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correlates between anatomy and positional behavior**

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**The Functional Morphology of the Prosimian Hindlimb:
Some Correlates Between Anatomy and Positional Behavior**

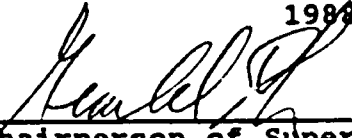
by

ROBERT LOUIS ANEMONE

**A dissertation submitted in partial fulfillment
of the requirements for the degree of**

Doctor of Philosophy

University of Washington

Approved by  1988
(Chairperson of Supervisory Committee)

Program Authorized
to Offer Degree Anthropology

Date December 16, 1987

Doctoral Dissertation

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Abstract

THE FUNCTIONAL MORPHOLOGY OF THE PROSIMIAN HINDLIMB:
SOME CORRELATES BETWEEN ANATOMY AND POSITIONAL BEHAVIOR

by Robert Louis Anemone

Chairperson of the Supervisory Committee: Professor Gerald G. Eck
Department of Anthropology

Recent years have witnessed a resurgence of interest in the functional morphology and ecology of the prosimian primates. Napier and Walker's (1967) vertical clinging and leaping hypothesis focused interest on the presence of saltatory adaptations in the hindlimb of certain prosimians. This dissertation presents a functional analysis of locomotor and postural adaptations in the hindlimb of leaping and quadrupedal prosimians designed to test morphological aspects of the vertical clinging and leaping hypothesis.

Osteological measurements were taken on the pelvis, femur, and tarsus of a total of 277 post-cranial skeletons representing 8 families and 16 genera. Lengths of the long bones and the skeletal trunk length (Biegert and Maurer 1972) were also collected for each specimen; the former were used in studies of overall limb proportions and skeletal allometry, and the latter was used as an estimator of bodily size. A series of ratios was calculated for the pelvic, femoral, tarsal, and limb proportion data, and multiple discriminant function analysis was utilized in the

analysis of pelvic and femoral data. Regression analysis was used to study allometric patterns in forelimb and especially hindlimb length.

My results indicate the presence of two very different morphological patterns in the hindlimb of extant prosimian leapers. Galagidae and Tarsiidae are linked by the possession of a series of specialized traits in the pelvis, proximal femur, and especially, by an elongate tarsus. The hindlimb among Indriidae and Lepilemuridae, along with that of other "hindlimb-dominant" Lemuriformes, demonstrates a very different gestalt. These different patterns can be seen in both bivariate and multivariate analyses, and in allometric investigations. The functional and biomechanical significance of hindlimb traits of leaping prosimians is discussed, along with the implications of these results for the vertical clinging and leaping hypothesis.

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Introduction

The publication in 1967 of Napier and Walker's seminal article on prosimian locomotion, in which they presented what has become known as the Vertical Clinging and Leaping (henceforth VCL) hypothesis, provoked a resurgence of interest in the anatomy, ecology, and evolution of the prosimian primates. One of the results of the interest engendered by this bold hypothesis has been a dramatic surge in research on prosimian ecology (Charles-Dominique 1977; Charles-Dominique and Bearder 1979; Crompton 1980, 1984; Doyle and Bearder 1977). This interest is best exemplified in the work of Charles-Dominique (1977) who has attempted to present a picture of the ecology of a series of sympatric prosimians that includes a consideration of positional behavior (used in the sense of Prost [1965] to include both locomotor and postural activities), habitat utilization, diet and foraging strategy, synecological relations, and predator-prey dynamics. Another area of increased interest has been the reconstruction of the positional behavior and other aspects of the ecology of extinct prosimians. Major contributions in this area include Jungers's (1976, 1978, 1980) work on subfossil Malagasy lemurs and Szalay and coworkers' analyses of Paleogene Primates (Szalay and Dagosto 1980; Szalay and Decker 1974; Decker and Szalay 1974; Dagosto 1983).

A third area of interest, and one which plays a crucial role in the integration of the previous two, is the study of the functional and comparative morphology of extant prosimian primates. It is clear that any hypotheses concerning the positional behavior of extinct taxa must be based on and tested against behavioral and morphological patterns visible among extant forms (Bock and von Wahlert 1965; Kay and Covert 1984). Similarly, classifications of behavioral variation (e.g., positional behavior) among living taxa can be supported or falsified on the basis of comparative and functional analyses of the anatomy that enables the attendant behaviors. Because the morphology of the hindlimb is crucial to discussions of primate positional behavior, aspects of the anatomy of this region have been studied by many workers, including Hall-Craggs (1965b, 1966a, 1966b, 1974), McArdle (1981), and Jouffroy (1962, 1975). The goal of this dissertation is to provide a functional and comparative analysis of the hindlimb of the extant prosimian primates that will:

1. Facilitate speculation on and provide a sound basis for the reconstruction of the positional behavior of extinct prosimian primates, and
2. Clarify the status of vertical clinging and leaping as a category of positional behavior among living prosimians.

The overall organization of this work is as follows. Chapter 1 begins with a review of previous classifications of prosimian locomotion, followed by a discussion of the

development and reception of the VCL hypothesis and a survey of previous work on the functional and comparative anatomy of the prosimian hindlimb. Chapter 2 contains a review of the available behavioral literature on the taxonomy, diet, habitat, and positional behavior of the prosimians. A presentation of the study materials and the methods of data collection utilized in this dissertation can be found in Chapter 3. Chapters 4 through 7 comprise the body of the dissertation; they contain the results of osteological and myological investigations on the hindlimb anatomy of most extant members of the Suborder Prosimii. These chapters deal separately with investigations on the pelvis, femur, tarsus, and overall limb proportions of extant prosimian primates. Finally, the results and their relevance are discussed in Chapter 8.

Chapter 1. Vertical Clinging and Leaping Among Prosimians

1.1. Introduction to Chapter 1

The classification of positional behavior and especially the VCL hypothesis (Napier and Walker 1967) are two of the major foci of the research involved in this dissertation. Chapter 1 begins with a brief discussion of early attempts at classifying prosimian positional behavior, and some of the pitfalls often encountered in these, and is followed by a discussion of the VCL hypothesis (Walker 1967, 1974, 1979; Napier and Walker 1967; Napier and Napier 1967). The response to the VCL hypothesis was rapid and critical, and I discuss some of the more cogent and influential published critiques (Cartmill 1972; Szalay 1972; Stern and Oxnard 1973), as well as an important but still unpublished contribution (Godfrey ms.). A summary of recent analyses of the morphology of the prosimian hindlimb that pertain to questions of positional behavior, and specifically to the status of leaping prosimians, concludes the chapter.

1.2. Early Classifications of Prosimian Locomotion

Attempts to classify the primates on the basis of locomotor behavior are nearly as old as the scientific study of the order itself. Many of the important primatologists of this century have been interested in the diversity of locomotor patterns among extant primates (e.g., Clark 1971; Jones 1916, 1929; Simpson 1935, 1940; Gregory 1912, 1920). In perhaps the earliest published

classification of primate locomotion, Mollison (1911) classified primates, including some prosimians, as either "Laufer" (runners), "Kletterer" (climbers), "Springer" (jumpers), or "Hangeler" (hangers). Although purportedly a classification of behavioral patterns, Mollison's work is actually based largely on limb and body proportions. Like many other published works on primate locomotor behavior it suffers from a lack of detailed observations of the behavior of the animals in nature. This problem is particularly acute in the study of prosimians and stems from their small body size, nocturnal activity patterns, and inaccessible habitats. In fact, much of the published work on prosimian locomotor behavior is based largely upon anecdotal observations in the field (often by untrained individuals), and on studies of animals in captivity, often supplemented by observations of skeletal morphology. The problems inherent in constructing "locomotor" classifications on the basis of skeletal morphology (often in the absence of adequate behavioral observations) are illuminated by a consideration of the locomotor category of brachiation.

In the voluminous literature on brachiation and brachiators, the contribution of Erikson (1963) typifies the pitfalls of using morphology as the basis of a locomotor classification. Stern and Oxnard (1973:5) define a "pseudo-

behavioral" classification as one

"in which a category owes its existence to the occurrence of similar morphology among its members, but derives its name from a behavior."

Relying almost exclusively on the evidence of overall limb proportions, Erikson (1963) classified New World monkeys as either springers, climbers, or brachiators. Rather than assuming (or asserting) that shared morphology reflects similar locomotor patterns among these animals, Erikson (1963) admitted the contrary: animals classified together on the basis of similar limb proportions often use different patterns of locomotion. This seeming contradiction is best demonstrated by Alouatta, a "brachiator" according to Erikson (1963:147):

"On functional grounds, the howler monkey Alouatta barely deserves inclusion in this group. On structural grounds, however, there are many reasons for including it with the brachiators...but it is much more exclusively a quadruped than the other three genera."

While Erikson (1963) was willing to accept this paradox, Napier (1963) went further in attempting to develop a theoretical basis for it. He argued that the term "brachiation" (and presumably other locomotor categories) bears equally valid behavioral and morphological connotations:

"A brachiator is one which brachiates, but it is also a primate with a well-recognised morphology that is peculiarly adapted in a particular way for arm-swinging" (Napier 1963:190).

He went on to state that since behavior can only be observed in living animals, to limit a locomotor category like brachiation to a behavioral meaning

"would be to render brachiator invalid as a phylogenetic concept, for only living animals could then be classified as brachiators" (Napier 1963:190).

I find several serious problems with Napier's (1963) argument for the use of morphology as a crucial element in the construction of locomotor categories. In the first place, pseudo-behavioral classifications simply do not work well, often lumping animals with widely dissimilar locomotor habits on the basis of perceived morphological similarities. Thus in explaining the inclusion of the great apes in the brachiator group, Napier (1963:185) stated:

"morphologically they are brachiators in spite of certain secondary modifications in living forms".

What Napier discretely referred to as "secondary modifications" involve nothing less than the fact that mature great apes simply do not brachiate in nature (Goodall 1971; MacKinnon 1974; Fossey 1983). More importantly, pseudo-behavioral classifications confound the analysis of the relationship between behavior and morphology. Rather than limiting the usefulness of locomotor categories to extant taxa, the use of observable behavior as the basis for the formation of locomotor categories is, in fact, a necessary prerequisite to

understanding the locomotor behavior of extinct taxa. It is only among living animals, where both form and function can be observed, that hypotheses relating specific morphological patterns to particular behaviors can be tested. Insights gleaned from analyses of "form-function complexes" (Bock and von Wahlert 1965) among extant primates must be the basis of any attempts to reconstruct the behavior of extinct primates (Kay and Covert 1984). Finally, referring to the variability or plasticity of primate locomotor abilities, Stern and Oxnard (1973:5) point out:

"The entire validity for attaching a behavioral name to a morphological category relies on a unique association between a given structural framework and a given behavior. In truth there is no logical requisite for such a unique relation."

The influential contribution of Ashton and Oxnard (1964) is illustrative of some other problems found in many classifications of primate positional behavior. The authors presented a classification based in parallel upon the usage and resultant stresses that the upper and lower limbs are (separately) subjected to during normal locomotion. In this scheme, habitual use of the forelimb in either tension or compression is what determines a taxon's primary locomotor type. On this basis, the authors constructed three categories of positional behavior for anthropoid primates (brachiators, semi-brachiators, and

quadrupeds), and two for prosimians (hangers and quadrupeds). While the hindlimb is nearly always used in compression during locomotion, Ashton and Oxnard (1964) determined that primates can be distinguished on the basis of the propulsive component of hindlimb use (i.e., to what degree do individuals of a taxon engage in leaping). Interestingly, they found a continuum from adept and frequent leapers to poor and/or infrequent leapers in each of the locomotor categories that they established on the basis of forelimb use.

While the concept behind Ashton and Oxnard's (1964) classification -- decouple the upper and lower limbs, analyze the major stresses operating on each, and base a classification on the observed patterns -- was both innovative and insightful, an examination of the resulting classification clearly indicates that it must be considered a failed attempt. Among the prosimians, the two categories (hangers and quadrupeds) are hopelessly imprecise as descriptors of behavior, and each includes animals with extremely dissimilar locomotor habits. Whether or not their forelimbs function mainly in tension, classifying lorises and indriids together as "hangers" makes little sense. In fact, two more dissimilar taxa with respect to positional behavior could hardly be found within any mammalian order.

The problem arises from the fact that Ashton and Oxnard (1964) were not really attempting to classify "behavior" as

such. Rather, they presented a classification of hypothesized biomechanical stresses on musculo-skeletal elements. In an earlier publication, Oxnard (1963:166) stated:

"To classify two animals as quadrupeds does not imply that they move in the same way" only that "within the great variation of locomotor patterns, there are within each group certain common factors relating to the function of the forelimb."

It should not be surprising that animals with extremely dissimilar habits might subject their upper and lower limbs to similar stresses since the only possibilities are tension, compression, or shear. Clearly, categories of positional behavior must be based on observed behavior, not on morphology or biomechanical stresses.

1.3. The Vertical Clinging and Leaping Hypothesis

Although not the first to note the occurrence of bipedal leaping among certain prosimians, Napier and Walker (1967) were the originators of the VCL hypothesis. In their 1967 article, based primarily on Walker's (1967) doctoral research, the authors presented their hypothesis in three distinct parts:

1. They proposed the existence of a "natural locomotor group" (Napier and Walker 1967) of prosimian primates that share a mode of positional behavior which includes clinging with upright posture to vertical arboreal supports and leaping, propelled mainly by the hindlimbs, between these supports. On the ground these animals engage in bipedal, kangaroo-like hopping.

2. In addition, they argued that vertical clinging and leaping prosimians share a suite of morphological characteristics (mainly but not exclusively in the hindlimb) that allows them to engage in this unique mode of positional behavior.

3. The final and perhaps most controversial part of the VCL hypothesis stems from the observation that the basic morphology shared by extant leapers was also present to some extent in all known Eocene prosimians. The authors concluded that "possibly it (vertical clinging and leaping) is to be regarded as the earliest locomotor specialization of primates and therefore preadaptive to some or possibly all of the later patterns of primate locomotion" (Napier and Walker 1967:204).

In their classification, Napier and Walker (1967; Walker 1967) placed each prosimian species in one of three categories of positional behavior: vertical clinging and leaping, arboreal quadrupedalism, or slow climbing quadrupedalism. Certainly the most discrete of these categories in both a taxonomic and a behavioral sense is the slow climbing quadrupedal group, composed of the four lorisid genera (Arctocebus, Perodicticus, Loris, and Nycticebus). Walker (1967:77) defined this behavior in the following way:

"An arboreal, quadrupedal, slow climbing form of locomotion in which no leaping is involved. The foot is placed directly behind the hand of the same side before the hand is released to make the next step....At any one time three extremities are usually involved in grasping the support."

The arboreal quadrupedal group is considerably more diverse, including the Lemuridae, Cheirogaleidae, and Daubentonia. Walker (1967:76) defined arboreal quadrupedalism in the following manner:

"A form of locomotion involving the use of all four limbs in climbing, walking and running. Leaping propensities vary from group to group. Ground locomotion is essentially the same as arboreal locomotion; the hands and feet are placed in a plantigrade position rather than grasping. The hindlimbs provide most of the propulsive effort and the forelimbs act as supporting struts for the body."

Finally, the VCL category contains Tarsius, Galago, Indriidae, Lepilemur, and Hapalemur. Walker (1967;76) defined VCL as follows:

"A leaping mode of progression through the trees in which the two hindlimbs, used together, provide the propulsive force of the locomotion. The trunk is held in a vertical position before and after each leap; vertical supports are preferred. On the ground this locomotor habit manifests itself in bipedal hopping with the trunk held erect and the arms almost never involved in support. Tail movements are often up and down but usually the tail is trailed inertly during a leap."

As will become amply clear to the reader in later sections of this dissertation, the slow-climbing lorisisds are easily distinguished on the basis of either behavior or morphology from both arboreal quadrupeds and vertical clingers and leapers. Much of our attention thus will necessarily focus on the more subtle distinctions between the latter two groups.

Looking first at extant leaping prosimians, Napier and Walker (1967; Walker 1967, 1974) presented a list of morphological traits that they suggest are functional adaptations for vertical clinging and leaping and serve to distinguish leaping prosimians from quadrupeds. All

vertical clingers and leapers were said to be small to medium-sized prosimians with long tails, except for Indri, which is the largest of the leapers and lacks a tail. Their hindlimbs are much longer than forelimbs, producing a low intermembral index (forelimb length as a percentage of hindlimb length), while a humerus shorter than the radius results in a high brachial index (radius length as a percentage of humerus length). Pelves have long ilia and short ischia, and the ilium is broad among the larger forms but narrow and bladelike among the smaller forms. Femora are long, straight, and provided with a cylindrical head, posteriorly projecting condyles, and a deep and narrow patellar groove that projects anterior to the shaft. In the tarsal region, the calcaneus and navicular are greatly elongated among small-bodied leapers, while the grasping pes is always provided with a strong and opposable hallux. Other features thought to be associated with vertical posture include a centrally placed foramen magnum, orthognathous facial region, and divergent mandibular rami.

One or more of these last three traits were offered as evidence for vertical clinging and leaping habits among Aeolopithecus (= Propithecus, Szalay and Delson 1979) and Parapithecus from the Fayum beds of the North African Oligocene (Napier and Walker 1967). Rather more substantial evidence for vertical clinging and leaping was

garnered for several Eocene Adapidae (Notharctus and Smilodectes) and Omomyidae (Hemiacodon, Necrolemur, Nannopithec, Omomys, Teilhardinia, and Tetonius). Based on admittedly scarce postcranial fossils, these forms were said to resemble modern vertical clingers and leapers by possessing such traits as an elongate calcaneus and navicular, low intermembral index, narrow and rodlike ilium, cylindrical femoral head and anteriorly projecting patellar groove, and a fused tibia and fibula (the latter only in Necrolemur and modern Tarsius) (Napier and Walker 1967). The authors went so far as to state that,

"Of all the fossil postcranial bones reputedly assigned to Eocene prosimians, none show the morphological feature of quadrupeds; all the skeletal characters point to these animals having been Vertical Clingers and Leapers" (Napier and Walker 1967:212).

