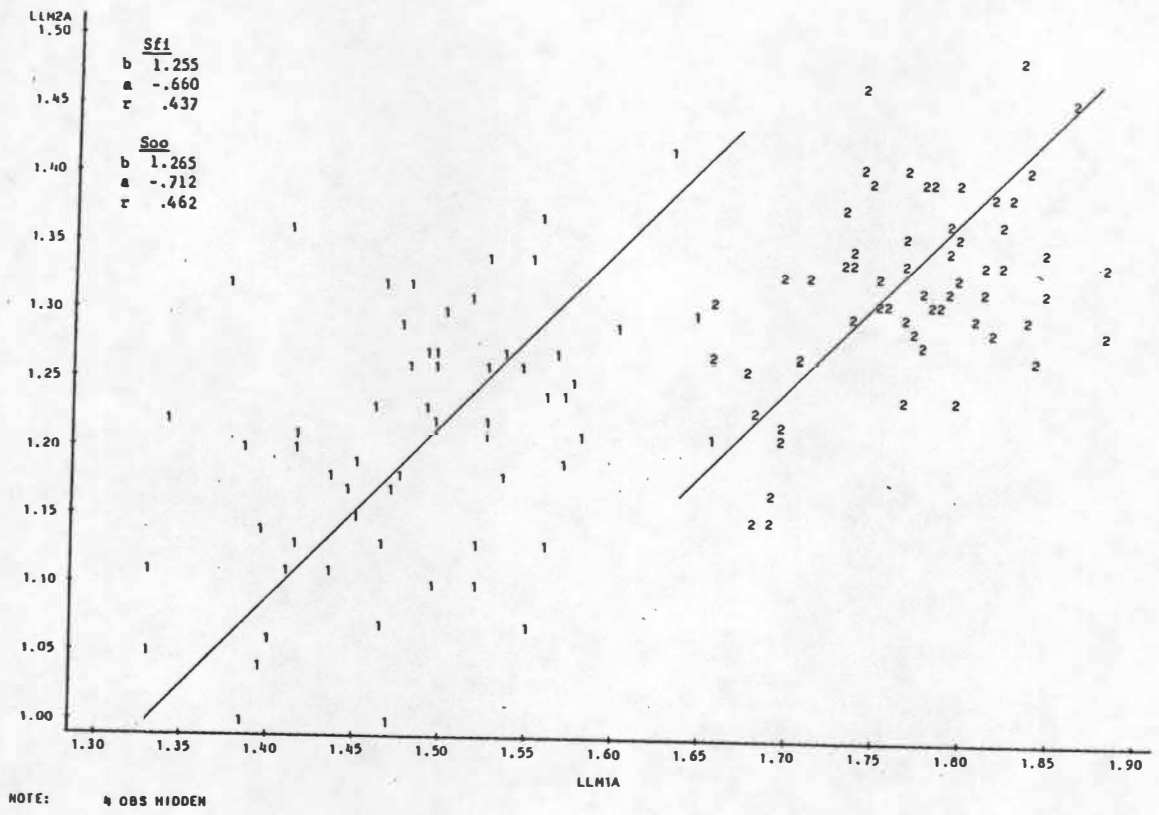

Figure 15. Plots of intraspecific RMA regressions of lower second molar area on lower first molar area for S. f. illigeri and S. o. oedipus.

Table 22. Principal components analysis of upper tooth areas.

	Raw PC I Loadings		Standardized Coefficients	
	Sfi	Soo	Sfi	Soo
I1	.2412	.3455	.6823	.9772
I2	.3803	.4404	1.0755	1.2458
C	.2190	.2950	.6193	.8343
P2	.3276	.4229	.9265	1.1961
P3	.3483	.4532	.9852	1.2820
P4	.2902	.3600	.8207	1.0183
M1	.2821	.1600	.7978	.4526
M2	.5974	.2452	1.6388	.6936

Raw Isometry: .3536

PC I Variance (% of total): Sfi 49.4
Soo 49.0

Vector Correlation: .9079

Vector Angle: 24.78°

in the oedipus sample, the loading for the second molar is very strongly negative (.4526).

As with the upper mesiodistal diameters, the second molar was deleted and the area analysis was redone (Table 23). The illigeri first component accounts for 53.4% of the total illigeri sample variance. The oedipus first component accounts for 55.1% of the total oedipus sample variance. The omission of the second molar increases the vector correlation to .9875, with a vector angle of 9.05°. There is a great deal of similarity in the intraspecific standardized coefficients for the anterior teeth (I1 through P2). In the cases of I1, C, and P2, the coefficients are nearly identical. The coefficients for P3 and P4 are fairly similar, but there are species differences in the scaling classifications. In the case of P3, the illigeri sample exhibits positive near- isometry (.1.0650), while the oedipus sample exhibits positive allometry (1.2533). In the case of P4, the oedipus sample exhibits negative near-isometry (.9748), while the illigeri sample exhibits negative allometry (.8049). The most divergent loadings occur in the first molar. Both species exhibit negative allometry (.7345 and .4352 for illigeri and oedipus, respectively), but the relative decrease of the first molar with increasing overall size occurs at a greater rate in oedipus.

Table 23. Principal components analysis of upper tooth areas, minus the second molar.

	Raw PC I Loadings		Standardized Coefficients	
	Sfi	Soo	Sfi	Soo
I1	.3642	.3547	.9636	.9383
I2	.5015	.4529	1.3269	1.1983
C	.3121	.2945	.8259	.7793
P2	.4319	.4417	1.1426	1.1687
P3	.4025	.4737	1.0650	1.2533
P4	.3043	.3684	.8049	.9748
M1	.2780	.1645	.7345	.4352

Raw Isometry: .3780

PC I Variance (% of total): Sfi 53.4
Soo 55.1

Vector Correlation: .9875

Vector Angle: 9.05°

Lower tooth areas. The PCA of lower tooth areas (Table 24) also produced a high correlation of species patterning. The first component percentage of the total intraspecific variance is 52.3% for illigeri and 47.1% for oedipus. The vector correlation is .9835, with a vector angle of 10.41°. The intraspecific standardized coefficients are most similar in the second premolar and in the posterior teeth (P4, M1, and M2). Differences in allometric classification occur with I1, C, P3, and M2. In the central incisor, the loadings are fairly similar. The illigeri sample exhibits positive near-isometry (1.0816), while the oedipus sample exhibits negative near-isometry (.9671). In the canine, the illigeri sample exhibits negative allometry (.8190), while the oedipus sample exhibits positive near-isometry (1.0807). In the third premolar, the illigeri sample exhibits positive allometry (1.1178), while the oedipus sample exhibits negative allometry (.8029). While the classifications for the second molar differ, the intraspecific loadings are quite close. The illigeri sample exhibits negative near-isometry (.9411), while the oedipus sample exhibits negative allometry (.8696). The intraspecific loadings are quite similar in the cases of the second premolar (both are positively allometric), the fourth premolar (both are negatively allo-

Table 24. Principal components analysis of lower tooth areas.

	Raw PC I Loadings		Standardized Coefficients	
	Sfi	Soo	Sfi	Soo
I1	.3824	.3419	1.0816	.9671
I2	.3963	.4841	1.1208	1.3692
C	.2898	.3821	.8190	1.0807
P2	.4201	.4356	1.1882	1.2319
P3	.3952	.2839	1.1178	.8029
P4	.3163	.2845	.8946	.8048
M1	.2634	.2387	.7450	.6752
M2	.3327	.3179	.9411	.8696

Raw Isometry: .3656

PC I Variance (% of total): Sfi 52.3
Soo 47.1

Vector Correlation: .9835

Vector Angle: 10.41°

metric), and the first molar (both are negatively allometric).

Summed Morphogenetic Areas -- RMA Analysis

The relationships between morphogenetic fields are described in terms of geometric similarity with RMA regression. The object of this phase of the analysis is to examine size-related changes in the relative proportions of morphogenetic fields. Intraspecific correlations for the field areas are shown in Table 25. The correlations are significantly different from zero in every case. A summary of the summed area regression statistics is found in Table 26.

Upper summed incisors on total postcanine area. Total incisor area consists of the sum of the areas of the central and lateral incisors. Total postcanine area consists of the sum of all of the premolar and molar reas. The RMA slopes for illigeri and oedipus are 1.178 and 1.340, respectively. The illigeri slope is not significantly different from isometry. The oedipus slope is significantly different from isometry and is classified as positively allometric. The z-statistic indicates that the slopes are not significantly different from each other. An examination of the regression plot (Figure 16) shows that the oedipus pattern is transposed below the illigeri pattern. This indicates that the oedipus incisors are less expanded,

Table 25. Correlations between summed tooth areas.*

		Upper Teeth r	P			Lower Teeth r	P
SI/PC	Sfi	.51777	.0001**	SI/PC	Sfi	.62879	.0001**
	Soo	.58460	.0001**		Soo	.55302	.0001**
C/PC	Sfi	.43824	.0004**	C/PC	Sfi	.39196	.0016**
	Soo	.42238	.0007**		Soo	.52020	.0001**
SP/SM	Sfi	.60887	.0001**	SP/SM	Sfi	.63526	.0001**
	Soo	.41703	.0008**		Soo	.40275	.0013**

* Abbreviations are as follows: SI -- summed incisor area, C -- canine area, PC -- total postcanine area, SP -- summed premolar area, SM -- summed molar area.

** Correlation is significantly different from zero at the 0.05 level.

Table 26. RMA regression statistics for summed tooth areas.*

		b	95% CI	zb	a
Upper:					
SI/PC	Sfi	1.178	.992 -- 1.434	-.8561	-1.841
	Soo	1.340	1.061 -- 1.618**		-2.615
C/PC	Sfi	1.109	.856 -- 1.362	-1.2987	-1.808
	Soo	1.374	1.055 -- 1.533**		-2.763
SP/SM	Sfi	.779	.576 -- .982**	-3.2447***	.771
	Soo	1.403	1.076 -- 1.729**		-.612
Lower:					
SI/PC	Sfi	1.263	1.013 -- 1.512**	-.8229	-2.142
	Soo	1.428	1.112 -- 1.743**		-2.931
C/PC	Sfi	1.339	1.026 -- 1.652**	-1.0307	-2.209
	Soo	1.579	1.234 -- 1.924**		-3.116
SP/SM	Sfi	1.017	.817 -- 1.216	-.3246	.303
	Soo	1.068	.818 -- 1.319		.333

* Abbrevations are as follows: SI -- summed incisor area, C -- canine area, PC -- total postcanine area, SP -- summed premolar area, SM -- summed molar area.