This evidence was further developed into a theory of the evolution of primate locomotion that considers vertical clinging and leaping to be the ancestral pattern among primates, preadaptive to quadrupedalism and, through quadrupedalism, to all the other forms of locomotion seen among members of the order (Napier 1967; Walker 1967, 1974, 1979).

1.4. The Critical Reaction to the VCL Hypothesis

In their cogent critique of the VCL hypothesis, Stern and Oxnard (1973) argued against all three of the main points mentioned in the previous section. Citing behavioral

variability at both intra- and interspecific levels, they questioned the existence of a "natural locomotor group" (Napier and Walker 1967:204) comprising extant leaping prosimians. The evidence for different methods of vertical clinging and leaping led Stern and Oxnard (1973) to investigate the possibility of different morphological adaptations to these behavioral patterns. Looking at ratios and indices of both hindlimb and forelimb measurements, log-transformed to control for correlations between variables and for differences in bodily size, the authors used canonical analysis in their investigation. Canonical analysis, a multivariate method of discriminant analysis, reduces a large number of correlated variables to a small number of independent axes which maximize the separation between groups in multivariate space. Combined with generalized distance measures such as Mahalanobis D-square, the use of canonical analysis can show the actual multivariate distance between group means (see Oxnard 1973 for a discussion of multivariate methods of data analysis). The results of Stern and Oxnard (1973) indicate the existence of at least two groups of leaping prosimians with different morphological adaptations to a saltatory way of life; Galago and Tarsius are closely linked and are well-separated from Lepilemuridae and Indriidae. Later studies by Oxnard and various coworkers (Oxnard, German and McArdle 1981; Oxnard, German, Jouffroy and Lessertisseur 1981),

using similar methods but with substantially larger sample sizes, confirmed these results. Recently, Oxnard (1984), while still noting morphological similarities between Tarsius and Galago, argued for the uniqueness of Tarsius among the extant leaping prosimians.

Stern and Oxnard's (1973) survey of the evidence for vertical clinging and leaping among Eocene prosimians similarly indicates the existence of two different morphological groups. One group, comprising mainly members of the family Adapidae, appears to resemble the living Malagasy leapers, while the other group resembles the modern tarsiers and galagos and includes members of the family Omomyidae. Although neither Stern nor Oxnard appear to have had access to many of the original fossils, their discussion of the evidence for vertical clinging and leaping among Eocene prosimians is sound. Since their analytical methods require much more complete specimens of fossil primates than are commonly available, they based their discussion on individual, usually qualitative traits of hindlimb morphology. In so doing they demonstrated that the evidence for a leaping way of life can only be sustained for certain Adapidae and Omomyidae among Eocene primates. Recent paleontological work (summarized in Szalay and Delson 1979) appears to support this more conservative viewpoint rather than that of Napier and Walker (1967).

Stern and Oxnard's (1973) conclusions are, however, problematic with respect to the behavioral and morphological variability among extant vertical clingers and leapers. The evidence that they amass in favor of intra- and inter-specific behavioral variability among leaping prosimians is trivial when compared to the obvious and adaptively important ways that the extant leapers resemble one another. Minor differences in the orientation of the body during flight or in the sequence or pattern of substrate contact at the end of the jump should not obscure the dominance of hindlimbpropelled leaping between vertical supports in the daily locomotor activities of these animals. The evidence for morphological variation, while clearly suggestive of behavioral and/or phylogenetic differences between leaping prosimians, is seriously deficient in one major respect; the multivariate analyses were never related to the actual morphological traits of the animals themselves. Thus, the authors never identified the traits that contributed to the discrimination in multivariate space between the Tarsiid-Galagid group and the Indriid-Lepilemur group. In noting this methodological problem, Oxnard, German and McArdle (1981:492) stated,

"In this study, each (discriminant) axis is a melange of variables which as a whole produce significant separations among the genera."

This very serious problem is present in all of the cited multivariate work on prosimians by Oxnard and his

coworkers. Since Oxnard's methods of data collection and analysis require essentially complete specimens, their application to fossil material is difficult. An understanding of the functional basis for morphological and behavioral differences between living primates is the key to reconstruction of the behavior of extinct taxa. Failing to provide this essential link, Oxnard's work is ultimately flawed and unsatisfying.

In an interesting series of papers, Cartmill (1972, 1974a, 1974b, 1975a) discussed the VCL theory in light of his own interest in arboreal adaptations among primates. In these publications, Cartmill attempted to debunk the "Arboreal Theory" of primate origins. In Cartmill's "Visual Predation Theory" the distinctive primate adaptations (grasping cheiridia, nails and tactile pads, reduced snouts and olfaction, increased reliance on vision with orbital frontation and stereoscopy) are explained not simply as the result of arboreal habits, but of the demands of visually-directed predation on insect and other invertebrate prey in an arboreal habitat. Cartmill questioned two aspects of the VCL hypothesis of Napier and Walker (1967) in reference to the fossil evidence for saltatory habits among Eocene prosimians. The first question was whether vertical clinging postures could be inferred from the presence of grasping adaptations in the hindlimb and pes; the second

concerned the argument for vertical clinging and leaping among all or nearly all Eocene prosimians.

While Napier and Walker (1967) linked grasping adaptations in the primate hindlimb with an habitual reliance on vertical postures among saltatory animals, Cartmill (1974b:67) explained these adaptations in light of his Visual Predation theory:

"The combination of a grasping first toe with a nonopposable thumb is not correlated with vertical clinging and leaping...it is found among didelphids and other arboreal mammals that clearly have no indriidlike or tarsierlike ancestors. It makes more sense to interpret the grasping foot as an adaptation to prolonged or cautious movement among slender branches and vines, in didelphids and early prosimians alike."

With respect to the question of vertical clinging and leaping among Eocene prosimians, Cartmill (1972, 1974a, 1975a) took a decidedly more conservative approach than that of Napier and Walker (1967). Cartmill agreed that the postcrania of the adapids Notharctus and Smilodectes resemble modern Indriidae, but argued that most of the Omomyidae (except perhaps the necrolemurines, which resemble Tarsius) are similar postcranially to the mainly quadrupedal Cheirogaleidae. Like Stern and Oxnard (1973), Cartmill (1972, 1974a, 1975) distinguished between at least two different morphological patterns among modern prosimian leapers; one characterized by elongated tarsal elements (Galagidae and Tarsiidae) and the other lacking this specialized trait (Indriidae and Lepilemuridae). As noted

above, these two patterns appear to have been present even in the Eocene among the Adapidae and Necrolemurinae, respectively.

Szalay's (1972) contribution to the VCL question also concerned the prevalence of vertical clinging and leaping among fossil prosimians. Szalay's viewpoint is of particular interest because of his wide experience with Paleogene primate fossils; his critique of the VCL hypothesis as applied to the fossil record is authoritative. Citing the work of Biegert (1963), Szalay (1972) quickly discounted the suggested correlation between a centrally placed foramen magnum and a shortened face with a reliance on vertical postures (Napier and Walker 1967). These traits are better explained as related to relative brain size and the possession of stereoscopic vision, and as such tell us little about positional behavior in Aeolopithecus and Parapithecus, contrary to Napier and Walker (1967). While agreeing that some Eocene prosimians are correctly identified as vertical clingers and leapers (among them Smilodectes, Notharctus, Hemiacodon, Necrolemur, and Microchoerus), Szalay (1972:33) stated that

"Citations by Napier and Walker of osteological characters allegedly known from the fossil record are based on inaccurate, outdated literature."

Furthermore, Szalay (1972) made the point that all of the Paleogene prosimian leapers date from the Early and Middle

Eocene, postdating by at least 20 million years the origin of the primates (Decker and Szalay 1974), and that the earliest postcranially known primate (Plesiadapis) was certainly not a leaper but an arboreal, quadrupedal, clawed climber (Szalay and Decker 1974).

While clearly demonstrating that the earliest primates were not leapers, Szalay seems unaware that Napier and Walker (1967) do not include Plesiadapis or any other Paleocene primate among their vertical clingers and leapers, or that the appearance of leaping specializations in the Paleocene is not a crucial part of the VCL hypothesis. Regardless of the situation in the Paleocene, if all or most Eocene primates were leapers, the hypothesis of Napier and Walker would be substantially upheld, since it is among the Adapidae and Omomyidae that all modern primates find their ancestors (Szalay and Delson 1979). The use of misidentified postcranial elements, the inclusion of non-primate material, and the use of morphological traits with no real connection to vertical clinging and leaping are, however, all valid criticisms of the VCL hypothesis (Szalay 1972). An obvious prerequisite to our understanding of the prevalence of vertical clinging and leaping in the fossil record is the finding of clear associations between behavior and morphology among its living practitioners. In summary, Szalay (1972: 33) states:

"The osteological characters that might be invariably associated with vertical clinging and leaping have not been deduced as yet, if such clear-cut features exist at all."

Godfrey's (ms.) contribution deals to a large extent with the behavior and morphology of extant leaping prosimians, especially the lemuriform leapers of the Malagasy Republic. She argues for the uniqueness of the indriid type of vertical clinging and leaping and that, with respect to both behavioral and morphological adaptations,

"Living indriids are far more similar to their more generalized hindlimb-dominated relatives (Lepilemuridae and Lemuridae) than they are to other animals (galagids and tarsiids) classified as vertical clingers and leapers by Napier and Walker (1967)." (Godfrey ms.:2).

Godfrey lists a series of traits which, she claims, link all "hindlimb-dominated" lemuriform primates in a morphological continuum and clearly separate lemuriform leapers from galagos and tarsiers.

Godfrey presents original and interesting ideas and working hypotheses. Especially helpful is the concept of a group of prosimians whose positional behavior and morphology can be described as "hindlimb-dominant." This group includes the quadrupedal Malagasy taxa and all of the prosimian leapers, but does not include the slow-climbing Lorisidae of Africa and Asia. Godfrey's hypothesis, that indriids resemble other Malagasy taxa more closely than they do the non-Malagasy leapers, is in direct

contradiction to the expectations of the VCL hypothesis of Napier and Walker (1967). She is not able, however, to convincingly falsify the VCL hypothesis owing to a major deficiency in her study, which deals exclusively with Malagasy taxa. Because her information on galagos and tarsiers appears to be second hand, her attempt to establish the uniqueness of the indriid version of VCL is weakened by her unfamiliarity with the galagid-tarsiid version. While there may indeed be differences in both the execution and the underlying morphology of vertical clinging and leaping between Indriidae and Galagidae/Tarsiidae, Szalay's (1972) assertion that they have not yet been clearly elucidated remains valid.

1.5. Previous Studies of Prosimian Hindlimb Anatomy

Much progress has been made during the last quarter century regarding the state of our knowledge of the functional and comparative morphology of prosimians. In a series of studies dealing with overall limb proportions and skeletal allometry, Jungers applied the "vertical support" model of Cartmill (1974b) to the extinct subfossil Megaladapis (Jungers 1976, 1978), to extant lemurs and lorises (Jungers 1979), and to the entire Primate order (Jungers 1985). Cartmill's (1974b) vertical support model predicts that a clawless, arboreal mammal can effectively minimize in one of two ways the gravitational torques

around its points of support while clinging to (or climbing on) a vertical support:

1. with long forelimbs adapted for powerful flexion, so as to subtend a large central angle as it grasps the support, and
2. with short, habitually flexed and adducted hindlimbs, allowing it to increase the frictional forces between its feet and the support surface.

Jungers's (1976, 1978) study of the scaling of limb proportions in three species of Megaladapis revealed that larger species possess relatively longer forelimbs and shorter hindlimbs than smaller species. This results from the forelimbs scaling in a positively allometric fashion, while the hindlimbs are negatively allometric. A byproduct of this allometric pattern is the possession of a higher intermembral index among the larger species. On this basis, Jungers (1976, 1978) argued that Megaladapis is best reconstructed as a "vertical clinger and climber" whose nearest modern analog might be Phascolarctos, the koala. The extremely short and robust hindlimbs, in conjunction with substantial body size, indicate that leaping could not have played a large role in the repertoire of locomotor behaviors of Megaladapis.

Further explorations of the vertical support model and skeletal allometry among extant lemurs and lorises can be found in two other papers by the same author (Jungers 1979, 1985). Jungers's research indicates that the most consistent trend in the scaling of primate limb proportions

is for the intermembral index to increase with increasing body size. At each level of comparison (i.e., all non-human primates, haplorhines, strepsirhines, individual families), the norm is for forelimb length to increase (relative to body size) at a faster rate than hindlimb length. This single result is achieved in differing ways in the various groups. Among strepsirhines, the forelimb is positively allometric but the hindlimb scales isometrically. There is a large amount of variability in forelimb and hindlimb scaling patterns among the families of strepsirhine primates.

Lorisidae are unique in exhibiting extreme negative allometry in both fore- and hindlimbs, while Cheirogaleidae alone show positive allometry in both pairs of limbs. Lemuridae, Indriidae, and Galagidae are similar in having higher scaling coefficients in the forelimb than the hindlimb, and thus the larger species in each of these families possess a higher intermembral index than do their smaller relatives. A closer look at the actual scaling relations of these three families shows that indriids are unique in showing negative allometry in both the forelimbs and especially the hindlimbs, while Galagidae and Lemuridae scale isometrically in the forelimb but negatively in the hindlimb. In these three families the relatively longer forelimb in larger species is judged, in the context of the

vertical support model, an aid in vertical clinging and climbing on supports of large diameter. The shorter hindlimbs are also predicted by this model, but can also be interpreted as aids to climbing on large diameter horizontal supports since they serve to bring the animal's center of gravity closer to the support surface (Jungers 1985).

In addition to his work on skeletal allometry and limb proportions, Jungers is one of the coauthors of an important paper that blends traditional descriptive and functional anatomy with biomechanics in an elegant analysis of the M. quadriceps femoris of Lemur fulvus (Jungers et al. 1980). Combining dissections and telemetered electromyography (EMG), the authors investigated three aspects of the morphology of this group of powerful thigh muscles in order to elucidate its relationship to positional behavior in lemurids. Their results indicate that the long, parallel fibers of M. vastus lateralis are of great importance in leaping: EMG findings revealed that M. vastus lateralis undergoes active force enhancement as it is stretched in hyperflexion prior to leaping, and that it is consistently the most important initiator of the leap. Conversely, M. vastus intermedius is composed of many short fibers which run to a central tendon that extends for much of the length of the thigh. As this tendon joins those of the other three parts of the M. quadriceps femoris to

form the patellar tendon, a cartilaginous "superior patella" is formed within it (Alezais 1900). Telemetered EMG indicates that the M. vastus intermedius is normally quiescent during leaping by L. fulvus, but shows high levels of electrical activity during postural behaviors in which the knee is highly flexed (e.g., vertical clinging). Jungers et al. (1980) concluded that the morphology of M. vastus intermedius may be adapted not to leaping itself, but to postural activities that are an integral part of the positional repertoire of all Malagasy prosimians. As for the adaptive significance of the possession of a superior patella, they state that it is

"most plausibly related to the complex tensile and compressive stresses generated in the tendon during the completely hyperflexed phase of leaping" (Jungers et al., 80:287)

Jouffroy's work can be conveniently discussed in three major areas: studies of prosimian limb proportions (Jouffroy and Lessertisseur 1979; Oxnard, German, Jouffroy and Lessertisseur 1981), application of cineradiography to the analysis of leaping behavior among galagids (Jouffroy and Gasc 1974; Jouffroy et al., 1973, 1974), and descriptive myology and osteology of lemuriformes (Jouffroy 1962, 1975).

Jouffroy and coworkers are responsible for pioneering studies in the application of the technique of

cineradiography to the analysis of prosimian locomotion (Jouffroy et al., 1973, 1974; Jouffroy and Gasc 1974). Simply put, this technique allows for frame by frame analysis of filmed X-ray records of limb excursions during locomotor behavior of captive animals. Applying this technique to the vertical leap of (a single individual of) G. alleni, they were able to distinguish between two very different kinds of leap. The symmetrical leap involves the use of both hindlimbs simultaneously and allows maximum height and distance to be gained. The more common asymmetrical leap, used for covering shorter distances, involves the lifting of one foot off the ground and the subsequent transfer of the entire body weight to the other foot. Propulsion is then gained through extension of the weight-bearing hindlimb. Although this captive specimen of G. alleni appeared to prefer using the asymmetrical leap, it is worth noting that Charles-Dominique (1977) noted the presence of only the symmetrical leap among free-living west African galagids. Similarly, Hall-Craggs's (1964, 1965a) film record of a captive specimen of G. senegalensis reveals only the symmetrical leap. Jouffroy and coworkers offered hypotheses concerning the adaptive significance of the two different leaps that must remain interesting speculations until both behavioral patterns are actually observed in free-living animals.

Unlike the work of Jungers (1978, 1979, 1985) on the allometry of primate limb proportions, Jouffroy's work deals with static ratios of limb and limb segment length among prosimians. Jouffroy's ratios include the intermembral index, forelimb and hindlimb length relative to precaudal vertebral column length, femoral and pedal length relative to overall hindlimb length and to precaudal vertebral length, and length of the metatarsus and tarsus relative to total length of the foot; all of these comparisons were made at the generic level (Jouffroy and Lessertisseur 1979). All of the relevant indices reveal that leaping taxa (indriids, galagids, and tarsiids) have the longest hindlimbs among prosimians. The ratios involving the relative length of hindlimb segments, however, reveal interesting differences between the leaping taxa. Tarsiers and galagos, and to a lesser extent Lepilemur and cheirogaleids, have a relatively long foot as a result of lengthening of the tarsus and, in comparison to the indriids, a relatively 'short' femur. Indriids, on the other hand, owe their great hindlimb length to lengthening of the femur, and have a relatively short foot. While the tarsus of indriids lacks any semblance of the elongation that marks that of the tarsiers and galagos, the metatarsus is relatively longer in indriids than in any other prosimian family. Lemuridae and Hapalemur possess neither the extremely long femur or metatarsus of Indriidae nor the

elongated tarsus of Tarsiidae and Galagidae. Lepilemur and Cheirogaleidae possess the longest tarsal regions among Malagasy taxa, although neither approximate the extreme elongation seen in Galagidae and Tarsiidae. Lepilemur does, however, approximate the Indriidae in the overall length of the hindlimb, and this is reflected in a low intermembral index.

The data first discussed in Jouffroy and Lessertisseur (1979) were further analyzed using the multivariate technique of discriminant analysis by Oxnard and German (Oxnard, German, Jouffroy and Lessertisseur 1981). Using the same methods as in their analysis of McArdle's (1981) data on the hip and thigh of prosimians (Oxnard, German and McArdle 1981), they attempted to further investigate the existence of several behavioral and morphological modes of vertical clinging and leaping among prosimians. Their results support the hypothesis that indriid and galagid-tarsiid leaping are marked by different morphological patterns and, presumably, by different behavioral patterns. Specifically, the results of this study indicate the existence of four different clusters in multivariate space: indriids, galagids and tarsiids, cheirogaleids, and a centrally located group consisting of lemurids and lepilemurids. As in other multivariate analyses by this group (e.g., Oxnard, German and McArdle 1981; Stern and

Oxnard 1973), an inherent problem is that the individual variables that contribute to the reported discrimination are never identified. While the multivariate approach of Oxnard and coworkers provides a plausible hypothesis, it seems to involve a necessary loss of information that does not occur in the simpler bivariate analyses (Jouffroy and Lessertisseur 1979).

It is in her descriptive studies of the osteology and myology of the Lemuriformes, however, that the clearest statement of Jouffroy's position on morphological adaptations to leaping may be found (Jouffroy 1962, 1975). Concerning the indriids, clearly the most proficient Malagasy leapers, Jouffroy (1975:188) states:

"The hindlimb is very long, but the two traits most characteristic of the group, which differentiate them totally from other prosimian vertical clingers and leapers such as Galago and Tarsius, are the great length of the femur and the shortness of the tarsus."

The cheirogaleines, according to Jouffroy "the most quadrupedal of the lemurs", are also the least specialized morphologically. However, she also mentions that

"The most spectacular, if not the only, specialization lies in the elongation of the tarsus of Microcebus, a leaping adaptation which one finds, in slightly different forms, in Lepilemur and especially in Galago and Tarsius." (Jouffroy 1975:188)

While Lepilemur resembles the Indriidae in having very long hindlimbs (owing not, as in indriids to extreme femoral elongation) they also resemble Microcebus in possessing a

longer tarsus than other Malagasy prosimians. The Lemuridae and Hapalemur,

"quadrupedal runners as much as leapers in most of their characters, form a group intermediate between Cheirogaleinae and Indriidae" (Jouffroy 1975:189).

Despite these interfamilial differences, Jouffroy (1962, 1975) notes that all Malagasy Lemuriformes are linked by a series of hindlimb traits that may be related to common aspects of positional behavior. The most interesting of these are the hypertrophied M. vastus lateralis combined with the presence of a superior patella in the tendon of M. vastus intermedius. As to the functional significance of these traits, Jouffroy (1975:167) states;

"The quadriceps femoris shows clear adaptations to jumping both in the strong development of vastus externus (=lateralis) and in the limitation of the origins of the two vasti in the region of the superior femoral epiphysis, as well as in the presence of a "superior patella'".

One of the earliest workers interested in the relation between hindlimb morphology and positional behavior among the Galagidae was E.C.B. Hall-Craggs. In a series of articles, Hall-Craggs (1964, 1965a, 1965b, 1966a, 1966b, 1974) pioneered the use of a wide range of innovative approaches to this problem, including high-speed cinematography, biomechanical analysis, gross dissection and histology, and physiological and histochemical studies of muscle tissue. This eclectic approach has been very

successful in explaining the functional significance of several characteristics of the hindlimb morphology of the galagids. Indeed, the work of Hall-Craggs is the necessary starting point for any biomechanical analysis of the hindlimb among leaping prosimians.

Using film speeds of close to one thousand frames per second, Hall-Craggs (1964, 1965a, 1965b) provided the first reliable description and biomechanical analysis of the leap of Galago senegalensis. His results indicate that the typical leap of G. senegalensis is bipedal and symmetrical, with the forelimbs playing no part in the propulsive effort. The highest jump observed was an almost vertical, standing jump of slightly more than seven feet; this jump started from a position in which the animal's center of gravity was approximately one and a half inches off the ground. Hall-Craggs also determined that the area of application of force against the ground was at the tarsometatarsal joints, not the metatarsophalangeal joints (contra Shultz 1963a, 1963b). This last point is of great importance for understanding the moment arms involved in plantarflexion at the ankle, an important component of leaping. Some of the biomechanical parameters that Hall-Craggs (1965a) was able to calculate were the take-off velocity and acceleration, ground reaction force and angle, and estimates of the total force generated and the amount of shortening in the M. quadriceps femoris and M. triceps

surae, two of the primary muscle groups involved in the leap. Cinematography revealed extreme flexion of all hindlimb joints prior to the leap, followed by complete extension. Osteometric analysis (Hall-Craggs 1965b) showed that Galagidae possess a relatively long hindlimb (indicated by the low intermembral index), and an extremely long tarsus due to elongation of the calcaneus and navicular. Hall-Craggs (1966) was also the first to note the presence of a synovial joint between the distal shafts of the calcaneus and navicular, and to suggest its involvement in rotational movements of the galagid foot.

Hall-Craggs's major contribution was to offer clear suggestions as to the functional significance of the osteological characteristics of leaping prosimians. The long hindlimb is clearly an adaptation for increasing the take-off velocity and thus the maximum distance (or height) of the leap.

"The take-off velocity, upon which so much depends, is attained by the animal while it is in contact with the ground and is related to the force applied to its centre of gravity either during this time or over the distance travelled by the animal during this time" (Hall-Craggs 1974:830).

A longer hindlimb allows force to be applied to the ground, and hence to the animal's center of gravity, for a longer time (or over a greater distance) during the propulsive effort of the jump. This results in a greater take-off

velocity. Since elongation of the tarsus occurs between the fulcrum of the tibio-talar joint and the point of application of force to the ground, it effectively increases the moment arm of the load or, simply, the load arm. Since this elongation has no direct effect on the moment arm of the plantarflexor musculature (*M. triceps surae*), or the lever arm, the net effect is a lowering of the "mechanical advantage" (lever arm/load arm) of the pedal plantarflexors (Smith and Savage 1956).

Hall-Craggs followed Smith and Savage (1956) in his interpretation of the functional effects of changes in the mechanical advantage of bone-muscle systems. These authors showed that, in general, a small mechanical advantage is best for fast movements, while a large mechanical advantage is best for slow, but powerful, movements. In addition, Schultz (1963a) has shown that a small mechanical advantage, while requiring a relatively powerful muscular contraction, results in a very large distal excursion for a given contraction. Hall-Craggs (1965b) concluded that the small mechanical advantage of galagid plantarflexors allows a full excursion of the tibio-talar joint with only a minimal departure from the initial resting length of the plantarflexor muscles (mainly *M. gastrocnemius*). This allows the muscles to operate in the most favorable region of the length-tension curve (i.e., close to resting length), where near maximal forces can be generated. The

bipinnate arrangement of muscle fibers in *M. gastrocnemius* is an integral part of this adaptation (Hall-Craggs 1966a, 1974), serving to greatly increase the cross-sectional area of the muscle and, hence, its maximum force (Gans and Bock 1965). Hall-Craggs clearly understood that the galagid tarsal region represents an elegant compromise between conflicting biomechanical demands. The small mechanical advantage, brought about mainly by distal elongation of the tarsus, requires large muscular forces from the plantarflexors. These muscular forces are realized by greatly increasing the cross-sectional area of the bipinnate *M. gastrocnemius*, and by allowing it to operate at or near its resting length. The small mechanical advantage in turn allows very rapid plantarflexion through a very large arc of motion with a minimal contraction, thus maximizing take-off velocity and acceleration. The overall result is the adept leaping behavior of the Galagidae.

Hall-Craggs (1974) was responsible for the first application of histochemical techniques to questions of form and function in the locomotor behavior of prosimian primates. In this preliminary contribution, Hall-Craggs found significant differences between *G. senegalensis* and *Loris tardigradus* in the composition of muscle fibers within *M. vastus medialis*. In the former taxon, nearly all of the fibers comprising *M. vastus medialis* are of the fast

twitch, glycolytic type; fast firing muscle fibers which also fatigue quickly. *M. vastus medialis* in the slow-climbing loroid is composed of a combination of fast twitch, oxidative-glycolytic fibers (fast firing, but fatigue resistant) and slow, oxidative fibers (slow firing and fatigue resistant) (Hall-Craggs 1974). The obvious parallels between these histochemical results and the positional behavior of galagos and lorises was noted by Hall-Craggs (1974) and further investigated by Sickles and Pinkstaff (1981a, 1981b) and Ariano et al. (1973).

Ariano et al. (1973) were the first authors to investigate muscle fiber types among prosimian primates. Using histochemical techniques involving the staining of sections of muscle fibers for the presence and activity of certain enzymes, three main fiber "types" have been found among mammals: fast-twitch, glycolytic (FG); fast-twitch, oxidative-glycolytic (FOG); and slow-twitch, oxidative (SO). Physiological studies have shown that these three fiber types are characterized by differences in speed of contraction and in resistance to fatigue (fibers utilizing oxidative metabolism are more fatigue-resistant than those relying on glycogen consumption) (Burke and Tsairis 1974; Buchthal and Schmalbruch 1980). Ariano et al. (1973) provide a catalogue of fiber types for hindlimb muscles of the guinea pig, rat, cat, lesser bushbaby (*G. senegalensis*), and slow loris (*N. coucang*). As did Hall-

Craggs (1974), they too found a higher proportion of SO fibers in Nycticebus, and a preponderance of FG and FOG fibers in Galago. On the basis of uniformly high proportions of SO fibers in Mm. soleus and vastus intermedius in all five taxa, Ariano et al. (1973) argued that analogous muscles in phylogenetically distant and functionally dissimilar mammalian taxa tend to have similar muscle fiber compositions.

Sickles and Pinkstaff (1981a, 1981b) dispute this hypothesis on the basis of their histochemical studies of hindlimb muscle fiber types among Tupaia glis, G. senegalensis, and N. coucang. Their results support a functional interpretation of muscle fiber types similar to that offered by Hall-Craggs (1974). In an exhaustive study of 30 hindlimb muscles, Sickles and Pinkstaff sampled over 65,000 muscle fibers from 18 individuals and found significant differences in fiber type composition between the three taxa and between hypothesized functional muscle groups within each taxon. One of the more notable results was the fact that FG fibers were totally absent from among the muscles sampled in the slow loris. The predominant fiber type found in Nycticebus was the slow oxidative (SO), as might be predicted in a slow and cautious climber like the slow loris. The lesser bushbaby and tree shrew retain all three fiber types, but show a high proportion of FG and

FOG fibers respectively, and relatively few SO fibers in most hindlimb muscles. Several hindlimb muscles, notably Mm. soleus, vastus intermedius, gluteus minimus, and the adductors of the thigh, are characterized by a preponderance of SO fibers in all three taxa. These muscles share a mainly postural role rather than acting as propulsive muscles during locomotion (Sickles and Pinkstaff 1981b). The propulsive muscles of the hindlimb in galagos and tree shrews are mainly composed of fast-twitch fibers and provide the rapid contractions necessary for their respective saltatory and rapid quadrupedal habits. The authors conclude that muscles used for running tend to be dominated by FOG fibers while those used for jumping are characterized mainly by FG fibers, and postural muscles are composed mainly of SO fibers.

Unlike many morphological studies that attempt to distinguish between taxa known to differ in positional behavior, McArdle's (1976, 1978, 1981) work includes a closer look at the diversity within two well-established taxonomic and locomotor groups: the Lorisidae and Galagidae. While the four genera of Lorisidae are universally recognized as slow and cautious climbers, recent ecological research summarized in McArdle (1981) indicates a dichotomy among these taxa in several aspects of behavior and ecology relative to body size. Two large-bodied species (Nycticebus and Perodicticus) are mainly

frugivorous dwellers of the forest canopy, while the two smaller taxa (Arctocebus and Loris) are primarily insectivorous inhabitants of the fine-branch forest niche. McArdle's (1981) results indicate that the larger genera are characterized by relatively short limbs with extensive, distally placed muscular insertions around the hip joint. The smaller taxa have long, thin limbs with reduced and proximally positioned muscular insertions. The hamstring muscles in the two smaller genera are also endowed with long muscle-free tendons and a pinnate arrangement of muscle fibers which effectively increases their cross-sectional area. McArdle (1981) hypothesized that the functional effect of proximal muscle insertions and long muscle-free tendons in Arctocebus and Loris is to reduce the lever arms and moment of inertia of the long hindlimb of these animals, thus increasing their speed of contraction. The pinnate arrangement of hamstring muscle fibers increases the cross-sectional area of these muscles, resulting in an increased maximum force generated (Gans and Bock 1965). Conversely, the large genera (Nycticebus and Perodicticus) may be maximizing the mechanical advantage and strength of hindlimb extension and flexion by increasing the moment arms of hip and thigh musculature through more distal insertions of these muscles.

McArdle's (1976, 1981) analysis of the Galagidae indicates the presence of morphological diversity relating to a spectrum of locomotor behavior among the six species of the genus. Behavioral analysis (summarized in McArdle 1981) places G. senegalensis and G. alleni at one extreme (most proficient leapers) and G. demidovii and G. crassicaudatus at the other (most quadrupedal). McArdle (1981) found morphological differences in overall body proportions and in the myology and osteology of the hip and thigh that correlate with the behavioral patterns among the Galagidae. With respect to limb proportions, the more proficient leapers are characterized by lower intermembral indices, relatively longer hindlimbs and pedal skeletons, and shorter forelimbs. Species at the quadrupedal end of the spectrum are characterized by more distal insertions of many of the muscles that cross the hip joint. This fact is also reflected in several of the osteological markers of muscle insertions, including the lesser and third trochanters (insertions of M. iliopsoas and Mm. tensor fasciae femoris and gluteus superficialis, respectively), which are both placed further distally relative to femoral length. Also, the ischium is shorter, tarsal elongation is greater, and the M. vastus lateralis is larger among the more specialized leaping galagos.

McArdle (1981) presents a strong argument for considering many of these traits as adaptations for leaping among the galagids. With respect to the great length of the hindlimb, he states:

"Since the muscular force (acceleration) required to achieve takeoff velocity in a leap is inversely proportional to the distance over which the force is applied (approximately equal to the length of a fully extended hindlimb), it is expected that the more proficient leaping galagos would have relatively longer hindlimbs." (McArdle 1981:58)

Speaking specifically of tarsal elongation, McArdle (1981:114) further states:

"In particular, a relatively longer tarsus is advantageous during leaping since it provides a bony lever to which the muscular force produced during extension of the hindlimb can be applied before losing contact with the substrate and also provides further elongation of the entire hindlimb."

More proximal muscular insertions of the major propulsive muscles of hip and thigh among the specialized leapers results in smaller lever arms for these muscles, and a lowered mechanical advantage. Hypertrophy of the *M. vastus lateralis* is also best interpreted as a leaping adaptation given its demonstrated importance in initiating the leap among lemurs (Jungers et al. 1980).

Ward and Sussman (1979) investigated the positional behavior and hindlimb anatomy of closely related species within the genus *Lemur* (*L. fulvus* and *L. catta*).

The value of studies of closely related taxa, in which

phylogenetic differences are controlled for, is clearly stated by the authors:

"Detailed analysis of subtle anatomical variations in congeneric but behaviorally distinct animals will be useful in identifying relationships between form and function, and the dynamics of morphological speciation in the fossil record " (Ward and Sussman 1979:576).

Sussman's (1974, 1975) observations of free-living L. fulvus and L. catta have in fact established that the behavioral repertoires, habitat preferences, and substrate utilization patterns of the two lemurids differ significantly. Lemur fulvus spends the overwhelming majority of its feeding and travel time high in the continuous forest canopy, while L. catta is most often found on the ground or in the lower, discontinuous parts of the canopy. Lemur fulvus generally runs along mostly horizontal terminal branches, while L. catta climbs along large oblique branches and jumps across gaps in the canopy. Lemur catta was never observed to engage in vertical clinging and leaping (contra Napier and Walker 1967).

The anatomical part of this study includes univariate and multivariate analyses of forty three measurements of the hindlimb skeleton, dissections of four cadavers of each species, and some preliminary investigations of joint mobility and bone density. The results indicate the existence of several significant morphological differences between the two species that may be related to the

behavioral differences noted above. L. catta possesses a longer femur, tibia, and fibula than L. fulvus, but the latter species exhibits a greater degree of mobility in flexion-extension of the leg and in inversion-eversion of the foot. In these aspects of joint mobility, the differences between L. fulvus and L. catta parallel those between arboreal and terrestrial cercopithecines (Ward and Sussman 1979). Dissections revealed that L. catta has a relatively larger group of leg flexor muscles, while the musculature devoted to eversion and inversion of the foot is more extensive in L. fulvus.

Ward and Sussman (1979) suggest that the longer hindlimb of L. catta may be related to terrestrial cursorial travel: an equally valid suggestion would relate the longer hindlimb to the ring-tailed lemur's penchant for saltation in the trees. The authors mention the increased mass moment of inertia that accompanies the increased length of the hindlimb in L. catta. In fact, since mass moment of inertia increases proportionally to the fifth power of length, even a small increase in length can greatly affect hindlimb biomechanics (Ward and Sussman 1979). They suggest that increased mass moment of inertia may be responsible for the more extensive femoral attachment of *M. flexor cruris lateralis* in L. catta, allowing deceleration of the femur at the end of hindlimb extension. The greater mobility and muscle mass devoted to eversion and inversion of the foot

in L. fulvus appears to be an arboreal adaptation, allowing greater variety of pedal postures in the variable and irregular arboreal habitat (Ward and Sussman 1979; Cartmill 1972, 1974a, 1974b). In summary, the authors note the relevance of form-function analyses of closely related species to the reconstruction of the behavior of extinct taxa:

"Ultimately our ability to extract paleoecological relationships from fossils is dependent upon the degree to which differences in behavior can actually be identified in the morphology of living closely related species, and at what level of precision" (Ward and Sussman 1979:576).