** Significantly different from isometry.

*** Slopes are significantly different.

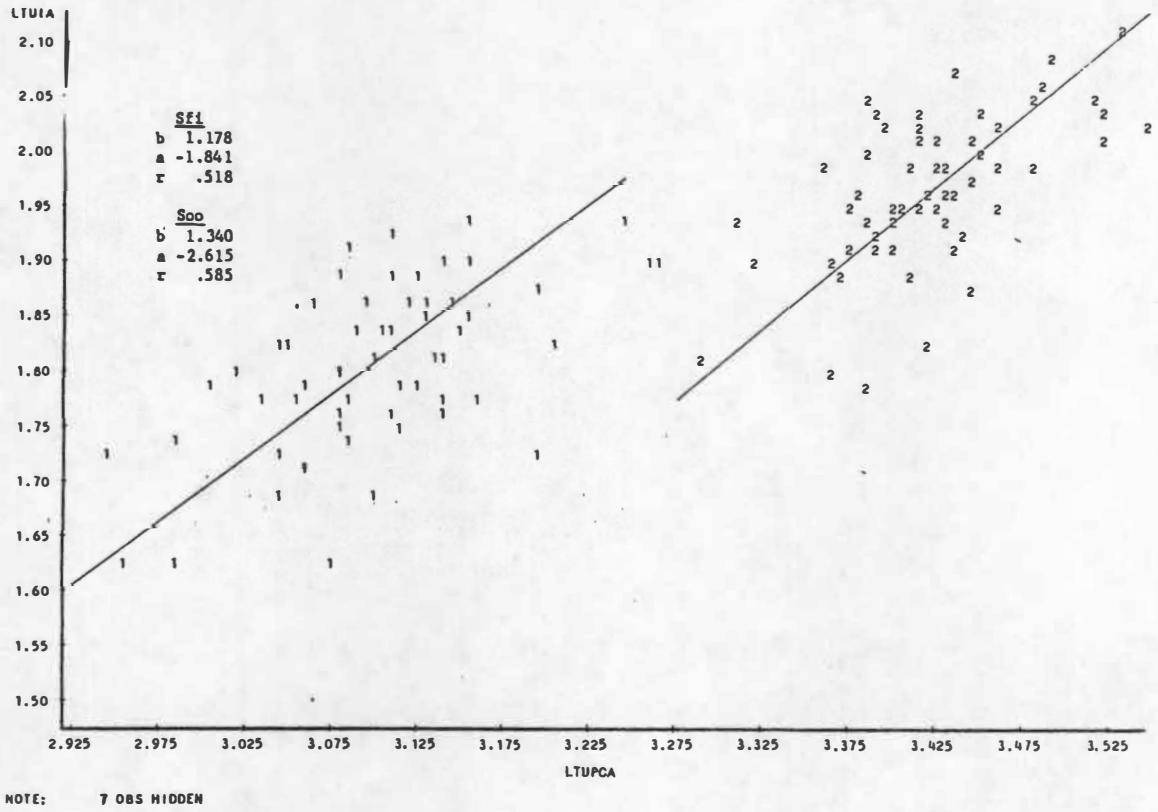

Figure 16. Plots of intraspecific RMA regressions of upper summed incisor on upper summed postcanine area for S. f. illigeri and S. o. oedipus.

relative to the postcanine area, than would be the case with hypermorphosis. Because of the insignificant z-statistic, the oedipus pattern considered to be post-displaced relative to the illigeri pattern, although they differ in scaling classification.

Upper canine on total upper postcanine area. The RMA slopes for illigeri and oedipus are 1.109 and 1.374, respectively. The illigeri slope is not significantly different from isometry. The oedipus slope is significantly different from isometry and is classified as positively allometric. The z-statistic indicates that the slopes are not significantly different from each other. The regression plot (Figure 17) shows that the oedipus mean falls close to an extension of the illigeri regression line. Because the slopes are not significantly different, the oedipus pattern cannot be classified as an acceleration, but is considered a hypermorphic extension of the illigeri pattern, although the scaling classifications differ.

Summed upper premolars on summed upper molars. THe RMA slopes for illigeri and oedipus are .779 and 1.403, respectively. The illigeri slope is significantly different from isometry, being classified as negatively allometric. The oedipus slope is also significantly different from isometry, but is classified as positively allometric. The z-statistic shows that the slopes are

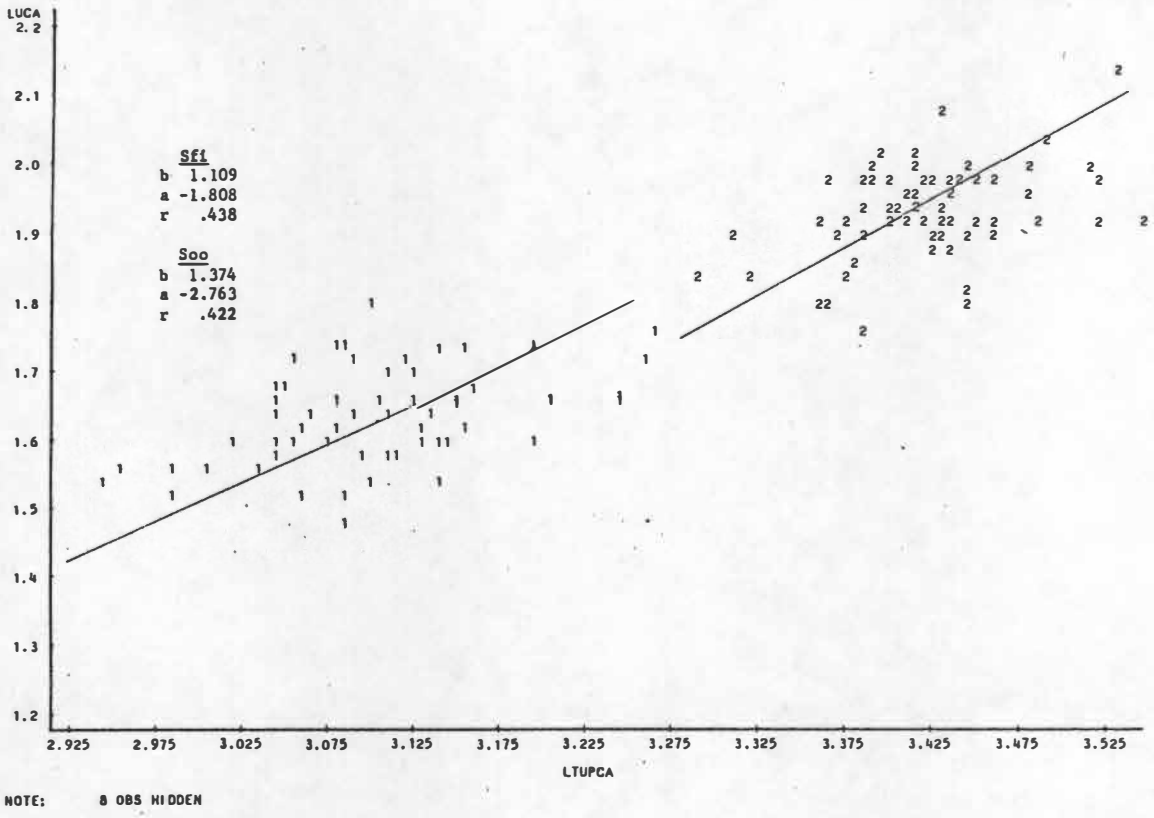

Figure 17. Plots of intraspecific RMA regressions of upper canine area on upper summed postcanine area for S. f. illigeri and S. o. oedipus.

significantly different from each other. The regression plot (Figure 18) shows that the oedipus mean is located above the extended illigeri line. This indicates that, on the average, oedipus premolars are more expanded, relative to molar size, than would be the case with hypermorphosis. The positively allometric oedipus pattern is interpreted as an acceleration of the negatively allometric illigeri pattern.

Summed lower incisors on total lower postcanine area. The RMA slopes for illigeri and oedipus are 1.263 and 1.428, respectively. Both slopes are significantly different from isometry and are classified as positively allometric. The z-statistic indicates that the slopes are not significantly different from each other. The regression plot (Figure 19) shows that the oedipus pattern is displaced below the extended illigeri pattern. The oedipus incisors are, therefore, less expanded, relative to the postcanine teeth, than would be the case with hypermorphosis. The positively allometric oedipus pattern is therefore interpreted as a post-displacement of the positively allometric illigeri pattern.

Lower canine on total lower postcanine area. The RMA slopes for illigeri and oedipus are 1.339 and 1.579, respectively. Both slopes are significantly different from isometry and are classified as positively ot

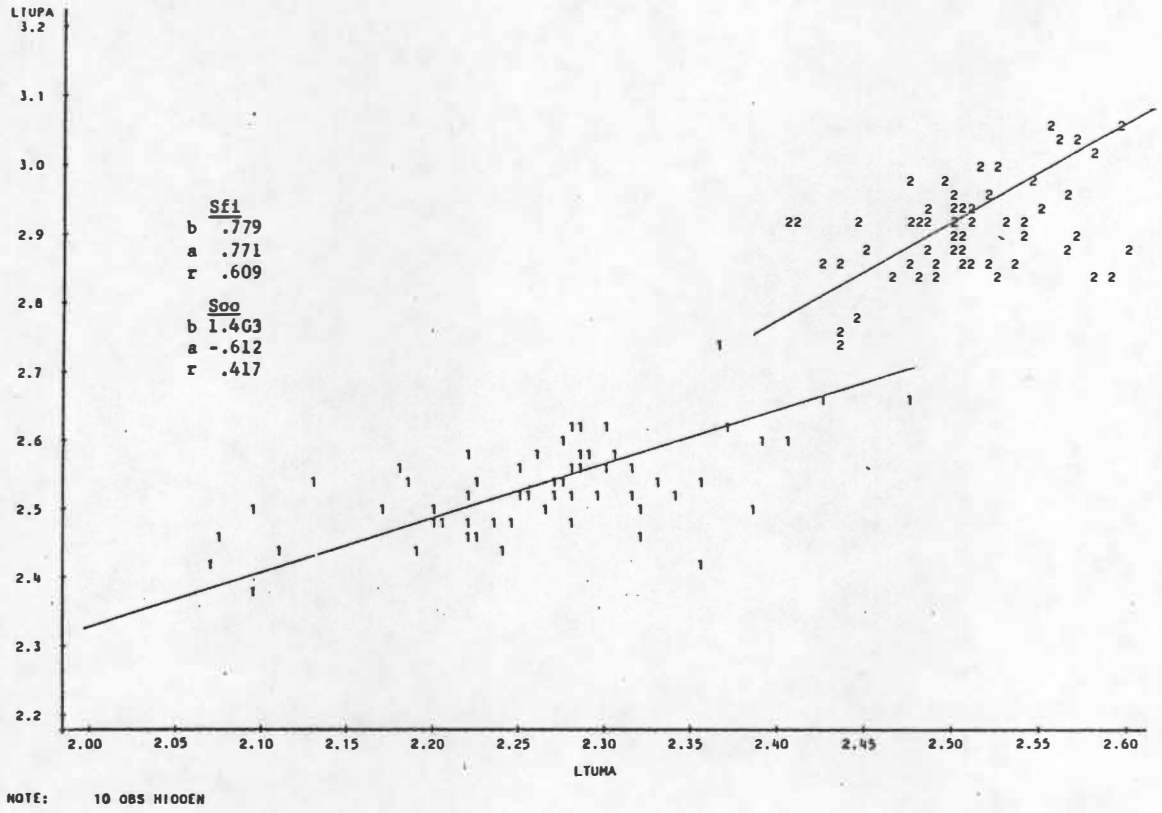

Figure 18. Plots of intraspecific RMA regression of summed upper premolar area on summed upper premolar area for S. f. illigeri and S. o. oedipus.

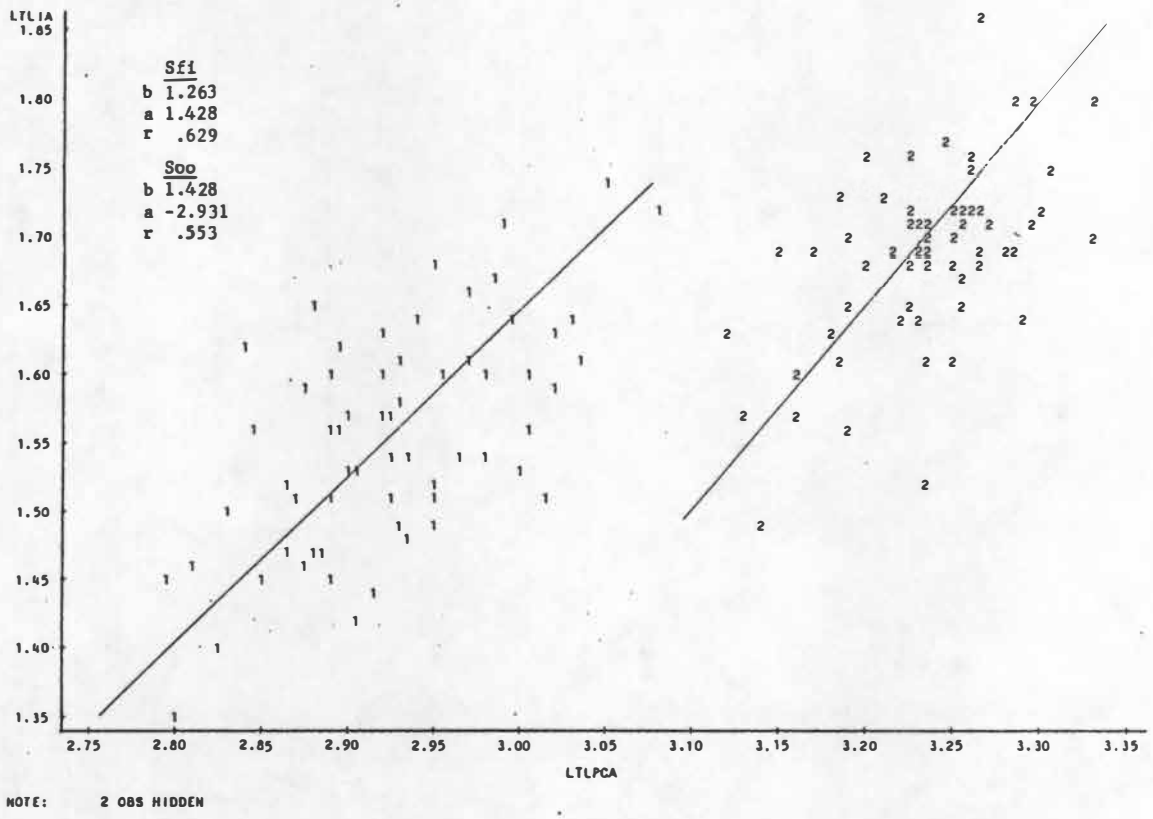

Figure 19. Plots of intraspecific RMA regressions of lower summed incisor area on lower summed postcanine area for S. f. illigeri and S. o. oedipus.

allometric. The z-statistic shows that the slopes are not significantly different from each other. The regressions plots (Figure 20) show that the oedipus pattern is displaced below the extended illigeri pattern. This indicates that the oedipus canine is, on the average, less expanded, relative to the postcanine teeth, than would be the case with hypermorphosis. The positively allometric oedipus pattern is therefore interpreted as a post-displacement of the positively allometric illigeri pattern.

Summed lower premolars on summed upper molars. The RMA slopes for illigeri and oedipus are 1.017 and 1.068, respectively. Neither slope is significantly different from isometry. The z-statistic indicates that the slopes are not significantly different. The regression plot (Figure 21) shows that the oedipus mean is displaced above the extended illigeri line. This indicates that the oedipus premolars are, on the average, more expanded, relative to the molars, than would be the case with hypermorphosis. The isometric oedipus pattern is therefore interpreted as a pre-displacement of the isometric illigeri pattern.

Summed Morphogenetic Areas -- PCA Analysis

The final phase of the analysis involves intraspecific PCA analyses of the summed areas of the four morphogenetic fields: incisors, canine, premolars,

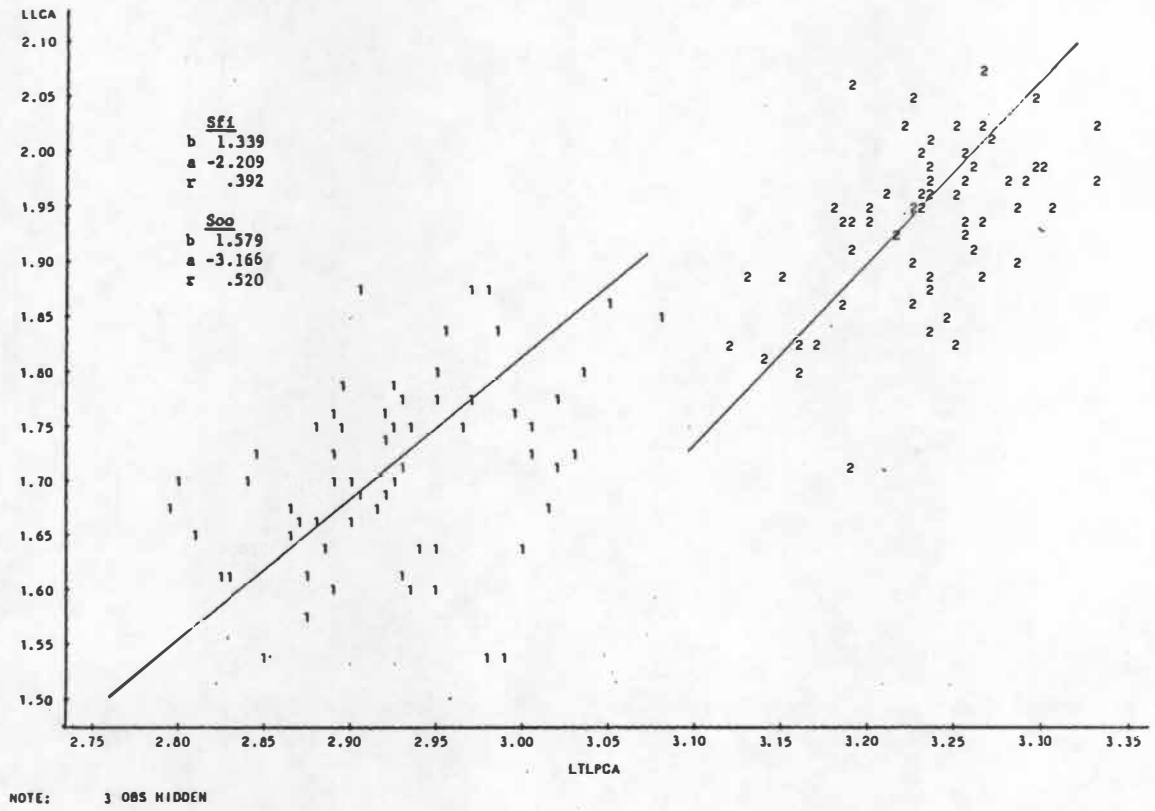

Figure 20. Plots of intraspecific RMA regressions of lower canine area on lower summed postcanine area for S. f. illigeri and S. o. oedipus.

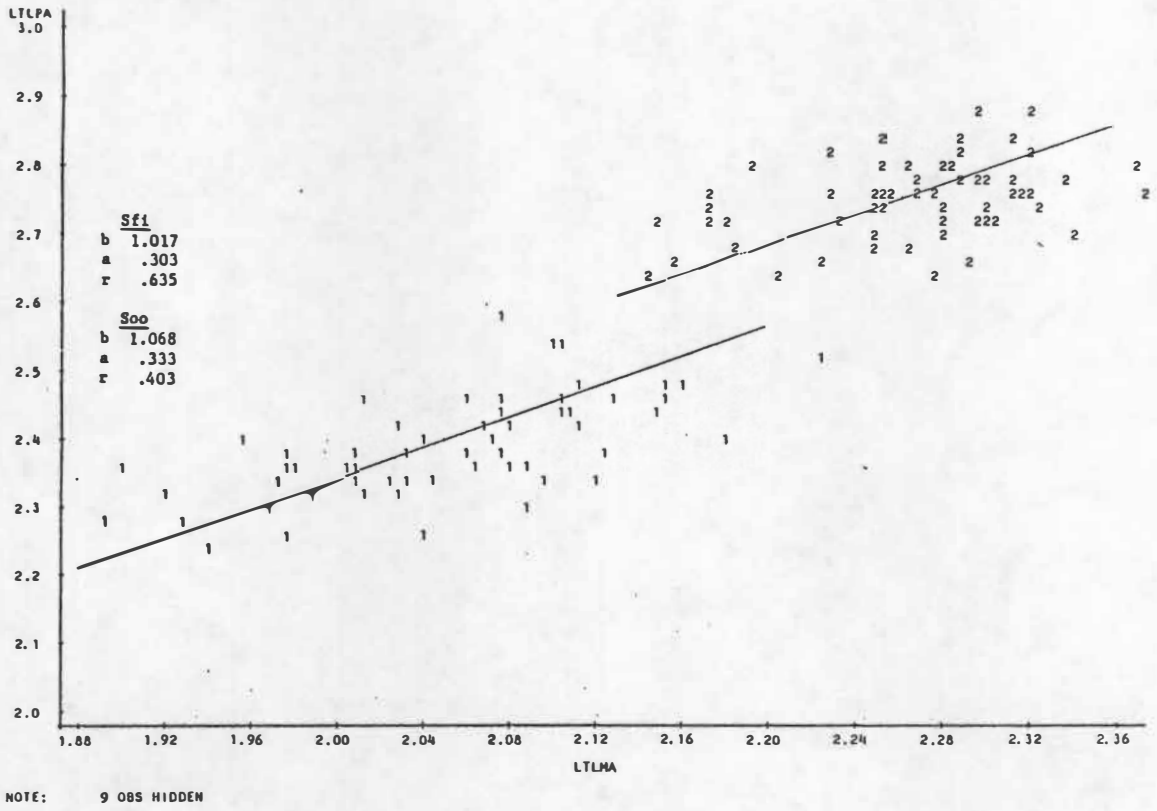

Figure 21. Plots of intraspecific RMA regressions of lower summed premolar area on lower summed molar area for S. f. illigeri and S. o. oedipus.

and molars. The object of this analysis is to see how the relative proportion of each morphogenetic type varies with overall size. Again, the upper and lower teeth were considered separately.

Upper summed areas. The results of the PCA on summed upper tooth areas are shown in Table 27. The percentage of the total intraspecific variation accounted for by the first component is 59.4% for illigeri and 60.8% for oedipus. The vector correlation is .9572 and the vector angle is 16.83°, indicating fairly similar intraspecific allometric patterning. The incisors are classified as isometric (1.0481) for illigeri and positively allometric (1.1872) for oedipus. The incisors show no size-related proportional change relative to the entire upper dentition area for illigeri, while the relative proportion of the oedipus incisors becomes greater with increasing size. The canine is classified as negatively allometric (.8810) in illigeri and positively allometric (1.1036) in oedipus. In illigeri, the canine becomes proportionally smaller with increasing size, while the canine becomes proportionally larger (at about the same rate) in oedipus. The scaling patterns are most alike in the premolars, with both loadings classified as isometric (.9842 in illigeri and 1.0320 in oedipus). Thus, there

Table 27. Principal components analysis for upper summed tooth areas.

	Raw PC I Loadings		Standardized Coefficients	
	Sfi	Soo	Sfi	Soo
I1-2	.5241	.5936	1.0481	1.1872
C	.4405	.5518	.8810	1.1036
P2-4	.4921	.5160	.9842	1.0320
M1-2	.5377	.2772	1.0755	.5544

Raw Isometry: .5000

PC I Variance (% of total): Sfi 59.3
Soo 60.8

Vector Correlation: .9572

Vector Angle: 16.83°

is no size-related change in relative premolar proportions in either species. The molars show the most divergent loadings: 1.0755 (positive near-isometry) for illigeri and .5544 (negative allometry) for oedipus. In illigeri, there is probably no size-related change in relative molar proportion. In oedipus, however, the allometric pattern is quite strong, with larger individuals (as measured on the first principal axis) having proportionally smaller molars.