1.6. Summary

The VCL hypothesis states that extant vertical clinging and leaping prosimians share a suite of morphological adaptations that can be found among Eocene prosimians, indicating that this behavior is the precursor to all later forms of positional behavior among the primates. The three major aspects of the VCL hypothesis can be labeled behavioral, morphological, and evolutionary. The critical response to this controversial hypothesis may have raised more questions than it answered. Behavioral variability among extant leaping prosimians led Stern and Oxnard (1973) to suggest the existence of two or more kinds of prosimian leaper. Similarly, the presence of morphological variability among both extant and extinct "leaping"

prosimians has been suggested by several authors, including Stern and Oxnard (1973), Cartmill (1972), Godfrey (ms.), and Szalay (1972). Problems with the morphological definition of vertical clinging and leaping among extant prosimian leapers were mentioned by each of these authors as being a serious barrier to the reconstruction of the positional behavior of extinct prosimians.

For the purposes of this dissertation I tentatively accept the behavioral aspect, and include in the extant VCL group all members of the families Indriidae, Tarsiidae, and Galagidae, as well as the genus Lepilemur. My goal is to test the morphological assertions of the VCL hypothesis on the basis of the morphology of the prosimian hindlimb. Although I do not explicitly test the evolutionary predictions, my results have clear implications for the reconstruction of the positional behavior of extinct primates. These implications are discussed in chapter 8.

A consideration of the previous morphological work on prosimian leapers (discussed in section 1.5.) indicates several patterns of analysis that reappear in my own research. Ward and Sussman (1979) and McArdle (1981) demonstrate the value of anatomical studies of closely related species with observably different patterns of positional behavior. Using, for the most part, traditional methods of analysis, these authors have looked for subtle morphological correlates of behavioral differences in

species of the genera Lemur and Galago. Although subtle, the anatomical differences are demonstrable, and often fit predictions based on known behavioral differences between taxa.

Standard techniques of osteometric analysis have been used by most of the authors cited in this chapter. When interpreted in the light of biomechanics, as exemplified by the work of Hall-Craggs (1965b), ratios of simple osteological measurements are easily interpretable and can provide much solid information. Interpretation of the results of multivariate analyses of osteometric data can be difficult, as is clearly seen in the work of Oxnard and his coworkers (Oxnard, German, Jouffroy and Lessertisseur 1981; Oxnard, German and McArdle 1981).

Attempts to understand the roles played by hindlimb muscles in various kinds of positional behavior include discussions of moment arms, moments of inertia, and the composition of muscle fibers. Jungers's analysis of M. quadriceps femoris of L. fulvus is notable for its elegant use of both dissection and telemetered electromyography to test functional hypotheses relating this muscle group to leaping (Jungers et al. 1980). Building on a theoretical base provided by the work of Gregory (1912) and Smith and Savage (1956), Hall-Craggs (1964, 1965a, 1965b) and McArdle (1981) discuss the functional biomechanics of changing

muscle lengths and attachment sites. Histochemical and physiological analyses of variation in fiber types reveal some interesting differences between prosimians of differing locomotor types, especially leapers and slow climbers (Hall-Craggs 1974; Sickles and Pinkstaff 1981a, 1981b; Ariano et al. 1973).

Standard appendicular indices of prosimian limb proportions have been an important part of many analyses of leaping prosimians, most notably in those of Jouffroy (Jouffroy and Lessertisseur 1979) and McArdle (1981). Since certain limb proportions (e.g., intermembral and brachial index) were among the original traits of VCLs defined by Napier and Walker (1967), their import to this analysis is clear. Allometric analysis provides additional information and fosters a better understanding of the patterns observed in ratios of limb proportions. Jungers's (1976, 1978, 1979, 1985) regression analyses illustrate variations in the relative length of limbs and their segments that are not apparent in analyses of standard appendicular indices.

As stated above, the major goal of this dissertation is to test the morphological aspect of the VCL hypothesis: namely, that extant leaping prosimians share a series of morphological traits related to their mode of positional behavior. While I have used many of the same methods and approaches used by other authors, the scope of this research is broader than most of these studies insofar as

my subject is the entire suborder. Many of the patterns noted in the work of previous authors are echoed in my research. Thus, while comparing the three families (and Lepilemur) of vertical clingers and leapers with quadrupedal taxa, I also discuss differences within genera (e.g., Lemur and Galago) and among genera of the same family. Osteometric data are analyzed by simple ratios and by multivariate analysis (multiple discriminant function analysis), and the results from these different methods are compared. Changes in the mechanical advantage of bone-muscle systems as a result of changes in muscular attachment sites are discussed along with their functional significance. A series of standard appendicular indices is computed that allows comparison of several measures of the relative lengths of hindlimb and forelimb segments among all prosimians. Finally, regression analysis is used to examine scaling patterns and allometry in both the hindlimb and forelimb.

Chapter 2. Locomotion, Diet and Habitat

2.1. Introduction to Chapter 2

Comparative analysis of the morphology of extant prosimians, if divorced from the ecological and behavioral milieu of the living animal, is surely a sterile and unsatisfying pursuit. By its very nature, functional anatomy involves correlation of morphological patterns with specific behaviors (e.g., locomotor or postural, dietary, agonistic) that can be observed in the field. In this chapter I review the data on diet, locomotion, and habitat preferences of prosimian primates. The underlying assumption is, of course, that behavioral variation can be associated in biomechanical terms with morphological variation in the lower limb. While it is clear that a simple one-to-one relationship between locomotor behavior and lower limb morphology should not be assumed a priori (Stern and Oxnard 1973), it is equally clear that a great deal of morphological variation can be explained by reference to differing patterns of locomotion and habitat utilization (Ward and Sussman 1979; Fleagle 1976, 1977). The behavioral data presented here have been collected by means of an extensive literature search, not from any original field observations of my own. I have however spent numerous hours watching many species of prosimian primate in captivity at several zoos and primate centers in this country.

2.2. Tupaiidae

There are five commonly recognized genera (Tupaia, Anathana, Urogale, Dendrogale, Ptilocercus) and approximately fourteen species in the Tupaiidae (Yates 1984; Roonwal and Mohnot 1977; Napier and Napier 1967; Hill 1953). Tree shrews range from India and South China through most of Southeast Asia, but, unlike Tarsiidae, never cross Wallace's Line (Jenkins 1974). Their taxonomic position and phylogenetic affinities have been for many years the subject of much controversy among anthropologists (see Luckett 1980 for a recent overview). Some authorities classify tree shrews as primates (Jones 1929; Walker 1964; Clark 1971; Simpson 1945), some as insectivores (Gregory 1951; Luckett 1980; Thorington and Anderson 1984; Van Valen 1965; McKenna 1966; Szalay 1968, 1969; Petter and Petter-Rousseaux 1979; Campbell 1974; Martin 1968; Hill 1953) and others would place them in their own order, Scandentia (Yates 1984; McKenna 1975). In a series of classic papers, Le Gros Clark (1924a, 1924b, 1925, 1926) established a series of anatomical similarities between tupaiids and lemurid primates. This evidence was used by Clark, Simpson (1945), and others to argue for inclusion of the Family Tupaiidae within the primates. While the work of George (1977) confirms Clark's anatomical findings, most modern workers explain these similarities as primitive retentions (Luckett 1980; Thorington and Anderson 1984; Szalay 1968,

1969; Campbell 1974) or as convergent adaptations to arboreality (Martin 1968), and hence of no value in formulating taxonomic hypotheses. Lockett's (1980) work on the embryology and placental relations of tupaiids provides definitive evidence of the non-primate nature of these interesting animals.

Regardless of their taxonomic status, tupaiids have long been considered, on the basis of proposed similarity in locomotor behavior and morphology with the earliest primates, to be good structural ancestors of modern primates (Clark 1971; Gregory 1951; Simpson 1945; Jenkins 1974). Additionally, as Jenkins (1974) argues, the arboreal and terrestrial variability in tupaiid locomotion may lead to insights concerning the extent of the arboreal adaptation of the earliest primates. For these reasons, and yet with taxonomic caveats, tupaiids are included in this study.

While tupaiids have not been intensively studied in the wild, they appear widely distributed throughout the primary and secondary tropical rain forests of Southeast Asia (Hill 1955). They are variably adapted to both arboreal and terrestrial habitats, all species being adept at locomotion both on the ground and in the trees, but the percentage of time spent in these two habitats varies between species. D'Souza (1974) notes that Tupaia minor is an arboreal claw-climber, unable to utilize the fine-branch milieu because

it lacks prehensile hands and feet. D'Souza (1974:173) characterizes the locomotion of T. minor as the "rapid running and hopping type", and stresses the importance of claws in climbing vertical supports. Roonwal and Mohnot (1977) describe the locomotion of Anathana ellioti and T. glis as a squirrel-like, rapidly scurrying type of above-branch quadrupedalism. All authors agree that while tupaiids are mainly insectivorous, they do on occasion eat some plant material (Roonwal and Mohnot 1977).

2.3. Tarsiidae

Hill (1955) follows Pocock (1918) in assigning Tarsiidae, along with the Anthropoid primates, to the Grade Haplorhini. Explaining most of the anatomical and behavioral similarities between tarsiers and strepsirhines as primitive retentions, both authors link tarsiers with higher primates on the basis of the shared derived condition of the rhinarium. This area of skin at the tip of the muzzle, including the upper lip and nasal region, is naked and associated with facial vibrissae and a functional organ of Jacobson in most generalized mammals and prosimian primates (Andrew and Hickman 1974). In tarsiers and anthropoid primates (the grade Haplorhini), the naked rhinarium is replaced by normal hairy skin, reduced vibrissae, and a vestigial organ of Jacobson. Additionally, the slit-like narial opening found in primitive mammals and strepsirhine primates is replaced in the Haplorhini by a

completely fused external narial opening (Hill 1955). Because this investigation is concerned with functional rather than evolutionary or taxonomic questions, however, the inclusion of the Tarsiidae is clearly warranted, whether one classifies them as haplorhines (Hill 1955; Petter and Petter-Rouseaux 1979) or prosimians (Napier and Napier 1967; Simpson 1945). Their status as vertical clingers and leapers par excellence makes them an integral part of any anatomical study of leaping among primates.

Three species of the genus Tarsius are presently recognized (Hill 1955; Niemitz 1984c; Napier and Napier 1967; Wolfheim 1983). They are found on many Southeast Asian islands stretching from the Philippines in the northeast (T. syrichta) to Sulawesi (T. spectrum), Borneo, Java and Sumatra in the southwest (T. bancanus). Their distribution is interesting in that it transgresses Wallace's Line, a fact that is "indicative of some considerable antiquity" according to Hill (1955:230). The best studied species remains T. bancanus (Fogden 1974; Niemitz 1979a, 1984a, 1984b, 1984d), while the behavior of T. spectrum in the wild is essentially unknown. All three species of tarsier are quite similar in postcranial anatomy, minor differences in limb proportions notwithstanding (Niemitz 1979b). Except where noted, the behavioral data summarized here refer to T. bancanus.

The diet of T. bancanus on Borneo comprises only animal prey, and includes both invertebrates (locusts, ants, beetles, cicadas) and vertebrates (birds, bats, snakes) (Niemitz 1984d). Tarsiers are most commonly found in the lowest 2 or 3 meters of both primary and secondary growth in inland and coastal tropical rain forests. Fogden (1974:160) states that T. bancanus is

"found to occur only in forest understorey with an abundance of vertical supports, particularly in the form of saplings 2-6 cm in diameter and 1-2 m apart. They apparently avoided very dense tangled vegetation, the forest canopy in general, and areas of relatively open secondary vegetation with few saplings and a dense herbaceous cover."

Tarsiers are perhaps the most specialized and proficient vertical clingers and leapers among the primates (Napier and Walker 1967). According to Niemitz (1979b:124),

"Tarsius bancanus in Borneo is an extreme nocturnal leaper... more than ninety five percent of all the locomotor activity of adult individuals takes place in the form of bipedal jumps from vertical to vertical support."

The great majority of this locomotor activity takes place between 0.3 and 3 meters above the ground (Niemitz 1979b). Napier and Walker (1967) similarly mention the tarsier's propensity for clinging to and leaping between vertical supports in the forest, and hopping bipedally when on the ground. They note that the tail is usually pressed against the vertical support during clinging postures, but trails inertly during active leaping. Upon landing, the

hindlimbs appear to contact the substrate before the forelimbs. Based on slight interspecific morphological variation and some behavioral data, Niemitz (1979b) speculates that the three species of Tarsius form a behavioral spectrum with respect to leaping ability from T. bancanus (most gifted leaper) to T. spectrum (least gifted leaper).

2.4. Lemuridae

Following Tattersall (1982), I recognize only two genera in Lemuridae, Lemur and Varecia. While Varecia is a monotypic genus (V. variegata), Lemur contains six extant species (L. catta, L. coronatus, L. macaco, L. mongoz, L. fulvus, and L. rubriventer), all of which are represented in my skeletal sample. The great majority of the "true lemurs" in this sample are, however, from the species L.catta and L. fulvus.

Lemur catta is found in the dry, deciduous forests of south-western Madagascar and in the semi-arid, xerophytic bush of the southern tip of the island (Tattersall 1982). Its diet is entirely vegetarian and varied, including the leaves, flowers, fruits, and buds of as many as 24 plant species (Jolly 1966). At Berenty in the arid southwest, where L. catta has been best studied (Sussman 1974, 1975, 1977; Jolly 1966), the pod of Tamarindus indicus, the kily tree, is an important year-round staple (Jolly 1966). Sussman (1974, 1975) mentions that L. catta prefers bush

and scrub forests of 3-7 meters in height, and utilizes all layers of the forest for travel and feeding. Lemur catta is the most terrestrial of the lemurs, using the ground mainly for travel through open areas of its habitat (Rand 1935; Sussman 1974, 1975; Jolly 1966). Its mode of arboreal locomotion is a combination of above-branch quadrupedalism and leaps between branches, characterized by Sussman (1974:86) as "a series of runs and leaps, in each case running up an oblique branch and leaping down to another." Jolly (1966) states that travel on the ground is usually in the form of quadrupedal running or galloping, with some bipedal hopping for short distances. While Jolly (1966:27) mentions that L. catta occasionally is seen leaping between vertical branches, she states that it does not "cling and rest on vertical trunks as Propithecus does."

Lemur fulvus includes seven distinct geographic subspecies found along the east and west coasts of Madagascar and on the island of Mayotte in the Comoro archipelago (Tattersall 1982). Rand (1935) made brief observations on the locomotion of three subspecies (L.f. albifrons, L.f. collaris, and L.f. rufus). He noted that while above-branch quadrupedalism was the preferred mode of locomotion, in the absence of horizontal branches, L. fulvus often leapt between vertical supports in a manner

reminiscent of the locomotion of indriids. Recent field studies include those of Harrington (1975) on L.f. fulvus, Sussman (1974, 1975) on L.f. rufus, and Tattersall (1977) on the Mayotte subspecies L.f. mayottensis. These studies present a uniform picture of the diet, habitat, and locomotor behavior of L. fulvus.

All three subspecies are entirely arboreal, preferring the upper reaches of the forest canopy for both feeding and travel. That they rarely come to the ground is indicated by Harrington (1975), who found that L.f. fulvus spends less than two percent of its time there. In Sussman's (1974, 1975) study area, L.f. rufus required continuous closed canopy deciduous forest of 7-15 meters in height, often dominated by the kily tree, Tamarindus indicus. The entirely vegetarian diet of L. fulvus is composed of leaves, buds, bark, fruit, and flowers. L.f. rufus appears to have a very restricted diet; Sussman (1974, 1975) found that 85% of its feeding time was spent on only three plant species. The other subspecies have more varied diets (Harrington 1975; Tattersall 1977). All three authors confirm Rand's (1935) description of the locomotion of L. fulvus. Harrington (1975:262), speaking of L.f. fulvus, states:

"L. fulvus moved primarily on horizontal branches, but also moved quite readily on vertical or oblique branches or vines. They also progressed by vertical clinging and leaping between tree trunks less than 30 cm in diameter."

Similarly, Tattersall (1977:470) states that while quadrupedal above-branch walking and running are clearly the preferred locomotor modes for L.f. mayottensis, the animals

"showed no aversion to moving through the avocet marron forest by leaping between vertical trunks... with great alacrity and agility."

The remaining species of the genus Lemur are substantially less well studied in their natural habitats. Lemur mongoz is found in a small area of northwest Madagascar and on the Comorian islands of Moheli and Anjouan (Tattersall 1982), and was the subject of a brief field study by Tattersall and Sussman (1975) at Ampijoroa in northwest Madagascar. It prefers the high canopy (10-15 meters) of wet, montane forest, where it feeds mainly on fruit, nectar, and perhaps pollen (Tattersall and Sussman 1975). Its locomotor pattern has been described by Tattersall and Sussman (1975) as basically similar to that of L. fulvus. The most common type of locomotion is rapid, above-branch quadrupedalism on small to medium sized horizontal and oblique branches. Jumps between horizontal and oblique supports are commonly used to cross gaps in the canopy. Vertical supports are rarely used, however, in either clinging postures or jumping. Lemur macaca is found in the wet, montane forests of the northwest coast of Madagascar, while L. rubriventer is found in dense rain

forests of the eastern coast of Madagascar. Both are poorly known but are said to be similar to L. fulvus in locomotion (Tattersall 1982). Finally, L. coronatus is restricted to the dry forests on the northern tip of Madagascar and has yet to be the object of a field study. Tattersall (1982:174) has stated that L. coronatus, like L. catta, "spends a substantial amount of time on the ground."

In addition to the six species of the genus Lemur, Lemuridae includes Varecia variegata, which is found in much of the wet forest of the eastern coast of Madagascar (Tattersall, 1982). Rand (1935:99) observed that the locomotion of V. variegata usually consisted of "walking along horizontal branches or springing from limb to limb". Tattersall (1982:175) states that in spite of its larger body size, V. variegata is "no less agile" in the trees than is Lemur. In addition to confirming a general pattern of above-branch quadrupedalism, Tattersall (1982:302) mentions that Varecia is unique among prosimians in the extent to which it relies on bipedal suspension in the trees, and that, with regard to its diet:

"No systematic observations have been made on the feeding behavior of Varecia. Petter et al. (1977) claim them to be frugivorous, which agrees with inferences from their dental morphology".

2.5. Cheirogaleidae

Tattersall (1982) includes five genera in the lemuriform family Cheirogaleidae. A complete lack of

access to skeletal representatives of three of these taxa (Allocebus trichotis, Mirza coquereli, Phaner furcifer) resulted in their absence from this study. Fortunately, the two genera that are included (Cheirogaleus and Microcebus) are well represented in museum collections, and relatively well studied in the field.

Species of Cheirogaleus and Microcebus are found throughout the forested regions of both eastern and western Madagascar (Tattersall 1982). Both C. major and M. rufus range throughout most of the eastern forest zone of Madagascar, and are sympatric in many areas. Cheirogaleus medius and M. murinus are found along the length of the western coast of the island, and are again often found in sympatry. During the most complete field study of any cheirogaleid, Martin (1972:52) discovered that M. murinus preferred to frequent what he called the

"fine branch niche... (made up of) relatively dense foliage zones containing large numbers of fine branches, narrow lianes, etc."

Martin (1972) discovered that vertical stratification of M. murinus populations in nature was determined by this preference for the fine branch niche. In undisturbed primary forest the fine branch niche may be as high as thirty meters, while in disturbed secondary growth it is often found at ground level. This preference for the fine branch niche explains why M. murinus is usually found high

in primary forests and at ground level in secondary. While Petter (1962, 1978) stated that M. murinus is primarily insectivorous, Martin (1972) discovered that less than 50% of the total diet of this species was composed of insects, and that a substantial portion of its diet was made up of fruit, flowers, and even leaves. Cheirogaleus, while less well studied in the wild than Microcebus, appears to have a diet composed mainly of fruit and gums, with some insects and leaves (Tattersall 1982; Petter 1962, 1978).

Several authors have described cheirogaleid locomotion as above-branch, arboreal quadrupedalism (Petter 1962; Napier 1976; Walker 1967). In their locomotor classification, Napier and Walker (1967:385) classified the Cheirogaleidae in the category and sub-type they called "quadrupedalism, branch running and walking type", which includes "climbing, springing, branch running and jumping". Martin (1972) noted that the great locomotor versatility of M. murinus is perhaps slighted by simply calling them "quadrupeds." In addition to slow and rapid above-branch quadrupedalism, Martin (1972:54) also found M. murinus to be capable of leaps of up to 3 meters, and of

"hopping over the ground in frog-like fashion (i.e., largely based on thrusts with the hindlimbs, but not fully bipedal)."

In evolutionary terms, Martin (1972:54) concluded that the extreme locomotor versatility of M. murinus, involving elements of both slow and rapid arboreal quadrupedalism and a tendency towards hindlimb-dominant activities, "may well represent a retention of the ancestral primate condition."

2.6. Lepilemuridae

While some taxonomists lump Hapalemur with the Lemuridae (Hill 1953; Petter and Petter-Rousseaux 1979), I follow Tattersall's (1982) classification and recognize the family Lepilemuridae as including the genera Lepilemur and Hapalemur. Lepilemur mustelinus, the only species in this genus recognized by Tattersall (1982), is widely distributed in the coastal forests of Madagascar, including the dry southern and northern extremes. Lepilemur possesses both morphological (enlarged caecum with bacterial flora) and behavioral (caecotrophy and low activity level) adaptations to a folivorous diet of extremely poor quality (Hladik and Charles-Dominique 1974; Hladik 1979). Tattersall (1982) recognizes two species in the genus Hapalemur, H. griseus and the extremely rare H. simus. The former includes a very common eastern subspecies (H.g. griseus), a western subspecies with only two known populations, both found in bamboo forests (H.g. occidentalis), and an extremely rare subspecies that has been found only in the reed marshes around Lac Alaotra (H.g. alaotrensis) (Tattersall 1982). Hapalemur simus is

known from only one site in the humid forest east of Fianarantsoa in the central part of the eastern coastal zone. All species of Hapalemur are herbivorous, often preferring bamboo shoots when available (Hladik 1979; Petter and Peyrieras 1975), while H.g. alaotrensis is said to feed on the pith and buds of papyrus and other leaves and shoots (Petter and Peyrieras 1975).

The locomotion of Lepilemur appears to be most similar to that of the Indriidae among other Malagasy taxa. Its preference for vertical supports, both at rest and during locomotion, has been confirmed by all authors who have personally observed Lepilemur in the field (Rand 1935; Petter 1962; Hladik and Charles-Dominique 1974). Tattersall (1982:176) described its locomotor behavior as follows:

"Sportive lemurs rarely come to the ground, but when there they get around almost invariably by hopping bipedally. In the trees they seem to travel in leaps almost exclusively, between vertical supports wherever possible.... Propulsion in leaping is provided solely by the hindlimbs, which leave the initial support last, but which then contact the landing support before the forelimbs."

Hapalemur griseus exhibits a kind of locomotion that is intermediate between the arboreal quadrupedalism of lemurids and cheirogaleids and the vertical clinging and leaping of Lepilemur and the indriids. Petter and Peyrieras (1975:283) state

"Like all lemurids, it (Hapalemur) can run quickly on the ground....The long hindlimbs and feet allow it to jump considerable distances from one vertical support to another."

Similarly, Tattersall (1982:175) states that individuals of H. griseus

"have been recorded as walking along horizontal and oblique branches, as well as clinging to and leaping between vertical supports. On the ground gentle lemurs generally move quadupedally rather than by hopping, but they can leap considerable distances between both horizontal and vertical supports."

2.7. Indriidae

The Madagascan Family Indriidae contains the genera Avahi, Indri, and Propithecus, all of which are represented in the skeletal sample of this study. Indriidae are widely recognized as the most specialized vertical clingers and leapers of all the Lemuriformes (Napier and Walker 1969; Tattersall 1982). They are found in a variety of forested habitats throughout the coastal zones of Madagascar, and are entirely vegetarian in diet.

Indri indri has the distinctions of being the largest of the lemurs and the only prosimian lacking a tail (Hill 1953). It is a diurnal creature with a very restricted distribution. Indri appears confined to humid montane forests in northeastern Madagascar, where it has been studied by Pollock (1975, 1977) and by Petter and Peyrieras (1974). Indri is frugivorous and folivorous, eating a wide variety of fruits, flowers, and leaves (Pollock 1975,

1977). Pollock (1975, 1977) found that Indri feeds in all levels of the forest (2-40 meters), usually in the terminal branch zone, but rarely comes to the ground. Pollock (1975) also noted that Indri uses both horizontal and oblique branches while moving or resting in primary forests: in secondary or disturbed forests it relies almost exclusively on vertical supports. Vertical postures and hindlimb-propelled leaps between vertical supports, however, are always preferred (Tattersall 1982; Pollock 1975, 1977; Petter and Peyrieras 1974).

Propithecus, another large-bodied, diurnal lemur, has been well studied in both humid gallery forests of western Madagascar and in the semi-arid bush of the south (Jolly 1966; Richard 1977, 1978). Tattersall (1982) recognizes two species in this genus, each with a number of geographic races or subspecies. P. diadema, the eastern species, contains five subspecies which are dispersed along the entire eastern coastal forest zone of Madagascar, but are not found in the dry south. P. verreauxi is composed of four subspecies which are distributed along the western coast and in the semi-arid southern sector. Nowhere are P. diadema and P. verreauxi found in sympatry.

Like Indri, Propithecus is an extremely proficient arboreal leaper. Leaps routinely cover distances as great as ten meters between vertical supports (Jolly 1966). While the preferred supports during locomotion and resting

are clearly vertical, Propithecus often uses horizontal and oblique supports during feeding, much of which takes place in the terminal branches of the forest canopy (Richard 1977, 1978; Jolly 1966). Propithecus rarely comes to the ground for feeding or travel, preferring to remain high (10-20 meters) in the canopy. Jolly (1966) found that populations of P. verreauxi at Berenty in southern Madagascar have a diet composed of the leaves, flowers, and fruits of twenty one plant species. The most popular food item at Berenty was the kily fruit (Tamarindus indicus). No insects or other animal matter have been reported to be part of the diet of Propithecus or of any other indriid.

Avahi laniger, of which Tattersall (1982) recognizes two subspecies, has yet to be the subject of a field study. Avahi laniger laniger is the eastern subspecies, broadly distributed along much of the eastern coastal forest but not in the far north of the island. The western subspecies, A.l. occidentalis, is confined to a restricted area of the northwestern coast. While nocturnal and of much smaller body size than either Indri or Propithecus, A. laniger is by all accounts an equally adept leaper.

2.8. Lorisidae

It is customary to distinguish between lorises and galagos at either the familial (Hill 1953) or more commonly, the subfamilial level (Napier and Napier 1967;

Petter and Petter-Rousseaux 1979; Wolfheim 1983). I follow Hill (1953) in recognizing the families Lorisidae and Galagidae within the superfamily Lorioidea. Lorisidae then includes two African (Arctocebus and Perodicticus) and two Asian (Loris and Nycticebus) genera. An interesting ecological parallel exists between the African and Asian lorises. On each continent, one genus (Arctocebus or Loris) is a small-bodied, insectivorous form that inhabits the fine-branch forest niche, while the other genus (Perodicticus or Nycticebus) is larger, omnivorous, and resides high in the forest canopy (Hladik 1979; Charles-Dominique 1974, 1977). All of the lorises are considered by Napier and Walker (1969) to be slow and cautious arboreal quadrupeds.

The Asian lorises have yet to be the subject of intensive ecological or behavioral studies. Loris tardigradus, the small Asian lorisid, inhabits the fine-branch niche of tropical rain forests of Sri Lanka and southern India (Roonwal and Mohnot 1977). Analyses of feces and of stomach contents show that the diet of L. tardigradus is mainly insectivorous, consisting of caterpillars, beetles, and orthopterans (Hladik 1979). Nycticebus coucang is widely distributed throughout southeast Asia from India to Thailand and along the island chains of Malaysia, Indonesia, and the Philippines (Roonwal and Mohnot 1977). It is typically found high in the canopy

in the densest part of the tropical forest, seldom venturing to the ground (McArdle 1981; Roonwal and Mohnot 1977). The diet of N. coucang is poorly known but appears to be omnivorous, including fruits, leaves, insects, bird eggs, and small birds (Hladik 1979; Roonwal and Mohnot 1977). The extremely rare and poorly studied N. pygmaeus is restricted to parts of Vietnam and Laos and is not represented in the skeletal sample employed in this study.

Arctocebus calabarensis and Perodicticus potto, the African members of the family Lorisidae, have been studied in nature to a much greater extent than have their Asian counterparts. They are distributed throughout the tropical rain forests of west and central Africa and have been observed in sympatry (along with three species of Galago) in Rio Muni (Jones 1969; Sabater Pi 1972), Nigeria (Jewell and Oates 1969), and Gabon (Charles-Dominique 1974, 1977; Charles-Dominique and Bearder 1979).

The smaller of the two African lorisisids, A. calabarensis, resembles L. tardigradus in several ecological traits (McArdle 1981). Like Loris, Arctocebus prefers the fine branch niche, being most commonly found near the ground (0-5 meters) in the dense undergrowth of disturbed secondary growth (Charles-Dominique 1974, 1977). Arctocebus also closely resembles Loris in its mainly insectivorous diet. Charles-Dominique (1974) found that

the diet of A. calabarensis in Gabon is composed of 85% small animal prey and 15% fruit. In contrast, the larger bodied P. potto prefers the upper reaches of the forest canopy in both primary (10-30 meters) and secondary (5-15 meters) forests. Perodicticus relies on a variety of support orientations and support diameters during arboreal travel and rarely comes to the ground (Charles-Dominique 1974, 1977; Jones 1969; Sabater Pi 1972). The omnivorous diet of these animals may be related to their larger bodily size (Hladik 1979). Again in Gabon, Charles-Dominique (1974, 1977) found that P. potto has a varied diet composed mainly of fruit supplemented by gums, insects and other small animal prey, and some leaves.

All lorises engage in a slow and cautious brand of arboreal quadrupedal locomotion that is unique among the primates. Relying on powerful manual and pedal prehension, lorises climb through the arboreal habitat in a quiet and deliberate manner that may be an adaptation for avoidance of visually-directed predators (Charles-Dominique 1977) or a cryptic means of hunting small animal prey (Hladik 1979). Since they rarely come to the ground and cannot leap across gaps in the forest canopy, lorises often take tortuous routes in search of a continuous pathway between trees (McArdle 1981; Charles-Dominique 1977). In his discussion of Arctocebus and Perodicticus, Charles-Dominique (1977:69) clearly describes the lorisid locomotor pattern:

"These animals are exclusive climbers, never leaping from one support to another... and always supported by at least two limbs on opposite sides of the body and the center of gravity is thus always located between the two points of support. This stability, combined with the power of the hands and feet, permits very slow movements during which the animal is never in a state of imbalance."

Descriptions of the locomotion of the Asian lorises are essentially identical to those of the African taxa.

Roonwal and Mohnot (1977:53) state that Loris

"moves along branches in a slow and deliberate manner. But it is incapable of jumping or hopping even short distances from branch to branch."

As for N. coucang, the same authors state that "it is a quadrupedal and a slow but ready climber, but it does not leap" (Roonwal and Mohnot 1977:59).

2.9. Galagidae

Most authorities today recognize two genera and five species within the Family Galagidae. The nominate genus contains four species (Galago alleni, G. crassicaudatus, G. demidovii, and G. senegalensis), while the genus Euoticus is monotypic (E. elegantulus). Just as disagreement exists as to the level of separation between bushbabies and lorises (i.e., subfamilial or familial level), there are different viewpoints concerning the lower-level taxonomy of the Galagidae. Some authors would split G. demidovii into the genus Galagoides (Hill 1953; Hall-Craggs 1965b), while others would lump Euoticus with the genus Galago (Napier

and Napier 1967; Petter and Petter-Rousseaux 1979). Perhaps the most unorthodox ideas on bushbaby systematics are those of Olson (1979), who would allocate G. crassicaudatus to two species of the genus Otolemur (O. crassicaudatus and O. garnetti). I shall follow the more conservative route of recognizing four species of the genus Galago and a single species of Euoticus (Simpson 1945; Wolfheim 1983; Walker 1964).

Galago alleni, G. demidovii, and E. elegantulus are usually found in sympatry with each other and with the lorisiid taxa A. calabarensis and P. potto in mature tropical rain forests of west and central Africa. They have been the objects of behavioral study by various workers in Gabon (Charles-Dominique 1974, 1977), Nigeria (Jewell and Oates 1969), and Rio Muni (Sabater Pi 1972; Jones 1969). Charles-Dominique's (1974, 1977) extremely detailed studies in Gabon are our most complete and most reliable source of information on the diets, habitats, and positional behaviors of these three taxa. Except where specifically noted, the following discussion is based upon the work of Charles-Dominique (1974, 1977).

In Gabon, G. alleni is normally found at or near ground level (0-2 meters) in the undergrowth of wet, primary tropical forests. In both postural and locomotor activities, G. alleni exhibits a strong preference for

vertical supports of small to medium diameter. Movement between these supports is usually in the form of rapid bipedal leaps. Charles-Dominique (1977:109) states that individuals of G. alleni move "almost exclusively by leaping between thin trunks and the bases of lianes, passing at great speed from one vertical support to another." In addition to its great skill at vertical clinging and leaping, G. alleni is also a very proficient quadrupedal runner, both along branch tops and on the ground. Through observation and analysis of gastric contents, Charles-Dominique (1974) established the mainly frugivorous and carnivorous nature of the diet of G. alleni (75% fruit, 25% animal matter). Prey items include "medium-sized beetles, slugs, moths, frogs, ants, orthopterans, termites, millipedes, pupae and caterpillars" (McArdle 1981:41). In addition to its use in locomotion, leaping is an important means of catching mobile prey in the arboreal habitat of G. alleni (McArdle 1981; Hladik 1979; Charles-Dominique 1974, 1977).

All who have studied G. demidovii in west Africa agree that the smallest of the bushbabies appears tied to dense foliage zones of the tropical rain forest. Both Jones (1969) and Jewell and Oates (1969) found G. demidovii low to the ground (below 10 meters) in the dense undergrowth of secondary forest. While confirming this in Gabon, Charles-Dominique (1974, 1977) noted that in primary forest, where

the dense foliage zone is found high in the forest canopy, G. demidovii is most often found at a height of between 10 and 30 meters. Clearly then, the fine branch niche itself rather than the canopy height or forest type, is the main determinant of the vertical distribution of G. demidovii. Charles-Dominique notes that the preferred supports during both locomotor and postural activities are very small-diameter foliage and lianes, approximately 50% of which are vertical. Again the best data on the diet of G. demidovii are found in the work of Charles-Dominique (1974, 1977) in Gabon, and are nicely summarized by Hladik (1979). The available data clearly indicate the insectivorous nature of G. demidovii: its diet is composed of insects (70%) fruits (20%) and gums (10%) (Charles-Dominique 1974, 1977; Charles-Dominique and Bearder 1979). These results have been confirmed by the investigations of Jewell and Oates (1969) on Nigerian populations of the species.

Jewell and Oates (1969) found the needle-clawed bushbaby, Euoticus elegantulus, at varying heights in the canopy of secondary forest, but rarely close to the ground. Charles-Dominique (1974, 1977), however, found E. elegantulus exclusively high in the canopy (15-35 meters) in the primary forests of Gabon. In Nigeria, Jewell and Oates (1969) found these animals to be mainly

insectivorous. Jones (1969) concurred on the basis of their seemingly 'short' digestive tract. Although he noted a substantial amount (20%) of small-animal prey in the diet of Euoticus in Gabon, Charles-Dominique (1974, 1977) found these animals to be mainly gummivores, with a diet composed mainly (75%) of the gums and saps of trees. Euoticus elegantulus relies on two well known anatomical specializations in its utilization of this excellent source of structural carbohydrate. The first is the dental comb, formed by the lower incisors and canines, which is used in puncturing tree bark and scraping the dried saps and gums that issue forth. The other is the uniquely keeled nails which function as claws and allow E. elegantulus to climb up and down vertical tree trunks of large diameter and to remain clinging to these vertical supports for long periods of time while feeding (Hill 1953; Cartmill 1974a, 1979).