Lower summed areas. The lower summed areas show more similarity in the intraspecific patterns than the upper summed areas. The results are shown in Table 28. The percentages of the total intraspecific variation accounted for by the first principal components are 60.9% for illigeri and 59.1% for oedipus. The vector correlation is .9898 and the vector angle is 8.18°. The incisor loadings are 1.1409 (positive allometry) for illigeri and 1.0900 (positive near-isometry) for oedipus. The illigeri incisors have a tendency to become proportionally larger as overall size inceases. The oedipus incisors probably show no size-related changes in relative proportion as overall size varies. The canines show the most divergent loadings: 1.0434 (isometry) for illigeri and 1.2667 (positive allometry) for oedipus. The illigeri canine probably shows no size-related changes in proportion. The oedipus canine,

Table 28. Principal components analysis of summed lower tooth areas.

	Raw Pc I Loadings		Standardized Coefficients	
	Sfi	Soo	Sfi	Soo
I1-2	.5705	.5450	1.1409	1.0900
C	.5217	.6334	1.0434	1.2667
P2-4	.5136	.4454	1.0272	.8908
M1-2	.3723	.3216	.7446	.6431

Raw Isometry: .5000

PC I Variance (% of total): Sfi 60.9
Soo 59.1

Vector Correlation: .9898

Vector Angle: 8.18°

however, shows an increase in relative proportion as overall size increases. The premolar loadings are more similar, but show differing classifications. The illigeri pattern (1.0272) is classified is isometric, while the oedipus pattern (.8908) is classified as negatively allometric. The illigeri premolars therefore show no size-related changes in relative proportion, with the oedipus premolars becoming relatively smaller with increasing overall size. The molars show fairly similar loadings (.7446 for illigeri and .6431 for oedipus) and are both classified as negatively allometric. In both cases, the molars become proportionally smaller with increases in overall size. This relative reduction occurs at a greater rate in oedipus.

CHAPTER VII

DISCUSSION

In discussing the results of this study, the null hypotheses should first be reviewed. As stated in the previous chapters, the first null hypothesis involved tests of sexual dimorphism in both species. Primatological and anthropological literature frequently assumes that, because the tamarins show little sexual dimorphism in external measures (such as weight and body length), they are similarly not dimorphic in other respects. The null hypothesis of no dental sexual dimorphism was tested by comparing the male and female tooth diameter means for non-transformed data. Male and female variances of log-transformed tooth diameters were also tested. Few significantly different means or variances were found in either species. The illigeri sample showed no significant differences in male and female means or logged-value variances. The oedipus sample showed two significant differences in male and female means: the buccolingual diameters of the upper central incisor and the upper canine. In both cases, the male means were greater. The oedipus sample showed no significant sex differences in logged-value variances. The species means (with pooled sexes) were significantly different in 31 of 32 cases (the exception

being the mesiodistal diameter of the upper first molar). The species logged- value variances were significantly different in four cases (UI2BL, UM2MD, LP2MD, and LM2BL). It was concluded that the sex differences were very small in magnitude when compared to the highly significant species differences. The sexes were therefore pooled in all subsequent analyses.

The other null hypothesis involved the comparison of intraspecific patterns of allometric variation. The null hypothesis tested throughout the allometric analysis was that the larger species (oedipus) exhibits patterns of variation which represent "extensions" of the patterns seen in the smaller species (illigeri). These comparisons were made in terms of geometric similarity. To rephrase the null hypothesis in the form of a question: In terms of proportions, does oedipus appear to be an "overgrown" form of illigeri? This question was addressed on several different levels: individual tooth diameters, individual tooth areas, and summed areas of morphogenetic fields. The comparisons of scaling patterns were approached with two different methods: RMA regression analysis and principal components analysis.

Individual Tooth Diameters

The first phase of the analysis involved the comparison of individual tooth shape variation through

RMA analysis. Because of the aforementioned problems with RMA, correlation analyses were first performed. Correlation coefficients were obtained to estimate the strengths of the relationships between the mesiodistal and buccolingual diameters of each tooth. In the allometric comparison, only those teeth in which both species showed coefficients which were significantly different from zero were examined. Only three teeth met this criterion, although there were a number of cases in which only one species showed a significant correlation. Because this is a comparative study, however, these cases were omitted from the analysis. The three teeth which showed significant patterns of size-related shape variation were the upper second molar, the lower central incisor, and the lower second molar. In terms of scaling, the null hypothesis of geometric similarity was rejected for both second molars. The scaling of M2 in oedipus was interpreted as neotenous, relative to the pattern of variation seen in illigeri. M2 shows an opposing pattern: the oedipus pattern is interpreted as an acceleration of the illigeri pattern. In the lower central incisor, the null hypothesis cannot be rejected. The oedipus pattern is interpreted as a hypermorphic extention of the illigeri pattern. This means that, in the case of I1, the oedipus teeth resemble "overgrown" illigeri teeth.

Overall, the low correlations seen between mesiodistal and buccolingual diameters in most teeth indicates that tooth shape tends to be independent of size. The three teeth which do show significant correlations in both species show diverse relationships between intraspecific patterns. This diversity suggests that the comparative scaling of individual teeth may be geometrically dissociated (McKinney 1984), although not much more can be said on the basis of three teeth.

The next step of the analysis involved principal components analyses of the individual tooth diameters. In these analyses, the buccolingual and mesiodistal measurements for each jaw were analyzed separately. The reason for this separation, as stated earlier, was that there is evidence for a degree of genetic distinction between the buccolingual and mesiodistal diameters of permanent teeth (Suarez and Bernor 1972; Suarez and Williams 1973; Lombardi 1975, 1978). Also, a principal components analysis combining the mesiodistal and buccolingual diameters would be very limited in its usefulness, given to results of the previous phase of the analysis. The general lack of correlation between tooth shape and size could possibly produce misleading results if the first component were interpreted as a "size" component. With the low size-shape correlations, the first component might be more reflective of random

variation within the sample than of systematic, size-related variation.

The intraspecific patterns of allometric variation were compared by obtaining vector correlations and angles. In terms of the null hypothesis that the intraspecific patterns should be the same, it was, in the strictest sense, rejected in every case, because none of the correlations were perfect. Such a perfect correlation is, however, an unreasonable expectation when dealing with biological data sets. The better way of examining the results might be to determine which patterns are the closest (or the most distant) from a perfect vector correlation.

The highest correlations occurred in the cases of the lower dentition (.9905 and .9529 for lower buccolingual and mesiodistal diameters, respectively). The vector correlation for the upper buccolingual diameters was slightly lower (.9520). A major divergence occurred in the upper mesiodistal diameters, where the vector correlation was only .6549. An examination of the standardized coefficients revealed that the second molar scaling was largely responsible for much of the difference. The upper second molar mesiodistal diameter was very positively allometric in illigeri and very negatively allometric in oedipus. These coefficients were so extreme in their allometric scaling that the

analysis was redone without the upper second molar diameters, as it was suspected that they were imparting biases on the loadings of the remaining variables. When the analysis was redone, the correlation coefficient increased to .9095. It is suggested, however, that the extremes in scaling seen with the mesiodistal diameter of the second molars of both species extend to produce scaling differences involving the second molar area in the individual area PCA and in the summed area PCA.

The next phase of the analysis involved the scaling of tooth areas within morphogenetic fields. This examination was performed with RMA regression. The purpose of this phase was to observe the interactions of morphologically similar teeth with variation in size. The null hypothesis was that the oedipus patterns of variation should be "extensions" of the illigeri patterns.

In six of seven cases, the null hypothesis could not be rejected. Recall that one test (M2 area on M1 area) was omitted because only one species had a significant correlation between variables. Isometric hypermorphosis was exhibited in comparisons of the upper incisors, the upper third premolar against the upper second molar, the lower incisors, and the lower third and fourth premolars against the lower second premolar. These results indicate that, in these cases, the oedipus

resemble "overgrown" illigeri. Because the patterns are isometric, the proportional relationships between tooth areas (within morphogenetic fields) are constant as size varies. Moreover, because the isometric patterns are hypermorphic, the same patterns are shared by the different-sized species.

The relationship between the oedipus and illigeri patterns when upper fourth premolar area is scaled against upper second premolar area is also hypermorphic, but the patterns of scaling differ from isometry. Both patterns are negatively allometric, indicating that, as size increases, the fourth premolar becomes proportionally smaller, relative to second premolar area. Because the slopes are not significantly different, the rate of proportional change may be considered the same in both species. Also, while a transformation of intercepts might be expected, in order to preserve function when allometric patterns occur at different sizes, it does not occur in this case. It is uncertain whether the lack of a transformation denotes a functional difference or whether the allometric patterns are functionally equivalent and are therefore not so strongly divergent from isometry as to require a transformation. An altogether different departure from the null hypothesis is seen in the scaling of lower second molar area on lower first molar area. In this

case, the intraspecific slopes are nearly identical (1.255 and 1.265 for illigeri and oedipus, respectively). There is, however, a transformation in intercepts which displaces the oedipus pattern below the extended illigeri pattern. This indicates that, for a given first molar area, the oedipus sample will have less relative expansion of the second molar than will be seen in the illigeri sample. In both species, the relative proportions of the first and second molars will remain fairly constant as size varies. Whether there is a functional reason for the transposition of intercepts is uncertain.

The next phase of the analysis involves principal components analyses of individual tooth areas. As mentioned before, the null hypothesis of a perfect vector correlation will probably always be rejected. Instead of speaking of a strict testing of the null hypothesis, it is probably better to speak in terms of relative proximity to a perfect correlation. As discussed in the previous chapter, the upper second molar was once again suspected of introducing a bias into the other loadings (as the results of extreme allometric scaling). Therefore, the analysis of the upper teeth was done twice, both with and without the second molar. With the second molar retained, the vector correlation (.9095) was fairly distant from a

perfect correlation, in comparison to the vector correlation of the lower tooth areas (.9835). When the second molar was removed, the vector correlation for the upper teeth became much higher (.9875), surpassing that of the lower teeth.

The conclusion reached from the PCA of tooth areas is that the species are very similar in the ways that tooth areas vary, relative to overall size. One interesting point is the manner in which the coefficients for the upper (minus M2) and lower teeth also tend to be quite similar, particularly in the illigeri sample. This is not unexpected, because the areas of occluding teeth tend to be quite highly correlated (Cochard 1981), so that occlusal function may be maintained.

The final RMA analysis involved the scaling of the summed areas of morphogenetic fields against each other. As with previous analyses, there was the null hypothesis that oedipus is a hypermorphic "extension" of illigeri. The null hypothesis is rejected in five of six cases.

In three cases (summed upper incisor area, summed lower incisor area, and lower canine area scaled against their respective summed postcanine areas), there are patterns of post-displacement associated with positively allometric scaling. These findings are in keeping with

the belief that transpositions help to preserve function at different sizes (Gould 1971). Post-displacement might, therefore, be reasonably expected in cases of positive allometry. The scaling patterns show that the upper and lower incisors and lower canine become larger, relative to the postcanine dentition, as size increases. This occurs in both species, although where the upper summed incisor area is concerned, the slope of 1.178 for illigeri is not significantly different from isometry.

The scaling of upper summed premolar area on upper summed molar area shows a dissociation of intraspecific patterns. The positively allometric oedipus pattern is accelerated, relative to the negatively allometric illigeri pattern. This contrast is indicative of an opposite scaling relationship between the summed areas. In the illigeri, the premolars are becoming smaller, relative to the molars, as size increases. In the oedipus, the premolars become larger, relative to the molars, as size increases.