As is briefly mentioned above, G. alleni is among the most specialized vertical clingers and leapers among the Galagidae. It prefers vertical supports and uses these to great advantage in rapidly leaping from one place to another, pivoting at great speed around the landing support as it prepares to take off again. Galago alleni attains a low trajectory during flight, and holds its body nearly horizontally. As it approaches the landing support, the tail is rapidly whipped downward and the trunk is pulled up to a vertical position, allowing the hindlimbs to contact the

substrate first and, presumably, to absorb most of the forces involved in landing. Horizontal distances of 2.5 meters can be covered with no loss in height (Charles-Dominique 1974, 1977). While G. alleni is a capable quadrupedal runner, it rarely runs, preferring to leap almost exclusively during locomotor activities.

In contrast to G. alleni, G. demidovii, appears to run and leap in roughly equal proportion, although not with equal facility or skill. Charles-Dominique (1977) states that G. demidovii is the best quadrupedal runner and the poorest leaper among the galagos. The most common form of locomotion used by the species in Gabon is quadrupedal running along the tops of horizontal supports. During quadrupedal locomotion the hindlimbs are used mainly for propulsion, while the forelimbs provide support and, with the tail, aid in the maintenance of balance. Some leaping is done from supports of all orientations, usually with a very low trajectory and a horizontal trunk in midflight. Landing is always initiated by, and most of the landing forces are absorbed by, the forelimbs. Charles-Dominique (1974, 1977) observed leaps of up to 1.5 meters in distance with no loss of height. It is interesting to note that Walker's (1974) study of captive G. demidovii indicated a very slight preference for leaping over quadrupedal running in an artificial arboreal setting.

While it also runs and leaps in roughly equal proportions, E. elegantulus appears unlike G. demidovii in being an excellent leaper and a relatively poor quadrupedal runner. Its posture in midflight is unique among the bushbabies. The trunk is kept nearly vertical during flight, allowing all four limbs to contact the substrate simultaneously on landing. Euoticus elegantulus uses large diameter supports of varying orientations to leap from, and is often seen to jump downward in a steep trajectory. Its large hands and tactile pads, in addition to the keeled nails, allow the maintenance of a powerful grip on vertical arboreal supports of large diameter. These adaptations allow E. elegantulus access to parts of the arboreal habitat that are unavailable to most other small primates (Cartmill 1974a, 1979). Charles-Dominique (1974, 1977) observed horizontal jumps of 2.5 meters with no loss of height.

Galago senegalensis and G. crassicaudatus are both distributed widely throughout the woodlands and grasslands of eastern and southern Africa. Wolfheim (1983:15) states that G. crassicaudatus

"is found in eastern and southern Africa. from southern Somalia to eastern South Africa and west to the Atlantic coast of Angola".

Galago senegalensis has an even more extensive distribution, being

"found throughout sub-Saharan Africa except in the Congo-Zaire River basin, the upper Guinea coast, and the southern tip of the continent" (Wolfheim, 1983:26).

Notwithstanding a brief study in Kenya (Nash 1983), most of our knowledge of the behavior and ecology of these taxa comes from work done in southern Africa. Both G. senegalensis and G. crassicaudatus have been the objects of intensive observation and analysis by Bearder (Bearder and Doyle 1974; Doyle and Bearder 1977; Charles-Dominique and Bearder 1979) in Zimbabwe (formerly Rhodesia) and by Crompton (1980a, 1980b, 1984) in the northern Transvaal. While G. senegalensis and G. crassicaudatus are found sympatrically in both eastern and southern Africa, they exhibit different habitat preferences. Bearder states that G. senegalensis appears better adapted to drier, open deciduous vegetation while G. crassicaudatus prefers "humid subtropical evergreen forests where trees bearing fleshy fruits are abundant" (Charles-Dominique and Bearder 1979:605). This conclusion has been amply confirmed by both Crompton (op. cit.) and Nash (1983). The work of Crompton is perhaps unique in the behavioral literature for its comprehensive treatment of seasonality in the life cycles of primate species. Unlike many field studies in which the animals are observed during a small part of the yearly round, Crompton's involved an entire year of observing G. senegalensis and G. crassicaudatus. In addition, his

collection and analysis of data on locomotion, diet, and habitat usage were designed to answer questions and test hypotheses relating to seasonal differences in resource availability and the resultant evolutionary pressures on the animals. Crompton's interesting results are of great relevance to this analysis of morphological and locomotor differences between prosimian taxa, and will be discussed below at some length.

Bearder's work in Zimbabwe shows G. senegalensis to be an extremely adaptable species living in a wide range of habitats between sea level and fifteen hundred meters; these include:

"semi-arid, steep-sided valleys, open woodland, orchard bush or scrub and isolated thickets with grassland" (Bearder and Doyle 1974:110).

Galago senegalensis, however, is most commonly found in Acacia thornveld; relatively open woodland-grassland dominated by the thorn tree, Acacia karoo. At times G. senegalensis penetrates riparian or montane forests, and it is usually in these settings where it is found in sympatry with G. crassicaudatus (Doyle and Bearder 1977). While G. senegalensis may be found as high as twelve meters, it generally inhabits the lower six meters of forest canopy, and frequently comes to the ground.

Within the arboreal habitat, G. senegalensis appears to utilize with equal facility broad supports of large diameter and small branches and trunks (Bearder and Doyle

1974). Nash (1983) and Crompton (1980a) note, however, a preference for small-diameter supports, while all investigators agree that vertical supports are used very frequently in both locomotor and postural activities. Bearder notes three fundamental types of locomotor behavior of both the lesser and the greater bushbabies: "jumping, hopping, and walking/climbing" (Doyle and Bearder 1977:13). Galago senegalensis most frequently jumps bipedally, often between vertical supports in the arboreal habitat. It also quite competently walks and runs in the trees, and is often observed moving quadrupedally above or below horizontal supports and climbing up and down vertical supports. When on the ground, G. senegalensis typically uses a kangaroo-like series of bipedal hops to move across gaps between trees or while foraging for insects.

All authors agree that the diet of G. senegalensis is mostly insectivorous, supplemented by the ingestion of tree gums, especially Acacia gum. Hladik (1979:332), discussing the seasonal importance of gums in the diet of both G. senegalensis and G. crassicaudatus, states that "both species of Galago rely on gums as the main source of energy, at least in winter, when fruits and insects are scarce." Galago senegalensis preys on insects, relying on its acute vision and hearing and extremely quick hands to catch insects in flight while in the trees, and

terrestrial insects while foraging on the forest floor.

Galago crassicaudatus occupies a number of different habitats both along the coastal zone and in the highlands, from sea level to about eighteen hundred meters in elevation (Bearder and Doyle 1974). It shows, however, more limited habitat preferences than G. senegalensis, being "mainly confined to dense evergreen indigenous forest and riparian bush" (Bearder and Doyle 1974:110), where the two species are at times found in sympatry. Although G. crassicaudatus is also found in cultivated fields and relatively open woodlands, it generally prefers wetter habitats than does G. senegalensis. Galago crassicaudatus is also usually found higher in the forest canopy than is G. senegalensis. It prefers the horizontal arboreal supports of large diameter that are commonly found between five and ten meters in the canopy (Crompton 1980a), and only rarely comes to the ground for foraging or travel between trees. Gaps between trees are usually negotiated by climbing or "bridging", and only rarely by jumping or descending to the ground.

A comparison of the locomotor behavior of G. crassicaudatus and the other species of the genus Galago points out the anomalous character of the former species. Bearder notes that while all galagos appear morphologically adapted to a saltatory mode of locomotion,

"The behavior of G. crassicaudatus belies its anatomical structure and provides an interesting exception to the general rule" (Charles-Dominique and Bearder 1979:605).

Indeed, some authors have tended to link the locomotor style of G. crassicaudatus more with that of the slow-climbing Lorisidae than with that of the vertical clinging and leaping Galagidae. Galago crassicaudatus most commonly climbs quadrupedally, running and walking along the tops of horizontal and oblique supports of large diameter. While all authors agree that G. crassicaudatus is quite capable of bipedal jumping, it does so only rarely. When on the ground, G. crassicaudatus most commonly engages in a clumsy sort of quadrupedal gallop involving the simultaneous motion of fore- and hindlimbs, and rarely engages in the bipedal hopping common among other bushbabies. Bearder and Doyle (1974:119) state that the primary arboreal locomotor technique of G. crassicaudatus is "quadrupedal running with occasional short jumps, or longer ones between trees", while its secondary mode is "slow, stealthy and quiet movement, sometimes beneath a branch".

The diet of G. crassicaudatus tends to be more varied than that of the primarily insectivorous G. senegalensis. While exhibiting a heavy reliance on gums throughout the year and on fruits in the summer, G. crassicaudatus supplements its diet with a variety of flowers, seeds, insects, and other small-animal prey. Doyle and Bearder

(1977) suggest that the most important limiting factor on the distribution of G. crassicaudatus is the availability of fruit, while Hladik (1979) stresses the importance of the year-long presence of gums, especially in the winter, when fruit is scarce in the highly seasonal environments that these animals typically inhabit.

Crompton's (1980a, 1980b, 1984) analysis of seasonality in the foraging strategy and ecology of G. senegalensis and G. crassicaudatus provides some interesting insights into the environmental pressures that these animals face, and the adaptive strategies that allow them to thrive in spite of these pressures. Crompton notes that G. senegalensis appears to undergo substantial seasonal changes in foraging behavior in its open and fairly dry habitat. During the summer months, the lesser bushbaby acquires the great proportion of its insect diet in the forest canopy. It relies on the "cantilevering strategy" also used so successfully by G. demidovii and E. elegantulus in western Africa (Charles-Dominique 1977), to capture insects in flight. "Cantilevering" involves maintaining a grasp with the hindlimbs on the substrate, leaping after a flying insect and grasping it with the forelimbs, and then returning to the original position. Through this entire maneuver, the hindlimbs never lose their grip on the substrate. Flying insects are much more scarce in the winter months and G. senegalensis must then rely to a

greater extent on gums (Hladik 1979) and on foraging on the ground for insects. Crompton (1980b) describes the foraging behavior of G. senegalensis as random and "birdlike", involving rapid movement between different food sources with no apparent regularity or discernable pattern. Galago crassicaudatus, in contrast, undergoes only slight changes in foraging behavior as a result of seasonal environmental change. Like G. senegalensis, it relies to a greater extent upon gums in winter, owing to the relative paucity of fruits, but continues to forage along regular arboreal routes, visiting the same gum and fruit sites night after night, often in the same order. In general, it does not make substantial changes to its seasonal routine.

Crompton then proceeds to tie these ecological differences to the body size and energetic requirements of the two species. On the one hand, G. senegalensis, with its small body size and rapid, saltatory locomotion and random foraging pattern, is subject to very high energetic requirements that seemingly must be met by a high-quality diet composed mainly of insects. On the other hand, G. crassicaudatus, with its large body size, slow and cautious locomotion, and regular foraging pattern can afford a lower quality, mainly frugivorous diet. An alternative explanation views the locomotor differences between the greater and the lesser bushbabies as different strategies

for predator avoidance. According to this explanation, G. crassicaudatus assumes a typically lorisid, passive or cryptic approach to the avoidance of predators. Not coincidentally, this strategy would almost certainly be more successful in a relatively closed canopy, and may explain why G. crassicaudatus appears less well adapted to open environments than G. senegalensis. Conversely, the lesser bushbaby takes a typically galagid, active predator avoidance strategy involving rapid, saltatory locomotion. This strategy allows G. senegalensis to inhabit relatively open environments. Certainly, these two points of view are not mutually exclusive.

2.10. Summary

This review of the diet, locomotion, and habitat preferences of Prosimii makes clear the great ecological diversity in the Suborder. While trends and correlations between aspects of prosimian ecology do exist, no simple patterns emerge from the observed diversity. In a discussion of "the nature and predictability of (the) relationship between primate diet and locomotion", Fleagle states:

"In animals with extreme dietary diversity and very flexible locomotor repertoires living in an extremely complex three-dimensional environment, we should be very lucky if we found any semblance of order at all" (Fleagle 1984:113).

In terms of locomotor patterns, the three groups of Napier and Walker (1967) make good sense as a first

approximation of the diversity among the prosimian primates. Thus we have the slow climbers, predominantly leaping forms, and the arboreal quadrupeds. Certainly the most distinct group in a behavioral sense consists of the slow-climbing Lorisidae; the leapers and the quadrupeds form a behavioral continuum of sorts in which intermediate forms (e.g., Hapalemur sp., M. murinus, G. crassicaudatus, and G. demidovii) engage in some combination of quadrupedalism and vertical clinging and leaping.

The animals classified by Napier and Walker (1967) as vertical clingers and leapers are distributed throughout Southeast Asia (Tarsiidae), sub-Saharan Africa (Galagidae), and Madagascar (Indriidae and Lepilemur). While leaping primates are usually said to be small-bodied (Napier and Walker 1967; Fleagle 1985), the Indriidae, and especially the genera Indri and Propithecus, are exceptions to this generalization. Furthermore the tiny mouse lemur, M. murinus, is at most a part-time leaper, while the smallest of the galagids, G. demidovii, is one of the more quadrupedal bushbabies. Fleagle (1985) argues that leaping is more common among small arboreal mammals for several mechanical reasons. Small animals are more frequently faced with gaps in the forest canopy that must be negotiated by leaps, while larger animals can often use suspension or bridging techniques to cross gaps. Small animals are also

more likely to find supports able to sustain the forces directed against them by the animal during leaping. Fleagle (1985) concludes that size-related differences in locomotor behavior may be viewed as adaptive responses which allow animals to inhabit similar environments and maintain functional equivalence in spite of physical constraints imposed by differences in body size. In contrast, gross differences in body size may be adaptive responses which allow entirely new locomotor adaptations and the utilization of different habitats and/or substrates.

Similar patterns emerge from considerations of dietary diversity among prosimians and from correlations between diet, body size, and locomotor pattern. Since many leaping prosimians are small primates, and since many small primates are insectivores (Kay and Covert 1984; Fleagle 1984), one might expect many leapers to be insectivorous. A consideration of the data on diet among prosimian leapers indicates, however, a full spectrum of dietary preferences including the totally insectivorous/carnivorous Tarsiidae, omnivorous Galagidae, herbivorous Indriidae, and folivorous Lepilemur. Fleagle (1984) states that the best example among primates of a clear correlation between a specific diet and a positional behavior is the ingestion of gums or other tree exudates among taxa adapted to vertical clinging. This correlation characterizes several prosimians (E. elegantulus, Phaner furcifer, G. senegalensis) and some

New World Platyrrhines (Cebuella and Saguinus), and is usually associated with

"a suite of common morphological adaptations (specifically small size, and either claw-like tegulae or pointed nails) which permit such postural abilities" (Fleagle 1984:110).

With respect to habitat and substrate preferences among leaping prosimians, perhaps the most that can be said is that the habitat of vertical clingers and leapers is generally dominated by the presence of vertical supports (Stern and Oxnard 1973). While these are often present in the understorey of tropical Asian forest in the guise of lianes, vines, and branches, they may also be present in the forest canopy of Madagascar or in the Acacia thornveld of South Africa.

Chapter 3 Materials and Methods

3.1. Data Collection: Materials

Table 1 lists the number of post-cranial skeletons of each species measured in this study, while Table 2 provides a list of the taxonomic abbreviations that were used. A total of 277 specimens representing 8 families and 16 genera were measured and analyzed. All specimens are in the Mammalogy collections at either the American Museum of Natural History in New York (AMNH), the United States National Museum of Natural History in Washington, D.C. (USNM), or the Museum of Comparative Zoology at Harvard University, Cambridge, Massachusetts (HMCZ). Whenever possible, specimens were limited to wild-shot, fully adult, not visibly pathological individuals. Owing to the relative paucity of prosimian skeletons in U.S. museums, however, (especially compared to the number of skins and skulls), these strictures were at times relaxed. While specimens with visible bony pathologies were never measured, some young adults (adult dentition erupted but some epiphyses unfused) and some lab and/or zoo animals were used. The decision to use these specimens was made if they looked normal and were from a rare taxon. Overall, nearly 75% of the 277 skeletons were wild-shot. The sexes were pooled in all analyses since prosimians do not exhibit significant postcranial sexual dimorphism, and because many museum specimens are of unknown gender.

Table 1. Specimen List.

TAXA	AMNH	USNM	HMCZ	TOTAL
Tupaiaidae				20
<u>Tupaia sp.</u>	8	12	0	20
Tarsiidae				8
<u>Tarsius sp.</u>	4	3	1	8
Lemuridae				41
<u>L. catta</u>	5	0	0	5
<u>L. coronatus</u>	1	0	0	1
<u>L. fulvus</u>	18	0	0	18
<u>L. rubriventer</u>	0	0	2	2
<u>L. sp.</u>	3	0	0	3
<u>V. variegata</u>	7	2	3	12
Cheirogaleidae				26
<u>C. major</u>	1	2	3	6
<u>M. murinus</u>	15	0	5	20
Lepilemuridae				38
<u>H. griseus</u>	4	5	7	16
<u>H. simus</u>	0	0	1	1
<u>L. mustelinus</u>	21	0	0	21
Indriidae				25
<u>A. laniger</u>	3	3	3	9
<u>I. indri</u>	3	0	1	4
<u>P. verreauxi</u>	7	0	2	9
<u>P. diadema</u>	1	0	2	3
Lorisidae				54
<u>A. calabarensis</u>	3	1	0	4
<u>L. tardigradus</u>	7	2	1	10
<u>N. coucang</u>	7	9	4	20
<u>P. potto</u>	10	9	1	20
Galagidae				65
<u>G. alleni</u>	1	2	0	3
<u>G. crassicaudatus</u>	10	14	0	24
<u>G. demidovii</u>	7	1	0	8
<u>G. senegalensis</u>	21	8	0	29
<u>E. elegantulus</u>	1	0	0	1
Totals	168	73	36	277

Table 2. List of taxonomic abbreviations.

Tupaiidae	TUP
<u>Tupaia sp.</u>	Tup
Tarsiidae	TAR
<u>Tarsius sp.</u>	Tar
Lemuridae	LEM
<u>L. catta</u>	L.cat.
<u>L. coronatus</u>	L.cor.
<u>L. fulvus</u>	L.ful.
<u>L. rubriventer</u>	L.ruf.
<u>V. variegata</u>	Var
Cheirogaleidae	CHE
<u>C. major</u>	Che
<u>M. murinus</u>	Mic
Lepilemuridae	LEP
<u>Hapalemur sp.</u>	Hap
<u>L. mustelinus</u>	Lep
Indriidae	IND
<u>A. laniger</u>	Ava
<u>I. indri</u>	Ind
<u>Propithecus sp.</u>	Pro
Lorisidae	LOR
<u>A. calabarensis</u>	Arc
<u>L. tardigradus</u>	Lor
<u>N. tardigradus</u>	Nyc
<u>P. potto</u>	Per
Galagidae	GAL
<u>G. alleni</u>	G.all.
<u>G. crassicaudatus</u>	G.cra.
<u>G. demidovii</u>	G.dem.
<u>G. senegalensis</u>	G.sen.
<u>E. elegantulus</u>	G.ele.

3.2. Data Collection: Measurements

All of the osteological measurements reported here were taken by me, the great majority while using Mitutoyo dial calipers calibrated to 0.05mm. Some long bones of the larger animals had to be measured with an osteometric board, and all long bone lengths were rounded to the nearest millimeter. Figures 1 and 2 show the anatomical points that define the measurements taken, as well as some other important landmarks, of the femur, pelvis, and calcaneus. These points are named and the measurements described in Tables 3 through 8. Several general considerations played important roles in the selection of the thirty osteological measurements used in this study. The ease, or indeed possibility, of consistently identifying landmarks and hence of accurately replicating measurements was always an important consideration. Several measurements were abandoned during data collection as a result of poor reproducibility. In addition, many measurements had a clear functional or biomechanical connection to the use of the lower limb during positional behavior. Some measurements were made in attempts to test specific ideas of other workers on correlations between hindlimb anatomy and behavior. More specifically, there were five general classes of measurement used in this study:

1. Long bone lengths were obtained for the analysis of limb proportions and of skeletal allometry. These include the maximum lengths of femur, tibia, radius, and humerus.
2. Joint surface morphology measures include height and breadth of the head of the femur, length of the pubic symphysis and height and breadth of the femoral condyles.
3. Biomechanical features measuring the distance of the insertions of various muscles to joint centers include the length of the ischium, pubis and ilium, the trochanters of the femur, and the posterior calcaneal length and load arm length in the tarsus.
4. Tarsal elongation, an important trait of some saltatorial prosimians, is gauged in all of the tarsal measurements.
5. General size, shape, and robusticity measures of hindlimb and pelvic bones include the width of the femoral neck, shaft, and greater trochanter, lengths of the iliac crest and ischio-pubic ramus, and total and dorso-ventral length of the pelvis.

3.3. Data Analysis: Ratios and Regressions

One of the simplest ways of correcting for isometric (but not allometric) aspects of variation in size involves the use of ratios (Oxnard 1978; McArdle 1981). In this study a total of 41 ratios were calculated in the analysis of the osteology of the femur (7), pelvis (20), tarsus (5), and of limb proportions (9) (see Tables 9-12). The BMDP (Dixon 1981) package of statistical programs was used in the analysis of these data. All analyses were performed on the Control Data Corporation Cyber 170/750 computer at the Academic Computing Center, University of Washington. Prior to calculating ratios, the data were initially screened and described with BMDP program 7D, "Description of groups with histograms and analysis of variance" (Dixon 1981). Variables

were grouped by family, genus, and for polytypic genera like Lemur and Galago, by species. The data were checked for outliers and for large deviations from univariate normality. The inherent limitations of biological samples drawn from museum collections can create problems in statistical analysis. Small and uneven sample sizes, ontogenetic and geographic variation, and non-random sampling are just a few sources of potential problems. With these limitations in mind, minor deviations from normality were not unexpected, and indeed did occur. Since many statistical techniques assume normally distributed data, the biologist faces a dilemma. A conservative approach might be to throw out data that deviate from normality, or to use only statistical techniques that make no assumptions concerning the distribution of the data. A more practical approach, and the approach taken in this study, is to be aware of marked deviations from normality if and when they occur, but in the event of reasonable approximations to the normal distribution, to use the standard statistical techniques and methods of analysis. Examination of the histograms indicated that most of the hindlimb variables in monotypic taxa represented by samples of reasonable sizes do approximate the normal distribution.

All ratios were calculated and analyzed using the BMDP 7D program, which plots histograms, calculates descriptive

statistics, and provides pairwise t-tests for all variables and groups. The skeletal trunk length (STL) of Biegert and Maurer (1972) was used as the denominator in many of the ratios used in this study. STL has been shown to be highly correlated with bodily size in both catarrhine (Biegert and Maurer 1972), and prosimian primates (Jungers 1979), and as such is here used as an estimator of bodily size. Ratios with STL as the denominator are attempts to measure the relative length of hindlimb bones or segments free of the effects of differences in bodily size. The length of the femur is also frequently used as a denominator, mainly in ratios involving pelvic and femoral variables. In most of these ratios, the numerator is a measure of a muscular lever arm, while femoral length is used as an approximation of the load arm of the lever. Consequently, these ratios are approximations of the mechanical advantage of a particular bone-muscle lever system. The tarsal ratios are all attempts to quantify the degree and nature of tarsal elongation which is such a striking characteristic of some prosimians. Some of the limb proportion ratios are standard appendicular indices, while others measure the relative length of the long bones and fore- and hindlimbs relative to skeletal trunk length. Comparisons were carried out at several different taxonomic levels, including family, genus and species. The discussion of each ratio begins at the family and proceeds to genus and species.

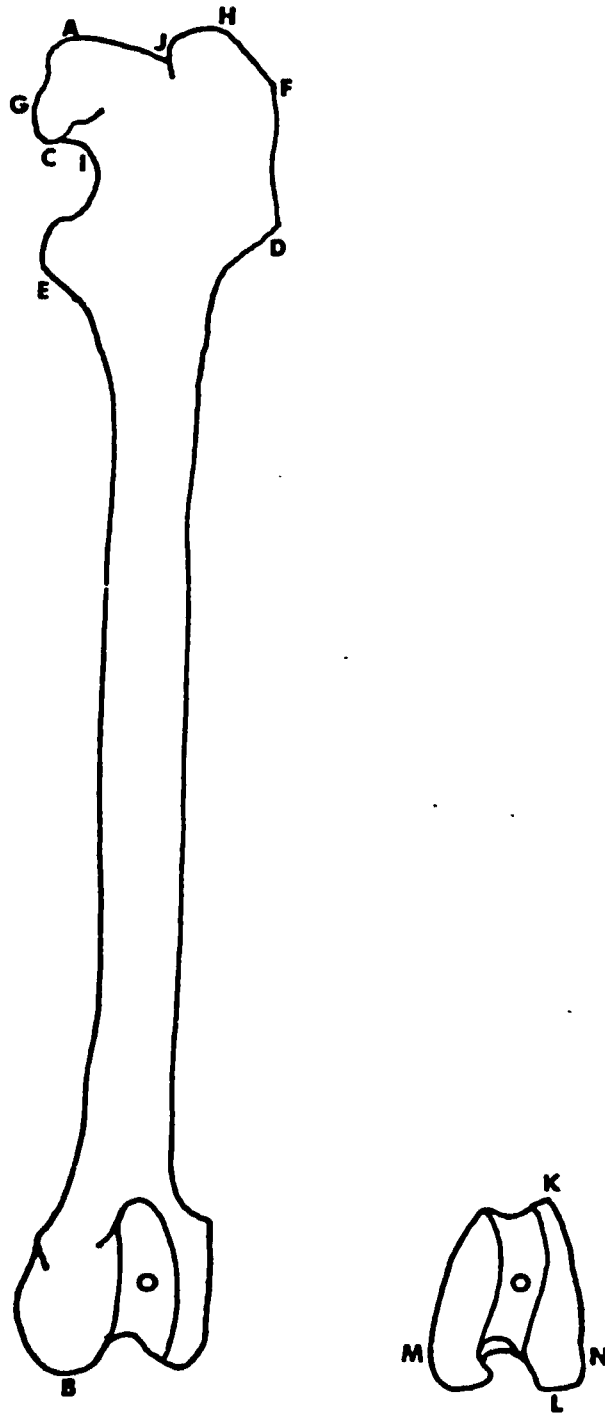


Figure 1. Anatomical points of measurement on left femur. Ventral and distal views. See Table 3 for description.

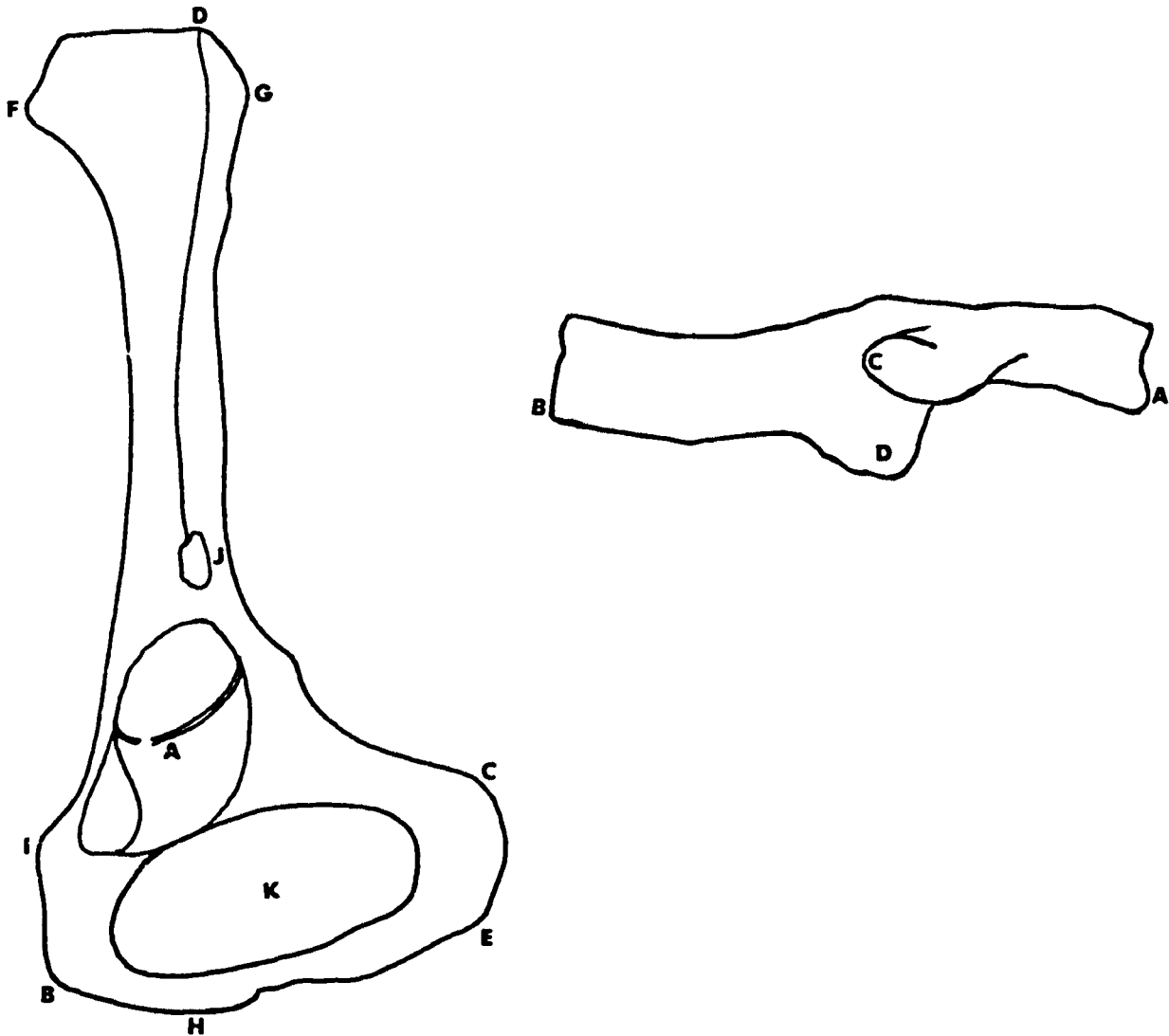


Figure 2. Anatomical points of measurement on right pelvis (lateral view) and calcaneus (superior view). See Tables 4 and 7, respectively, for description.

Table 3. Anatomical Points on the Femur.

- A. Most proximal point on femoral head.
- B. Most distal point on femoral condyles.
- C. Most distal point on femoral head.
- D. Most distal point on third trochanter.
- E. Most distal point on lesser trochanter.
- F. Most lateral point on greater trochanter.
- G. Most medial point on femoral head.
- H. Most proximal point on greater trochanter.
- I. Most distal non-articular point on neck.
- J. Most proximal non-articular point on neck.
- K. Most ventral point on femoral condyles.
- L. Most dorsal point on femoral condyles.
- M. Most medial point point on femoral condyles.
- N. Most lateral point on femoral condyles.
- O. Patellar groove.

Table 4. Anatomical points on the pelvis.

- A. Anatomical center of acetabulum.
- B. Ischial tuberosity.
- C. Most proximal point on pubic symphysis.
- D. Most proximal point on iliac crest.
- E. Most distal point on pubic symphysis.
- F. Posterior superior iliac spine.
- G. Anterior superior iliac spine.
- H. Most distal point on ischio-pubic ramus.
- I. Ischial spine.
- J. Anterior inferior iliac spine.
- K. Obturator foramen.

Table 5. Femoral Measurements.

1. Femoral length. Maximum length of femur from horizontal plane of femoral condyles to most proximal point of femur. Measured between points A and B or points H and B.
2. Height of femoral head. Maximum proximo-distal length of femoral head. Measured between points A and C.
3. Breadth of femoral head. Maximum ventro-dorsal length of femoral head. Points of measurement not pictured.
4. Distal extent of third trochanter. Maximum distance from most proximal point of femoral head to most distal point of third trochanter. Measured between points A and D.
5. Distal extent of lesser trochanter. Maximum distance from most proximal point of femoral head to most distal point of lesser trochanter. Measured between points A and E.
6. Diameter of femoral neck. Maximum proximo-distal length of non-articular area of femoral neck. Measured between points I and J.
7. Head-greater trochanter length (1). Maximum distance from most medial point of femoral head to most lateral point of greater trochanter in a plane perpendicular to femoral shaft. Measured between points F and G.
8. Diameter of femoral shaft. Maximum ventro-dorsal width of femoral shaft, taken at midlength. Points of measurement not pictured.
9. Ventro-dorsal length of femoral condyles. Maximum ventro-dorsal length of femoral condyles. Measured between points K and L.
10. Medio-lateral length of femoral condyles. Maximum medio-lateral length of femoral condyles. Measured between points M and N.
11. Width of greater trochanter. Maximum ventro-dorsal width of greater trochanter, taken on lateral aspect of femur. Points of measurement not pictured.
12. Head-greater trochanter length (2). Maximum distance from distal and medial point of femoral head to most proximal point of greater trochanter. Measured between points C and H.

Table 6. Pelvic Measurements.

1. Ischial length. Maximum length of the ischial ramus from center of acetabulum to most caudal point on ischial tuberosity. Measured between points A and B.
2. Pubic length. Maximum length of the superior pubic ramus from the center of the acetabulum to the most cranial point on the pubic symphysis. Measured between points A and C.
3. Iliac length. Maximum length of the ilium from the center of the acetabulum to the most cranial point on the iliac crest. Measured between points A and D.
4. Pubic symphyseal length. Maximum cranio-caudal length of pubic symphysis. Measured between points C and E.
5. Ventro-dorsal pelvic length. Maximum length of the pelvis between the ischial tuberosity and pubic symphysis. Measured between points B and C.
6. Iliac crest length. Maximum ventro-dorsal length of iliac crest. Measured between points F and G.
7. Pelvic length. Maximum length of pelvis from the ischiopubic ramus to the iliac crest. Measured between points D and H.
8. Ischiopubic ramus length. Maximum length of ischiopubic ramus from the ischial tuberosity to the most distal point of the pubic symphysis. Measured between points B and E.

Table 7. Anatomical points on the calcaneus.

- A. Most posterior point on the calcaneal tuberosity.
- B. Most anterior point on cuboid articular surface.
- C. Most anterior point on lateral talar facet.
- D. Sustentaculum tali.

Table 8. Tarsal Measurements.

1. Calcaneal length. Maximum length of the calcaneus. Measured between points A and B.
2. Anterior calcaneal length. Length from cuboid articular surface to most anterior point of lateral talar facet. Measured between points B and C.
3. Posterior calcaneal length. Length from calcaneal tuberosity to most anterior point of lateral talar facet. Measured between points A and C.
4. Calcaneo-cuboid length. Maximum length of articulated calcaneus and cuboid. Points of measurement not pictured.
5. Length of cuboid. Maximum length of cuboid bone. Not pictured.
6. Length of navicular. Maximum length of navicular bone. Not pictured.
7. Load arm length. Maximum length from most anterior point on lateral talar facet to most anterior point on cuboid. Measured on articulated calcaneus and cuboid, not pictured.

Table 9. Femoral Ratios. See Table 5 for a description of the numbered measurements on the femur.

<u>Ratio Names</u>	<u>Measurements</u>
F1. Relative Femoral Length	1/STL
F2. Hip Flexor Index	5/1
F3. Gluteal Index	4/1
F4. Condylar Index	9/10
F5. Femoral Head Index	2/3
F6. Greater Trochanter Index 1	7/1
F7. Greater Trochanter Index 2	12/1

Table 10. Tarsal Ratios. See Table 8 for a description of the numbered tarsal measurements.

<u>Ratio Name</u>	<u>Measurements</u>
T1. Calcaneal Index	3/2
T2. Mechanical Advantage	3/7
T3. Relative Calcaneal Length	1/STL
T4. Relative Cuboid Length	5/STL
T5. Relative Navicular Length	6/STL

Table 11. Pelvic Ratios. See Table 6 for a description of the numbered pelvic measurements.