The null hypothesis is also rejected in the lower postcanine dentition When the lower summed premolar areas are scaled against lower summed molar areas, the patterns are geometrically similar, but there is a transposition of intercepts. The intraspecific slopes are nearly identical (1.017 and 1.068 for illigeri and

oedipus, respectively) and are very close to isometry. Because the slopes are isometric, the transposition cannot be interpreted as an attempt to preserve function at different sizes. In oedipus, the premolars are more expanded, relative to molar size, than the premolars in illigeri. This is the only case in which the relative proportions of the summed areas are not affected by variations in size.

The scaling of the upper canine against the summed upper postcanine area is the sole case in which the null hypothesis of hypermorphosis is not rejected. Although the oedipus slope is significantly different from isometry and the illigeri slope is not, the slopes are not significantly different and must be considered hypermorphic.

Finally, the summed morphogenetic areas for the upper and lower dentition were subjected to principal components analysis. The first component variance percentages for the upper teeth were 59.3% for illigeri and 60.8% for oedipus. The percentages for the lower teeth were 60.9% for illigeri and 59.1% for oedipus. The vector correlations for the upper and lower analyses were .9572 and .9898, respectively. The vector angles for the upper and lower analyses were 16.83° and 8.18°, respectively. With the upper summed areas, the greatest similarity is in the scaling of the summed premolar

areas (both species scale isometrically). The greatest divergence is seen in the molars (positively near-isometry in illigeri and strongly negatively allometric in oedipus). This contrast of similarity and difference is reflective of the geometric dissociation between upper premolars and molars which was seen in the RMA analysis. The incisors and canines also show differences in scaling classification, although these did not produce significant differences in the RMA analysis.

In the lower dentition, the greatest difference is in the classification of the canine. The oedipus coefficient is positively allometric (1.2667), while the illigeri pattern is isometric (1.0434). Actually, there are scaling classification differences in three of the four morphogenetic fields, but the coefficients are quite similar in these cases. This is a good example of how correlation vectors are good indicators of multivariate similarity, but are not sensitive to arbitrary allometric scaling classifications.

It is interesting to note that, in all three principal components analyses, the intraspecific scaling patterns were more similar in the lower dentition. This was due, in part, to the divergent patterning of the upper second molars of both species.

Making Biological Inferences

Perhaps the most difficult part of any allometric analysis is attempting to make biological sense of all of the scaling phenomena which are observed. The results of this study raise interesting questions involving the nature of intraspecific allometry.

The first question which arises in looking at intraspecific scaling variation is why intraspecific variation should exist at all. Given the narrow size ranges of the tamarin taxa used in this study, why should there be any significant shape variation within either species? Some researchers have encountered difficulties when making assumptions about functional equivalence in interspecific studies. But with intraspecific studies, especially in the case of dental allometry in taxa that have essentially no sexual dimorphism, the assumption that different-sized members of the same sample used their teeth in the same way does not seem unreasonable at all.

One interpretation of intraspecific dental allometry might involve size-related functional differences in the relationship between tooth size and body mass. Theoretically, the teeth of larger animals should be relatively larger because of relatively greater metabolic demands. In the tamarins, however, there are few or no significant intraspecific

correlations between tooth size and body mass. Harrill (1986) has recently shown, in a study relating postcranial measurements to body mass, that the weight estimates for this sample appear to be realistic and that the lack of correlation with teeth cannot be entirely blamed on captive environment or provisioned diet. One solution to the problem of finding relationships between tooth size and body size might be to find an independent variable other than body mass. Jungers (1984) has recently suggested scaling tooth size against recorded metabolic rate in a sample of animals for which such data might be avaliable. This makes sense, because size-related metabolic variation is what is actually being inferred in many studies which scale tooth size against body mass.

Interspecific studies (for example, Kay 1975) which make functional connections between tooth size and body mass have been fairly successful in reaching conclusions which make a functional connections between the two. Intraspecifically, however, the functional connection between tooth size and body size may not be as strong. In fact, there is always the possibility that tooth size and body size may not be functionally related (in modern human populations, for example).

This study of dental allometry is different from most in that it involves internal scaling. Allometric

(non-isometric) scaling was evident in both taxa, particularly in the summed area RMA analysis. The question of how allometric patterns within the dentition originate and whether they are functionally related to anything remains unresolved. For example, why should large illigeri have smaller premolars, relative to their molars, than small illigeri? Why should large oedipus show such a divergent pattern when the same variables are considered? Large oedipus have larger premolars, relative to their molars, than small oedipus.

The best means of addressing these questions might be in studies of the morphogenesis of the dentitions of primates, with the aim of determining how variation in the onset, rate, and duration of dental development affects both the size and size-related shape of the permanent teeth. The most interesting aspect of the comparison of illigeri and oedipus is not just in recognizing that differences exist, but in thinking about how these differences may have arisen. There is currently not enough dietary or developmental data to make a fully adequate study of dental scaling variation in these taxa. In that light, this study should probably best be regarded as exploratory. The fact is that there appear to be fundamental developmental differences underlying the observed differences in intraspecific scaling. In addition, the intraspecific

patterns seen within species may represent variation in developmental pathways which may occur as part of natural intraspecific variation.

The answers to the questions posed above may be more fully investigated with larger and more complete data sources and with refinements of investigative techniques. The author would like to encourage further comparative studies of intraspecific dental scaling (especially in closely-related species) as a means of better understanding the processes by which the frequently seen interspecific differences in dental scaling arise.

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APPENDICES

APPENDIX A

MEASUREMENT DEFINITIONS

Table A-1. Measurement definitions. The nomenclature for anatomical landmarks follow Hershkovitz (1977).

The Maxillary Dentition

Incisors (Central and Lateral)

Maximum Mesiodistal Diameter (UI1MD and UI2MD): the distance between the most mesial and most distal points on the crown, taken along the incisal edge (from the mesiostyle to the distostyle).

Maximum Buccolingual Diameter (UI1BL and UI2BL): the distance between the buccal and lingual surfaces of the crown, taken at the level of the cementoenamel junction, in a plane perpendicular to the incisal edge and the maximum mesiodistal diameter.

Canine

Maximum Mesiodistal Diameter (UCMD): the distance between the mesial and distal surfaces of the crown, taken between the mesiostyle and the distostyle.

Maximum Buccolingual Diameter (UCBL): the distance between the the buccal and lingual surfaces of the crown, taken at the cementoenamel junction, in a plane perpendicular to the maximum mesiodistal diameter (UCMD).

Premolars

Maximum Mesiodistal Diameter (UP2MD, UP3MD, and UP4MD): the distance between the mesial and distal surfaces of the crown, taken between the mesiostyle and distostyle.

Maximum Buccolingual Diameter (UP2BL, UP3BL, and UP4BL): the distance between the buccal and lingual surfaces of the crown, taken in a plane perpendicular to the maximum mesiodistal diameter (UP2MD, UP3MD, and UP4MD).

First Molar

Maximum Mesiodistal Diameter (UM1MD): the distance between the mesial and distal surfaces of the crown, along a line extending through the eocone (paracone) and the metacone.

Table A-1 (Continued)

Maximum Buccolingual Diameter (UM1BL): the distance between the buccal and lingual surfaces of the crown, in a plane perpendicular to the maximum mesiodistal diameter (UM1MD).

Second Molar

Maximum Mesiodistal Diameter (UM2MD): the distance between the mesial and distal surfaces of the crown, in a plane perpendicular to the maximum buccolingual diameter (UM2BL).

Maximum Buccolingual Diameter (UM2BL): the distance between the buccal and lingual surfaces of the crown, along a line extending through the eocone (paracone) and the protocone.

The Mandibular Dentition

Central Incisor

Maximum Mesiodistal Diameter (LI1MD): the distance between the mesial and distal surfaces of the crown, taken along the incisal edge (from the mesiostylid to the distostylid).

Maximum Buccolingual Diameter (LI1BL): the distance between the buccal and lingual surfaces of the crown, taken at the level of the cementoenamel junction, in a plane perpendicular to the maximum mesiodistal diameter.

Lateral Incisor

Maximum Mesiodistal Diameter (LI2MD): a tangent line is drawn from the cementoenamel junction on the mesial surface to the most mesial point of the incisal edge (the mesiostylid). The measurement consists of the perpendicular distance between this tangent and the most distant point on the distal surface.

Maximum Buccolingual Diameter (LI2BL): the distance between the buccal and lingual surfaces of the crown, taken at the level of the cementoenamel junction, in

a plane perpendicular to the incisal edge (from the mesiostylid to the distostylid).

Canine

Maximum Mesiodistal Diameter (LCMD): the distance between the mesial and distal surfaces of the crown, taken between the mesiostylid and the distostylid.

Maximum Buccolingual Diameter (LCBL): the distance between the buccal and lingual surfaces of the crown, taken at the cementoenamel junction, in a plane perpendicular to the maximum mesiodistal diameter (LCMD).

Second Premolar

Maximum Mesiodistal Diameter (LP2MD): the distance between the mesial and distal surfaces of the crown, taken along the line of the anterior segment of the eocristid (mesiostylid to eoconid).

Maximum Buccolingual Diameter (LP2BL): the distance between the buccal and lingual surfaces of the crown, in a plane perpendicular to the maximum mesiodistal diameter (LP2MD).

Third and Fourth Premolars

Maximum Mesiodistal Diameter (LP3MD and LP4MD): the distance between the mesial and distal surfaces of the crown, from the mesiostylid to the distostylid, along the line of the eocristid.

Maximum Buccolingual Diameter (LP3BL and LP4BL): the distance between the buccal and lingual surfaces of the crown, in a plane perpendicular to the maximum mesiodistal diameter (LP3MD or LP4MD).

First and Second Molars

Maximum Mesiodistal Diameter (LM1MD and LM2MD): the distance between the mesiodistal surfaces of the crown, perpendicular to the line between the eoconid and the hypoconid.

Table A-1 (Continued)

Maximum Buccolingual Diameter (LM1BL and LM2BL): the distance between the buccal and distal surfaces of the crown, in a plane perpendicular to the maximum mesiodistal diameter (LM1MD or LM2MD).

APPENDIX B

INTRASPECIFIC CORRELATION MATRICES

SAGUINUS FUSCICOLLIS ILLIGERI

	UI1BL	UI1MD	UI2BL	UI2MD	UCBL	UCMD	UP2BL	UP2MD	UP3BL	UP3MD	UP4BL
UI1BL	1.0000										
UI1MD	0.0866	1.0000									
UI2BL	0.4208	0.2601	1.0000								
UI2MD	0.0107	0.4763	0.2864	1.0000							
UCBL	0.3098	0.3587	0.2207	0.2012	1.0000						
UCMD	0.2125	0.3603	0.3050	0.3431	0.4994	1.0000					
UP2BL	0.4662	0.4142	0.3726	0.4442	0.4153	0.5867	1.0000				
UP2MD	0.1639	0.3348	0.2358	0.3242	0.2188	0.5016	0.3625	1.0000			
UP3BL	0.3128	0.3503	0.2820	0.3437	0.3168	0.5815	0.6472	0.3367	1.0000		
UP3MD	0.3139	0.3313	0.2980	0.2541	0.0978	0.3195	0.3922	0.6179	0.3410	1.0000	
UP4BL	0.1678	0.4163	0.1700	0.4047	0.2845	0.4205	0.3522	0.2546	0.6124	0.3989	1.0000
UP4MD	0.0206	0.1775	0.2705	0.2516	-.0831	0.2558	0.0942	0.5485	0.2180	0.6216	0.2166
UM1BL	0.2841	0.3439	0.2834	0.2334	0.1194	0.3923	0.4039	0.1957	0.4988	0.3857	0.5929
UM1MD	-.1040	0.2556	0.1678	0.2745	-.0359	0.2252	0.3309	0.1671	0.4882	0.2574	0.2734
UM2BL	0.1412	0.2105	0.1907	0.1977	0.2461	0.2174	0.3602	0.1940	0.4722	0.3147	0.4584
UM2MD	-.1197	0.2583	0.1769	0.2359	-.1018	0.0501	0.0922	0.1253	0.3685	0.3006	0.3746
LI1BL	0.5128	0.4293	0.5176	0.3352	0.2720	0.4561	0.5495	0.4085	0.4929	0.4373	0.3935
LI1MD	0.1866	0.5497	0.1272	0.4127	0.2240	0.3845	0.4471	0.3232	0.1761	0.4425	0.3359
LI2BL	0.4326	0.4992	0.4945	0.3798	0.4099	0.5181	0.6372	0.3799	0.5807	0.4301	0.5560
LI2MD	0.2578	0.4638	0.2378	0.3661	0.2701	0.4812	0.2970	0.3436	0.3636	0.4505	0.4838
LCBL	0.3592	0.0570	0.2341	0.0859	0.4184	0.4350	0.3495	0.2854	0.4562	0.1977	0.3008
LCMD	0.3175	0.3366	0.3839	0.1596	0.4464	0.5076	0.4037	0.3070	0.3952	0.2091	0.2354
LP2BL	0.3925	0.4302	0.3481	0.4062	0.4854	0.6012	0.6925	0.4187	0.6347	0.3953	0.4389
LP2MD	-.0153	0.1268	0.0325	0.3334	0.0944	0.3050	0.1386	0.3638	0.1882	0.3826	0.3551
LP3BL	0.3323	0.3230	0.3539	0.3410	0.3378	0.3923	0.6025	0.3399	0.5775	0.4804	0.4988
LP3MD	0.1978	0.1900	0.1682	0.1694	0.0589	0.2971	0.3071	0.3438	0.3868	0.5696	0.4251
LP4BL	0.1638	0.4636	0.2628	0.4729	0.2923	0.3781	0.4899	0.4138	0.5889	0.5537	0.6698
LP4MD	0.0385	0.1266	-.0420	0.1474	0.0033	0.2422	0.0878	0.2718	0.1041	0.3223	0.3293
LM1BL	0.1890	0.3413	0.2057	0.3704	0.1304	0.2104	0.2126	0.2326	0.3614	0.3150	0.4956
LM1MD	0.2310	0.1303	0.3587	0.1018	0.2064	0.0322	0.2694	0.1808	0.3733	0.3403	0.3051
LM2BL	0.1195	0.3885	0.1112	0.2920	0.0845	0.3038	0.3810	0.2710	0.3870	0.4723	0.4715
LM2MD	-.1445	0.3016	0.2707	0.2196	0.0920	0.3074	0.2516	0.3634	0.3069	0.4346	0.4104
CRBW	0.1730	0.0298	0.3594	-.1052	0.0722	-.1634	-.0172	-.0143	0.0089	-.1475	-.0407

	UP4MD	UM1BL	UM1MD	UM2BL	UM2MD	LI1BL	LI1MD	LI2BL	LI2MD	LCBL	LCMD
UI1BL											
UI1MD											
UI2BL											
UI2MD											
UCBL											
UCMD											
UP2BL											
UP2MD											
UP3BL											
UP3MD											
UP4BL											
UP4MD	1.0000										
UM1BL	0.2143	1.0000									
UM1MD	0.4177	0.3719	1.0000								
UM2BL	0.1172	0.4641	0.2190	1.0000							
UM2MD	0.4053	0.3478	0.5288	0.4757	1.0000						
LI1BL	0.2839	0.4265	0.1587	0.1762	0.1222	1.0000					
LI1MD	0.2181	0.3215	0.0902	0.2992	0.1338	0.4253	1.0000				
LI2BL	0.1423	0.4221	0.1990	0.3326	0.1798	0.7985	0.4857	1.0000			
LI2MD	0.2828	0.3709	0.1490	0.1396	0.1315	0.4702	0.3959	0.5676	1.0000		
LCBL	0.1200	0.1728	0.0185	0.2233	-.0101	0.4269	0.1356	0.4709	0.3165	1.0000	
LCMD	0.2515	0.2071	0.1262	0.2305	0.0731	0.4322	0.3190	0.3867	0.2738	0.6343	1.0000
LP2BL	0.1973	0.4468	0.2770	0.3906	0.1110	0.6179	0.4983	0.6614	0.5340	0.5535	0.5711
LP2MD	0.4386	0.0244	0.0999	0.1256	0.1749	0.1403	0.2702	0.1186	0.1443	0.3381	0.3297
LP3BL	0.1773	0.3478	0.3726	0.2343	0.1602	0.4161	0.2764	0.6006	0.2100	0.3456	0.4236
LP3MD	0.4504	0.2987	0.2914	0.2964	0.2615	0.3161	0.3578	0.3572	0.3697	0.1353	0.1792
LP4BL	0.3063	0.3719	0.4056	0.3376	0.3267	0.4911	0.4307	0.6063	0.3865	0.2788	0.2208
LP4MD	0.3728	0.1900	0.1934	-.1189	0.0415	0.0003	0.1261	0.1036	0.4325	-.0176	-.1483
LM1BL	0.2408	0.4363	0.4302	0.1608	0.3893	0.3764	0.3192	0.3819	0.4542	0.0346	0.0904
LM1MD	0.2839	0.3397	0.3729	0.2071	0.0348	0.3947	0.0497	0.3936	0.0840	0.1357	-.0056
LM2BL	0.2180	0.3343	0.4153	0.3481	0.3404	0.2871	0.5561	0.3375	0.2816	0.2164	0.3290
LM2MD	0.3826	0.2232	0.3808	0.3192	0.2772	0.1246	0.0888	0.2355	0.2540	-.1402	-.0022
CRBW	0.0459	-.0940	-.1155	0.0432	0.0655	0.1647	-.2374	0.1147	-.1815	0.1137	0.1899

	LP2BL	LP2MD	LP3BL	LP3MD	LP4BL	LP4MD	LM1BL	LM1MD	LM2BL	LM2MD	CRBW
UI1BL											
UI1MD											
UI2BL											
UI2MD											
UCBL											
UCMD											
UP2BL											
UP2MD											
UP3BL											
UP3MD											
UP4BL											
UP4MD											
UM1BL											
UM1MD											
UM2BL											
UM2MD											
LI1BL											
LI1MD											
LI2BL											
LI2MD											
LCBL											
LCMD											
LP2BL	1.0000										
LP2MD	0.1264	1.0000									
LP3BL	0.4238	0.2437	1.0000								
LP3MD	0.3959	0.3032	0.1908	1.0000							
LP4BL	0.5043	0.3276	0.6719	0.3273	1.0000						
LP4MD	-.0137	0.3739	0.1435	0.3034	0.2592	1.0000					
LM1BL	0.1940	0.0423	0.4030	0.3048	0.5462	0.2873	1.0000				
LM1MD	0.2941	-.0269	0.4129	0.3313	0.5261	0.0899	0.4199	1.0000			
LM2BL	0.3093	0.5246	0.4682	0.4493	0.5283	0.2345	0.4597	0.1250	1.0000		
LM2MD	0.1421	0.1851	0.3503	0.3971	0.4462	0.3311	0.3332	0.3971	0.3889	1.0000	
CRBW	0.0199	-.1504	0.1088	-.2472	-.0791	-.3619	-.1261	0.0441	-.2200	0.0714	1.0000

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	UI1BL	UI1MD	UI2BL	UI2MD	UCBL	UCMD	UP2BL	UP2MD	UP3BL	UP3MD	UP4BL
UI1BL	1.0000										
UI1MD	0.5012	1.0000									
UI2BL	0.2999	0.1679	1.0000								
UI2MD	0.3908	0.4134	-.1215	1.0000							
UCBL	0.5867	0.3114	0.4984	0.2540	1.0000						
UCMD	0.2667	0.3017	0.1733	0.2178	0.0777	1.0000					
UP2BL	0.2872	0.1063	0.2875	0.3430	0.3510	0.3789	1.0000				
UP2MD	0.5599	0.5825	0.2139	0.3008	0.3047	0.6145	0.2286	1.0000			
UP3BL	0.3642	0.1958	0.1659	0.4510	0.1513	0.3832	0.5203	0.2411	1.0000		
UP3MD	0.6581	0.6542	0.3416	0.3000	0.3127	0.4186	0.2868	0.7478	0.3552	1.0000	
UP4BL	0.4516	0.4547	0.3322	0.5999	0.3329	0.3917	0.5766	0.4617	0.7334	0.5567	1.0000
UP4MD	0.2714	0.3345	0.2111	0.3440	-.1051	0.1808	0.0989	0.4052	0.3112	0.5397	0.4065
UM1BL	0.2775	0.1451	0.2623	0.1784	0.2697	0.2073	0.3105	0.2434	0.3859	0.2330	0.3570
UM1MD	0.3677	0.5797	0.2958	-.0066	0.2754	0.0748	0.0577	0.2099	0.1220	0.4830	0.2766
UM2BL	0.2065	0.1694	0.1444	0.1820	0.1672	0.0169	-.2197	0.1337	0.1502	0.1517	0.1403
UM2MD	0.0585	0.1459	0.2077	-.2641	0.0065	0.4879	0.0079	0.1277	-.0059	-.0433	-.1064
LI1BL	0.6094	0.3873	0.5165	0.1610	0.3959	0.3641	0.4243	0.3333	0.4124	0.4169	0.4665
LI1MD	0.3622	0.4695	0.1792	0.3917	0.0468	0.1290	0.1072	0.4361	0.4599	0.6107	0.6113
LI2BL	0.5838	0.1992	0.4742	0.1005	0.3754	0.2356	0.5305	0.4314	0.3933	0.4783	0.4187
LI2MD	0.6093	0.6644	0.4977	0.3694	0.5657	0.2372	0.5045	0.4601	0.3511	0.6302	0.5252
LCBL	0.3811	0.1568	0.4197	0.2688	0.4710	0.4374	0.5255	0.2103	0.3339	0.2432	0.5528
LCMD	0.1973	0.5145	0.1115	0.3515	0.0562	0.3092	0.1422	0.3737	0.1372	0.3262	0.2683
LP2BL	0.3254	0.4283	0.3199	0.3184	0.4758	0.3844	0.5280	0.2908	0.3392	0.3618	0.6433
LP2MD	0.5763	0.4899	0.4370	0.4864	0.5798	0.5152	0.5283	0.6908	0.3132	0.5751	0.5513
LP3BL	0.2246	0.4199	0.2757	0.3368	0.5757	0.2730	0.3319	0.2035	0.1481	0.2579	0.2837
LP3MD	0.3012	0.1645	0.2397	0.2460	0.2529	0.2767	0.4385	0.3447	0.2931	0.4815	0.4903
LP4BL	0.1208	0.2344	0.2761	0.4296	0.2765	0.1907	0.3700	0.1358	0.4382	0.2489	0.4814
LP4MD	0.2141	0.0008	0.4568	0.0566	0.3008	0.3125	0.1185	0.4108	0.2627	0.3360	0.2709
LM1BL	0.0369	0.3707	0.1033	0.1278	0.0558	-.0818	0.1403	0.2404	-.1115	0.3528	0.0374
LM1MD	0.5025	0.3844	0.2613	0.4661	0.4955	0.3756	0.4481	0.2695	0.3576	0.4848	0.3442
LM2BL	0.2306	0.4524	0.4986	0.0241	0.4524	-.0221	0.2605	0.2420	0.0503	0.2209	0.3006
LM2MD	0.2001	-.1501	0.0832	-.1917	0.2395	0.0431	0.4562	0.0545	0.1078	0.0535	0.0961
CRBW	-.4241	-.3718	-.0536	-.0756	-.2021	-.1134	0.0965	-.3294	0.0633	-.5358	-.0729

	UP4MD	UM1BL	UM1MD	UM2BL	UM2MD	LI1BL	LI1MD	LI2BL	LI2MD	LCBL	LCMD
UI1BL											
UI1MD											
UI2BL											
UI2MD											
UCBL											
UCMD											
UP2BL											
UP2MD											
UP3BL											
UP3MD											
UP4BL											
UP4MD	1.0000										
UM1BL	0.0095	1.0000									
UM1MD	0.2236	0.0957	1.0000								
UM2BL	0.1138	-.1671	-.0038	1.0000							
UM2MD	-.0906	0.0437	0.0822	0.2984	1.0000						
LI1BL	0.0084	0.3496	0.2479	0.1366	0.2804	1.0000					
LI1MD	0.4943	0.1191	0.1254	0.3971	-.1279	0.2906	1.0000				
LI2BL	0.2717	0.2561	0.2134	0.1769	0.1902	0.6798	0.3072	1.0000			
LI2MD	0.3247	0.2553	0.5085	-.1902	-.1116	0.5664	0.3416	0.4035	1.0000		
LCBL	0.0665	0.0911	0.2821	0.0337	0.0948	0.5120	-.0271	0.4097	0.4135	1.0000	
LCMD	0.4440	-.1182	0.2756	-.0524	0.0755	0.1981	0.3726	0.0257	0.4240	0.0525	1.0000
LP2BL	-.0004	0.3345	0.4587	0.0081	0.0590	0.4403	0.2634	0.3160	0.5529	0.6604	0.0143
LP2MD	0.3368	0.1583	0.3300	0.1475	0.1358	0.4452	0.2275	0.4850	0.5553	0.4464	0.5266
LP3BL	-.0115	0.0668	0.4689	0.1143	0.0976	0.1266	-.1505	0.1045	0.3581	0.5249	0.3354
LP3MD	0.3194	0.1736	0.0910	-.2052	-.3929	0.3252	0.2418	0.2241	0.4876	0.2677	0.1723
LP4BL	0.1518	0.0784	0.1962	0.1915	-.0066	0.1853	0.3322	0.0880	0.3383	0.3641	0.3542
LP4MD	0.4092	0.1083	0.1172	0.0324	-.0961	0.1507	0.0506	0.3120	0.1936	0.1576	0.2052
LM1BL	0.2944	0.1216	0.3022	-.1136	-.0783	-.0406	0.0002	0.1945	0.2347	-.1228	0.0454
LM1MD	0.1832	0.1306	0.3437	0.2114	0.0350	0.3507	0.3210	0.2082	0.5367	0.2375	0.4359
LM2BL	0.2769	0.1252	0.4978	0.2012	0.3597	0.2616	0.1395	0.3787	0.4272	0.2272	0.2150
LM2MD	0.1508	-.0053	0.0265	-.0070	0.2242	0.1359	-.1209	0.5022	0.0493	0.2302	-.1731
CRBW	-.2495	-.1270	-.2317	0.1501	0.2818	-.2886	-.2961	-.0671	-.4127	-.1141	-.3357

	LP2BL	LP2MD	LP3BL	LP3MD	LP4BL	LP4MD	LM1BL	LM1MD	LM2BL	LM2MD	CRBW
UI1BL											
UI1MD											
UI2BL											
UI2MD											
UCBL											
UCMD											
UP2BL											
UP2MD											
UP3BL											
UP3MD											
UP4BL											
UP4MD											
UM1BL											
UM1MD											
UM2BL											
UM2MD											
LI1BL											
LI1MD											
LI2BL											
LI2MD											
LCBL											
LCMD											
LP2BL	1.0000										
LP2MD	0.3443	1.0000									
LP3BL	0.3475	0.5881	1.0000								
LP3MD	0.3905	0.3757	0.0017	1.0000							
LP4BL	0.4610	0.3628	0.4151	0.1873	1.0000						
LP4MD	-.0096	0.5593	0.1849	0.5512	0.1453	1.0000					
LM1BL	-.0257	0.3612	0.2150	0.0161	-.0197	0.1588	1.0000				
LM1MD	0.4152	0.6002	0.4359	0.4481	0.4735	0.2605	0.0748	1.0000			
LM2BL	0.4052	0.4396	0.3289	-.0120	0.2219	0.0698	0.3700	0.1862	1.0000		
LM2MD	0.0676	0.2139	-.0287	0.1317	-.2729	0.1479	0.1833	0.0376	0.3444	1.0000	
CRBW	-.1112	-.1261	-.0170	-.4834	-.0304	-.1637	-.0680	-.3344	0.1452	0.0897	1.0000

APPENDIX C

INTRASPECIFIC CORRELATION MATRICES

SAGUINUS FUSCICOLLIS ILLIGERI

	UI1BL	UI1MD	UI2BL	UI2MD	UCBL	UCMD	UP2BL	UP2MD	UP3BL	UP3MD	UP4BL
UI1BL	.00902										
UI1MD	949E-6	.01332									
UI2BL	.00426	0.0032	.01136								
UI2MD	977E-7	.00527	.00293	0.0092							
UCBL	.00263	0.0037	0.0021	.00172	.00797						
UCMD	.00216	.00446	.00348	.00353	.00478	.01148					
UP2BL	.00441	.00476	.00395	.00424	.00369	.00626	.00992				
UP2MD	.00158	.00393	.00255	.00316	.00199	.00546	.00367	.01033			
UP3BL	.00383	.00522	.00388	.00425	.00365	.00804	.00832	.00442	.01664		
UP3MD	.00208	.00267	.00222	0.0017	610E-6	.00239	.00273	.00439	.00307	.00488	
UP4BL	.00204	.00616	.00232	.00497	.00326	.00577	.00449	.00332	.01012	.00357	.01641
UP4MD	121E-6	.00127	.00178	.00149	-.0005	.00169	580E-6	.00345	.00174	.00269	.00172
UM1BL	.00338	.00498	.00379	.00281	.00134	.00527	.00504	.00249	.00807	.00338	.00952
UM1MD	-0.001	.00294	.00178	.00263	-.0003	.00241	.00329	.00169	.00628	.00179	.00349
UM2BL	.00201	.00365	.00305	.00285	0.0033	0.0035	.00538	.00296	.00914	0.0033	.00881
UM2MD	-.0015	.00388	.00246	.00295	-.0012	699E-6	0.0012	.00166	.00619	.00273	.00625
LI1BL	.00475	.00483	.00538	.00314	.00237	.00477	.00534	.00405	0.0062	.00298	.00492
LI1MD	.00121	.00432	924E-6	0.0027	.00136	.00281	.00303	.00224	.00155	.00211	.00293
LI2BL	.00371	0.0052	.00476	.00329	0.0033	.00501	.00573	.00349	.00676	.00271	.00643
LI2MD	.00157	.00343	.00162	.00225	.00155	.00331	0.0019	.00224	.00301	.00202	.00397
LCBL	.00374	720E-6	.00273	902E-6	.00409	.00511	.00381	.00318	.00645	.00151	.00422
LCMD	.00361	.00466	.00491	.00184	.00478	.00652	.00482	.00374	.00611	.00175	.00362
LP2BL	.00423	.00564	.00421	.00443	.00492	.00732	.00783	.00483	0.0093	.00314	.00639
LP2MD	-.0002	.00192	455E-6	0.0042	.00111	.00429	.00181	.00485	.00319	.00351	.00597
LP3BL	.00329	.00389	.00394	.00342	.00315	.00439	.00626	.00361	.00778	0.0035	.00667
LP3MD	.00157	.00184	0.0015	.00136	441E-6	.00267	.00256	.00293	.00418	.00333	.00456
LP4BL	.00155	.00533	.00279	.00452	0.0026	.00403	.00486	.00419	.00756	.00385	.00854
LP4MD	290E-6	.00116	-.0004	.00112	231E-7	.00206	693E-6	.00219	.00107	.00179	.00335
LM1BL	.00153	.00336	.00187	.00303	993E-6	.00192	.00181	.00202	.00397	.00188	.00541
LM1MD	.00216	.00148	.00376	960E-6	.00181	339E-6	.00264	.00181	.00473	.00234	.00384
LM2BL	.00105	.00416	0.0011	0.0026	700E-6	.00302	.00352	.00255	.00463	.00306	0.0056
LM2MD	-.0014	.00347	.00288	0.0021	820E-6	.00329	0.0025	.00369	.00395	.00303	.00525
CRBW	.00512	.00107	.01193	-.0031	.00201	-.0055	-.0005	-.0005	357E-6	-.0032	-.0016

	UP4MD	UM1BL	UM1MD	UM2BL	UM2MD	LI1BL	LI1MD	LI2BL	LI2MD	LCBL	LCMD
UI1BL											
UI1MD											
UI2BL											
UI2MD											
UCBL											
UCMD											
UP2BL											
UP2MD											
UP3BL											
UP3MD											
UP4BL											
UP4MD	.00382										
UM1BL	.00166	.01573									
UM1MD	.00258	.00465	.00994								
UM2BL	.00109	.00873	.00328	.02251							
UM2MD	.00326	.00568	.00686	.00929	.01695						
LI1BL	.00171	.00522	.00154	.00258	.00155	.00951					
LI1MD	919E-6	.00275	613E-6	.00306	.00119	.00283	.00464				
LI2BL	794E-6	.00478	.00179	0.0045	.00211	.00703	.00299	.00815			
LI2MD	.00112	.00298	952E-6	.00134	0.0011	.00294	.00173	.00328	.00411		
LCBL	813E-6	.00237	202E-6	.00367	-.0001	.00456	.00101	.00466	.00222	0.012	
LCMD	.00186	.00311	.00151	.00415	.00114	.00505	.00261	.00419	0.0021	.00833	.01438
LP2BL	.00139	.00636	.00314	.00665	.00164	.00684	.00386	.00678	.00389	.00689	.00778
LP2MD	.00356	401E-6	.00131	.00247	.00299	0.0018	.00242	0.0014	.00121	.00486	.00519
LP3BL	.00114	.00455	.00388	.00367	.00218	.00424	.00197	.00566	.00141	.00395	0.0053
LP3MD	.00233	.00314	.00243	.00372	.00285	.00258	.00204	0.0027	.00198	.00124	0.0018
LP4BL	.00189	.00464	.00403	.00504	.00423	.00477	.00292	.00545	.00247	.00304	.00264
LP4MD	.00183	.00189	.00153	-.0014	429E-6	236E-8	681E-6	741E-6	0.0022	-.0002	-.0014
LM1BL	.00127	.00466	.00366	.00206	.00432	.00313	.00185	.00294	.00248	323E-6	924E-6
LM1MD	.00173	.00419	.00365	.00305	445E-6	.00378	333E-6	.00349	529E-6	.00146	-67E-6
LM2BL	.00125	.00389	.00384	.00484	.00411	0.0026	.00351	.00282	.00167	0.0022	.00366
LM2MD	.00236	.00279	.00379	.00478	0.0036	.00121	604E-6	.00212	.00162	-.0015	-26E-6
CRBW	883E-6	-.0037	-.0036	.00202	.00266	0.005	-0.005	.00322	-.0036	.00388	.00709

	LP2BL	LP2MD	LP3BL	LP3MD	LP4BL	LP4MD	LM1BL	LM1MD	LM2BL	LM2MD	CRBW
UI1BL											
UI1MD											
UI2BL											
UI2MD											
UCBL											
UCMD											
UP2BL											
UP2MD											
UP3BL											
UP3MD											
UP4BL											
UP4MD											
UM1BL											
UM1MD											
UM2BL											
UM2MD											
LI1BL											
LI1MD											
LI2BL											
LI2MD											
LCBL											
LCMD											
LP2BL	0.0129										
LP2MD	.00188	.01722									
LP3BL	.00503	.00334	0.0109								
LP3MD	.00377	.00333	.00167	.00701							
LP4BL	0.0057	.00428	.00698	.00273	.00991						
LP4MD	-.0001	.00389	.00119	.00201	.00205	.00629					
LM1BL	.00188	473E-6	.00359	.00218	.00464	.00194	.00727				
LM1MD	.00328	-.0003	.00424	.00273	.00515	701E-6	.00352	.00363			
LM2BL	.00326	.00638	.00453	.00349	.00488	.00172	.00363	.00114	.00859		
LM2MD	.00161	.00242	.00365	.00332	.00443	.00262	.00284	.00389	0.0036	.00996	
CRBW	702E-6	-.0061	.00354	-.0064	-.0025	-.0089	-.0033	.00135	-.0064	.00222	.09695

TOTAL VARIANCE = 0.4389476

SAGUINUS OEDIPUS OEDIPUS

	UI1BL	UI1MD	UI2BL	UI2MD	UCBL	UCMD	UP2BL	UP2MD	UP3BL	UP3MD	UP4BL
UI1BL	.00572										
UI1MD	.00376	.00982									
UI2BL	.00176	.00129	.00602								
UI2MD	.00297	.00412	-.0009	.01011							
UCBL	.00513	.00357	.00447	.00295	.01336						
UCMD	.00277	.00411	.00185	.00301	.00123	.01887					
UP2BL	.00246	0.0012	.00253	.00391	0.0046	.00591	.01288				
UP2MD	.00471	.00643	.00185	.00337	.00392	0.0094	.00289	.01239			
UP3BL	.00317	.00224	.00148	.00522	.00202	.00607	0.0068	.00309	.01328		
UP3MD	.00554	.00722	.00295	.00336	.00402	0.0064	.00362	.00927	.00456	0.0124	
UP4BL	.00405	.00535	.00306	.00716	.00457	.00639	.00776	0.0061	.01003	.00736	.01408
UP4MD	.00168	.00271	.00134	.00283	-0.001	.00203	918E-6	.00369	.00293	.00492	.00395
UM1BL	.00204	0.0014	.00198	.00174	.00303	.00276	.00342	.00263	.00432	.00252	.00411
UM1MD	.00306	.00632	.00252	-73E-6	0.0035	.00113	720E-6	.00257	.00155	.00591	.00361
UM2BL	.00139	.00149	996E-6	.00163	.00172	206E-6	-.0022	.00132	.00154	0.0015	.00148
UM2MD	246E-6	804E-6	896E-6	-.0015	420E-7	.00373	500E-7	790E-6	-38E-6	-.0003	-.0007
LI1BL	.00294	.00245	.00256	.00103	.00292	.00319	.00307	.00237	.00303	.00296	.00353
LI1MD	.00176	.00298	892E-6	.00253	347E-6	.00114	780E-6	.00311	0.0034	.00436	.00465
LI2BL	.00302	.00135	.00252	692E-6	.00297	.00222	.00412	.00329	0.0031	.00365	0.0034
LI2MD	0.0033	.00471	.00276	.00266	.00468	.00233	0.0041	.00366	.00289	.00502	.00446
LCBL	0.0033	.00178	.00373	0.0031	.00624	.00688	.00683	.00268	.00441	0.0031	.00752
LCMD	0.0019	.00648	0.0011	.00449	826E-6	0.0054	.00205	.00529	.00201	.00462	.00405
LP2BL	.00306	.00528	.00309	.00398	.00684	.00657	.00745	.00403	.00486	.00501	0.0095
LP2MD	.00413	0.0046	.00322	.00464	.00636	.00671	.00568	.00729	.00342	.00607	0.0062
LP3BL	0.002	.00491	.00252	.00399	.00785	.00442	.00444	.00267	.00201	.00339	.00397
LP3MD	.00198	.00142	.00162	.00215	.00255	.00331	.00433	.00334	.00294	.00467	.00507
LP4BL	.00119	.00304	0.0028	.00564	.00418	.00342	.00549	.00198	0.0066	.00362	.00747
LP4MD	.00167	800E-8	.00365	586E-6	.00358	.00442	.00138	.00471	.00312	.00385	.00331
LM1BL	196E-6	.00258	564E-6	904E-6	453E-6	-.0008	.00112	.00188	-.0009	.00276	312E-6
LM1MD	.00351	.00352	.00188	.00433	0.0053	.00477	0.0047	.00277	.00381	.00499	.00378
LM2BL	.00114	.00292	.00252	158E-6	.00341	-.0002	.00192	.00175	377E-6	0.0016	.00232
LM2MD	.00148	-.0015	632E-6	-.0019	.00271	580E-6	.00507	594E-6	.00122	583E-6	.00112
CRBW	-.0107	-.0123	-.0014	-.0025	-.0078	-.0052	.00366	-.0123	.00244	-.0199	-.0029

	UP4MD	UM1BL	UM1MD	UM2BL	UM2MD	LI1BL	LI1MD	LI2BL	LI2MD	LCBL	LCMD
UI1BL											
UI1MD											
UI2BL											
UI2MD											
UCBL											
UCMD											
UP2BL											
UP2MD											
UP3BL											
UP3MD											
UP4BL											
UP4MD	.00669										
UM1BL	754E-7	.00942									
UM1MD	.00201	.00102	.01208								
UM2BL	827E-6	-.0014	-37E-6	0.0079							
UM2MD	-.0004	236E-6	502E-6	.00147	.00309						
LI1BL	440E-7	.00216	.00174	774E-6	994E-6	.00407					
LI1MD	.00259	741E-6	884E-6	.00226	-.0005	.00119	.00411				
LI2BL	.00152	0.0017	.00161	.00108	724E-6	.00297	.00135	.00469			
LI2MD	0.0019	.00177	0.004	-.0012	-.0004	.00258	.00157	.00198	.00512		
LCBL	623E-6	.00101	.00355	343E-6	604E-6	.00374	-.0002	.00321	.00339	.01313	
LCMD	.00462	-.0015	.00385	-.0006	534E-6	.00161	.00304	224E-6	.00386	765E-6	.01617
LP2BL	-43E-7	.00404	.00627	895E-7	408E-6	.00349	0.0021	.00269	.00492	.00941	226E-6
LP2MD	.00261	.00146	.00344	.00124	716E-6	.00269	.00138	.00315	.00377	.00485	.00635
LP3BL	-.0001	765E-6	.00608	0.0012	640E-6	952E-6	-.0011	844E-6	.00302	.00709	.00503
LP3MD	.00227	.00147	871E-6	-.0016	-.0019	.00181	.00135	.00134	.00304	.00267	.00191
LP4BL	.00162	994E-6	.00282	.00222	-48E-6	.00154	.00278	787E-6	.00316	.00545	.00588
LP4MD	.00345	.00108	.00133	296E-6	-.0005	990E-6	334E-6	0.0022	.00143	.00186	.00269
LM1BL	.00169	830E-6	.00234	-.0007	-.0003	-.0002	923E-9	937E-6	.00118	-0.001	406E-6
LM1MD	.00139	.00117	.00349	.00174	180E-6	.00207	0.0019	.00132	.00355	.00252	.00513
LM2BL	.00147	791E-6	.00356	.00116	0.0013	.00109	582E-6	.00169	.00199	0.0017	.00178
LM2MD	.00121	-50E-6	285E-6	-61E-6	.00122	848E-6	-.0008	.00337	345E-6	.00258	-.0022
CRBW	-.0068	-.0041	-.0085	.00446	.00523	-.0061	-.0063	-.0015	-.0099	-.0044	-.0143

	LP2BL	LP2MD	LP3BL	LP3MD	LP4BL	LP4MD	LM1BL	LM1MD	LM2BL	LM2MD	CRBW
UI1BL											
UI1MD											
UI2BL											
UI2MD											
UCBL											
UCMD											
UP2BL											
UP2MD											
UP3BL											
UP3MD											
UP4BL											
UP4MD											
UM1BL											
UM1MD											
UM2BL											
UM2MD											
LI1BL											
LI1MD											
LI2BL											
LI2MD											
LCBL											
LCMD											
LP2BL	.01547										
LP2MD	.00406	.00899									
LP3BL	0.0051	.00658	.01391								
LP3MD	.00423	0.0031	178E-7	.00758							
LP4BL	.00749	0.0045	0.0064	.00213	.01707						
LP4MD	-.0001	.00546	.00225	.00494	.00196	.01061					
LM1BL	-.0002	.00241	.00178	983E-7	-.0002	.00115	.00495				
LM1MD	.00478	.00526	.00475	.00361	.00572	.00248	486E-6	.00855			
LM2BL	.00328	.00271	.00253	-68E-6	.00189	468E-6	.00169	.00112	.00424		
LM2MD	823E-6	.00199	-.0003	.00112	-.0035	.00149	.00126	341E-6	0.0022	.00958	
CRBW	-.0046	-0.004	-.0007	-.0141	-.0013	-.0056	-.0016	-.0103	.00316	.00293	.11161

TOTAL VARIANCE = 0.4279759

VITA

Theodore Millaway Cole, III was born in Waynesboro, Virginia on April 19, 1962. He attended elementary schools in that city and in Fishersville, Virginia and was graduated from Wilson Memorial High School in June 1980. He entered Virginia Polytechnic Institute and State University in September 1980 and attended that school until June 1983, studying engineering and English.

In September 1983, he transferred to the University of Tennessee, Knoxville, where he received a Bachelor of Arts degree in Anthropology in August 1984. He began graduate studies at the University of Tennessee in September 1984. During this period, he served as curator of the UT Saguinus Collection. He was awarded a Masters of Arts degree in Anthropology in June 1986.

The author is member of the American Association of Physical Anthropologists. He will begin his doctoral studies in Anthropology at the State University of New York at Stony Brook, where he has been awarded a Graduate Council Fellowship, in September 1986.

ERRATUM

In the printing of this manuscript, a portion of the text was accidentally deleted. The first paragraph of page 17 (CHAPTER II) should properly read:

Relationships among extant taxa. There is no general agreement among researchers about how the extant callitrichines should be organized phylogenetically. Studies which help to elucidate the phylogenetic relationships between taxa are rare, especially those which attempt to demonstrate how congeneric species are related. While the placement of marmosets (Callithrix) and tamarins (Saguinus) in separate genera is nearly universal (but see Rosenberger (1983) for a discussion of the biological reality of this division), the placements of the pygmy marmoset (Cebuella), the lion tamarin (Leontopithecus or Leontideus), and Goeldi's monkey (Callimico) remain unresolved. The division of callithichids into "long-tusked" and "short-tusked" groups is a potential source of confusion. Sussman and Kinzey (1984:421) state that these terms "are especially useful in distinguishing two adaptively different groups, but not necessarily two phylogenetic clades."