<u>Ratio Names</u>	<u>Measurements</u>
P1. Relative Ischial Length 1	1/STL
P2. Relative Ischial Length 2	1/7
P3. Relative Ischial Length 3	1/3
P4. Ischial Mechanical Advantage	1/Femoral length
P5. Relative Pubic Length 1	2/STL
P6. Relative Pubic Length 2	2/7
P7. Relative Pubic Length 3	2/3
P8. Pubic Mechanical Advantage	2/Femoral length
P9. Relative Iliac Length 1	3/STL
P10. Relative Iliac Length 2	3/7
P11. Pubic Symphysis Length 1	4/STL
P12. Pubic Symphysis Length 2	4/7
P13. Dorso-Ventral Pelvic Length 1	5/STL
P14. Dorso-Ventral Pelvic Length 2	5/7
P15. Ischiopubic Ramus Length 1	8/STL
P16. Ischiopubic Ramus Length 2	8/7
P17. Iliac Crest Length 1	6/STL
P18. Iliac Crest Length 2	6/7
P19. Iliac Crest Length 3	6/3
P20. Relative Pelvic Length	7/STL

Table 12. Limb Proportion Ratios.

<u>Ratio Names</u>	<u>Measurements</u>
LP1. Intermembral Index	Humerus + Radius/Femur + Tibia
LP2. Crural Index	Tibial length / Humeral length
LP3. Relative Tibial Length	Tibial length / STL
LP4. Relative Hindlimb Length	Humeral length / STL
LP5. Brachial Index	Radial length / Humeral length
LP6. Relative Forelimb Length	Humerus + Radius / STL
LP7. Relative Humeral Length	Humeral length / STL
LP8. Relative Radial Length	Radial length / STL

While ratios may present significant information regarding limb proportions, a complete picture must take into account the scaling trends within related taxa of different bodily size. For example, Jungers (1979) has shown that while the crural indices of lemurids, indriids, and lorisisids are similar, the actual scaling of femoral and tibial length among the three families is far from uniform. Skeletal allometry was investigated in this study by least-squares regressions of logarithmically transformed data in order to ascertain the relationship between limb length and bodily size, as approximated by STL. These regressions were calculated using BMDP program 6D, "Bivariate Scatter Plots". This program provides the slope of the regression equation and the correlation between the variables. The plots presented here were printed using the SPSS "Plot" procedure.

3.4. Data Analysis: Discriminant Function Analysis

In addition to the univariate and bivariate analyses described above, multivariate analysis was utilized with the osteological data from the pelvis and the femur. The particular usefulness of multivariate statistics is that they allow the simultaneous handling of many variables (both independent and dependent) that may be correlated with each other to varying degrees. A large and complex data set can be analyzed in a single step, rather than by a series of univariate or bivariate analyses. In addition,

multivariate analyses may reveal aspects of the data that would not be seen in a simpler analysis. It is axiomatic that while two variables taken singly may not separate two groups, two variables taken together may reveal complete separation of the groups (Oxnard 1978). Since multivariate statistics are much more complex than univariate or bivariate statistics, the pitfalls that an investigator can encounter are more numerous, and the difficulties of interpreting the results can also be greater. Used judiciously and interpreted carefully, multivariate morphometric analyses can be a valuable addition to statistical treatment of biological data.

Multivariate statistics were used in this analysis for a very specific purpose and to test a specific hypothesis. The purpose was to see how various groups of prosimians were arrayed in multivariate space on the basis of hindlimb osteology. Groups of particular interest in this analysis were those classified by positional behavior. Generally I hoped to discover that the same patterns of hindlimb bony morphology revealed in the bivariate and univariate analyses could be demonstrated by the multivariate analyses. The hypothesis to be tested was central to this entire thesis, and related the patterns of hindlimb morphology demonstrated by the statistical analysis to the categories of positional behavior established from the observed

behaviors of the living animals. Are all of Walker's "vertical clingers and leapers" clearly separated from the non-leapers, and are the various taxa arrayed in a recognizable pattern relative to their habitual positional repertoires? Finally, what are the particular measurements (predictor variables) that allow discrimination between prosimian taxa of differing positional behaviors (especially leapers and quadrupeds)?

The appropriate method of addressing these kinds of questions is clearly discriminant analysis. Multiple discriminant function analysis is a multivariate technique whose purpose is to distinguish between two or more groups on the basis of a series of predictor variables. The statistical algorithm finds the linear combination of these variables that maximizes the between-group variance while at the same time minimizing the within-group variance. This is the first discriminant axis, sometimes called the first canonical variate or axis (discriminant analysis and canonical analysis are synonyms). It will then find the next best linear combination of variables, orthogonal (hence uncorrelated) to the first axis, that accounts for the next greatest part of the between-group variance, and so on until all of the between-group variance is accounted for. The number of discriminant axes required to account for all of the variance will be either equal to the number of variables or to one less than the number of groups.

The greater part of the variance is, however, usually accounted for in the first two or three discriminant axes, and later axes are usually disregarded as not adding significant information to the analysis. The value of discriminant analysis can be plainly seen in the reduction of dimensionality of the data from the number of variables or groups to two or three axes that account for most of the significant variation between groups.

Two different "canned" packages of statistical programs were used in the multivariate analysis, SPSS (Nie et al. 1975) and BMDP (Dixon 1981). While the algorithms are similar, the discriminant programs in these packages provided some differences in statistical output and in plotting capabilities that made it useful to run analyses using both. The results of the two different programs were compared and found to be essentially identical in all cases, and so the discussion and results reported here are from the SPSS runs. A stepwise analysis was chosen for both the BMDP and the SPSS discriminant analyses, as opposed to the alternative or direct method. The former method adds variables into the discriminant function in stepwise fashion in the order in which the variables add the most to the between-group separation. This is determined by comparison of the F-statistics from a one-way analysis of variance (ANOVA) performed at each step. A direct

discriminant analysis forces all the variables into the algorithm simultaneously, regardless of their relative importance as discriminators.

The BMDP program (7M) plots bivariate scattergrams of the first two discriminant axes for all cases with group means and for group means only. In addition to printing eigenvalues and canonical coefficients, program 7M also provides two different classificatory matrices on the basis of Mahalanobis' D-square distances from group means. All cases incorrectly classified are detailed, and the percent classified correctly is shown. The D-square values were useful in checking for outliers. Although it does not provide any plots, the SPSS DISCRIMINANT program was used because it provides correlations between variables and each discriminant axis. This is a valuable aid in interpreting the contribution of each variable to the separation along the various discriminant axes. The plots presented use the SPSS discriminant results and were drawn on a Macintosh computer using Microsoft Chart software. Both univariate and bivariate plots were made for the first three discriminant axes for all discriminant runs on Chart.

One of the more difficult and certainly the most important part of multivariate analysis is the interpretation of the results. In the case of discriminant analysis, the problem is to evaluate the importance of the various predictor variables in the separation along the

first two or three discriminant axes. The next step is to relate those variables that most strongly affect the discrimination to the living animals and to explain the separation in terms of biomechanics and function. Unfortunately, the literature on discriminant analysis indicates that there is no single accepted method for evaluating the contribution of predictor variables. Three methods seem to be accepted by many workers, but all with certain caveats. Finding it difficult to justify the use of any one of these methods to the exclusion of the other two, I have used all three. This seems to be the method least fraught with the danger of misinterpretation. Concordance between the three methods will allow greater confidence in the interpretation, while serious discordance will be reason for caution in interpreting the significance of predictor variables.

The first method is simply to rank the importance of the predictor variables by the order in which they are entered into the stepwise discriminant analysis. As stated above, the order of entry of variables into the discriminant analysis is on the basis of F-statistics computed from a one way analysis of variance at each step. The variable with the highest F-statistic is added at each step. Then the ANOVA is recalculated for all the other variables not yet entered, and again the variable with the highest F-

statistic is added, and so on. Both the BMDP and the SPSS manuals specifically state that this method adds variables in the order in which they best discriminate between the groups (Dixon 1981; Nie et al. 1975). The major problem with this assumption is that the F-statistics "represent the ability of each predictor variable by itself to predict group membership" (Tabachnick and Fidell 1983:298). Consequently, they do not take into account correlations among the variables. In addition, it is not possible to connect the order of entry of variables to the discrimination produced along any specific axis. Another possible indication of the relative contribution of different variables to the discrimination is in the relative magnitude of their canonical coefficients (Nie et al. 1975:443). These coefficients do not, however, take into account interaction between variables, and so can be misleading. The final method, and perhaps the most intuitive, is to examine the correlations between each predictor variable and the various discriminant functions or axes. The highest absolute correlations are considered to indicate the most important variables for a particular discriminant axis, with a minimal r value of 0.30 being judged significant (Tabachnick and Fidell 1983:321). In the tables and discussion that follow, all three of these methods will be referred to and used in the attempt to evaluate the relative contributions of the different

variables to the overall separation provided by the discriminant analyses.

Another frequent difficulty in multivariate statistical analyses of biological data involves the question of size. Since animals are of varying bodily size, and since many aspects of shape seem to be correlated with size, there is a real need to be able to separate size-dependent from size-independent aspects of morphology. For example, if we could scale a tree shrew (Tupaia) up to the size of a sifaka (Propithecus), would the relative length of its ischium resemble that of sifakas or of tree shrews? Many investigators have gone to great lengths to "correct" for differences in bodily size (e.g., Corruccini 1972, 1973; Manaster 1979), using complicated mathematical approaches to "cook" their data. I have chosen to use a different method in an attempt to control for the great range in prosimian bodily sizes. The multivariate analyses were done on three different sets of data, and because of small sample sizes for many genera, were compared at the taxonomic level of the Family. First, the raw data were analyzed, then a logarithmic transformation was done on the raw data, and lastly simple ratios using the skeletal trunk length or STL (Biegert and Maurer 1972) as the denominator were calculated. Results of each of these three discriminant analyses are discussed below.

Chapter 4. The Prosimian Pelvis

4.1. Introduction to Chapter 4

The pelvis is of central importance to any discussion of the functional anatomy of the mammalian hindlimb. One might rightly expect to find ample evidence of locomotor specializations on this complex bone from which arise many important muscles of the lower limb. Walker (1967, 1974; Napier and Walker 1967) has suggested several pelvic traits as adaptations to vertical clinging and leaping among prosimians. Among these are a long ilium with prominent anterior and posterior iliac spines, and a short ischium. With regard to the width of the ilium, Napier and Walker (1967:210) state that,

"An allometric function is revealed in a study of the ilia; the larger animals have widely splayed iliac blades but in the smaller vertical clingers the iliac blades are narrow."

In this chapter I test the validity of these claims and seek a functional explanation of the pelvic morphology or morphologies of vertical clinging and leaping prosimians.

A consideration of VCL behavior reveals three salient aspects of muscular function around the hip joint:

1. both femora are flexed, laterally rotated, and adducted during vertical clinging postures;
2. during the propulsive phase of the leap both femora are rapidly and powerfully extended and medially rotated;
3. rapid femoral flexion at the hip occurs in mid-flight during the recovery phase as the hindlimb prepares to bear the initial and major stresses of landing.

This chapter begins with a comparative examination of the pelvic osteology of the prosimians. The discussion is organized by family, and is followed by a consideration of the muscles that arise from the pelvis to insert on the bones of the lower limb proper. Discussion of the statistical analysis of the twenty pelvic ratios and of the discriminant analysis follows. Finally, in a section on the functional anatomy of the pelvis, I attempt to relate the statistical, osteological, and muscular information to biomechanical theory in order to more fully understand leaping adaptations in the prosimian pelvis. A brief summary ends this chapter by returning to Walker's (1967, 1974) original diagnosis of the pelvis in vertical clingers and leapers in light of the results reported here. What are the common traits, if any, of the pelvis among leaping prosimians, and what is their functional significance?

4.2. Osteology

Before describing the pelvic morphology of the various families of prosimian primates, I briefly discuss the overall pelvic "gestalt" for the entire suborder. In addition to mentioning both variable and invariant traits of prosimian pelvic morphology, I note whether particular characteristics were studied only qualitatively or also quantitatively in this work. See Figure 2 and Table 4 for the named landmarks on the prosimian pelvis, and Table 6

for a list of the pelvic measurements used in this study.

While all prosimians possess long and narrow iliac blades, some of the Malagasy taxa, especially Indriidae, have dorso-ventrally expanded iliac crests. This expansion along the cranial border of the pelvis is usually the result of a large and projecting anterior superior iliac spine. This trait was both described qualitatively and measured (iliac crest length, measurement 6). In addition to the anterior superior iliac spine, all prosimians have an anterior inferior, and a posterior superior iliac spine. The two superior iliac spines normally correspond to the ventral and dorsal edges of the iliac crest and are joined by an interspinous ligament. The M. tensor fasciae femoris arises from the iliac crest of all prosimians, while the M. sartorius arises from the interspinous ligament among some Malagasy prosimians. The anterior inferior iliac spine is on the gluteal (lateral) surface of the ilium close to the cranial lip of the acetabulum, and provides origin to the M. rectus femoris. These bony landmarks are variably developed among prosimians; their presence and relative development are noted for all taxa. All prosimians lack a posterior inferior iliac spine. The gluteal surface of the ilium is slightly to very concave, especially in its cranial part, among most prosimians. In addition, the cranial part of the ilium is laterally flared above the sacro-iliac joint in most prosimians, giving the bone a

decidedly sigmoidal shape in ventral view. The blade of the ilium is also rotated laterally to a variable extent from the plane of the ischio-pubic ramus. This feature makes the gluteal surface face dorsally, as opposed to laterally, to a variable extent, and would seem to affect the direction of pull and hence the function of the gluteal musculature. The sacro-iliac joint is positioned on the dorsal aspect of the medial surface of the ilium in all prosimians. Its position relative to the cranial edge of the ilium varies considerably among prosimians. This feature was measured in a few specimens of each group.

The pubis is, among prosimians, a less complex part of the pelvic girdle than the ilium. The lengths of both the superior pubic ramus and of the ischio-pubic ramus were measured (measurements 2 and 8, respectively). The former measurement is a close osteological approximation of the moment arm of the adductor musculature, which arises along its length. The pubic symphysis was both measured (measurement 4) and described as being horizontal or caudally sloping. The absence or presence of pubic tubercles on the superior pubic ramus was noted, as was the outline of the pelvic inlet (V-shaped or more gently curved or rounded). The relative lengths of the pubic rami influence the shape of the obturator foramen, which varies from oval to triangular in shape.

All prosimians have a stout ischial ramus with a well developed ischial tuberosity and ischial spine. There is, however, a significant amount of variation in the length of the ischium (measurement 1) and in the orientation of the ischial tuberosity. As the bulk of the hindlimb extensor musculature arises from the ischium and especially from its tuberosity, ischial length is a good approximation of the moment arm of these muscles. In some taxa, the tuberosity is projected dorsally. This brings the origin of the hamstring muscles to a more dorsal position relative to the acetabulum, and should be of functional significance in hindlimb extension.

4.2.1. Lorisidae

The lorisid ilium is a long and straight bone, slender dorso-ventrally, but thick medio-laterally. The iliac crest is only very slightly expanded dorso-ventrally, resulting in the bone's narrow, rodlike appearance. The medio-lateral thickness of the ilium among the Lorisidae is a trait that distinguishes this family from all other prosimians. The gluteal surface of the ilium is quite flat and the ilium is laterally rotated between 40 and 50 degrees from the plane of the ischio-pubic ramus. The narrow gluteal surface faces mainly laterally but also somewhat dorsally as a result of the squared off dorsal border of the ilium. Unlike other prosimians, the cranial part of the ilium is not laterally flared. The sacro-iliac joint among the Lorisidae has an

extremely cranial position on the ilium, with a roughened area for ligamentous attachment extending to the iliac crest. The iliac spines are poorly developed. The anterior inferior iliac spine is variable in development, implying a weak *M. rectus femoris*. It is often absent from the African taxa, but may be moderate in size, particularly in large individuals of *Nycticebus*. When the anterior inferior iliac spine is present among Lorisidae it is separated from the lip of the acetabulum by 5 to 10 millimeters. The anterior and posterior superior iliac spines are the thickened ventral and dorsal ends of the iliac crest. Among Lorisidae they are very poorly developed and sometimes non-existent, indicating a weak attachment of *M. tensor fasciae femoris*.

The lorisid pubis is a thin, elongate bone with a very distinctive morphology. Both its superior and ischio-pubic rami are long and thin, and there are normally no pubic tubercles on the superior ramus. The length of the pubis provides a large moment arm for the adductor musculature. As a result of the length of the pubis, the obturator foramen has a distinctive elongate oval shape. The pelvic inlet is very narrow and V-shaped in all lorisisds. A unique feature of the lorisid pubis is the extremely short cranio-caudal length of the pubic symphysis. This character is probably in some way related to parturition, although its significance was not investigated in this study.

The ischium among lorisids is also quite distinctive. The ischial spine and ischial tuberosity are both consistently well developed as in all prosimians, but the ischium as a whole is very short. Interestingly, lorisids most closely resemble the specialized prosimian leapers with respect to this short ischium and the attendant small moment arm for femoral extension at the hip. In addition, the tuberosity has a rounded posterior border that projects dorsally to the acetabulum and extends onto the ischio-pubic ramus.

There exists significant intergeneric variation among Lorisidae in several pelvic characteristics including the width of the iliac crest, the development of the anterior inferior iliac spine, and the position of the ilium relative to the ischium and pubis. Nycticebus and Loris show moderate expansion while Perodicticus and Arctocebus show little or no expansion of the iliac crest. The anterior inferior iliac spine is either absent from or very poorly developed in Arctocebus and Perodicticus. It is somewhat better developed in Loris and best developed in Nycticebus, where it is still only moderate in size when compared with the anterior inferior iliac spine of other prosimians. The angle at which the ilium joins the superior pubic ramus (ventral to the acetabulum) distinguishes Loris from the other lorisid genera. In Loris this angle is either acute or right, while in the other taxa it is always

obtuse. Arctocebus most closely approximates Loris in this trait. Its significance is not known.

4.2.2. Galagidae

Among the galagos, the ilium is a long, narrow, and rodlike structure with a moderate degree of dorso-ventral expansion along its cranial margin. The gluteal surface of the ilium is only slightly concave, mainly in its cranial third. As in lorises, the blade of the ilium is laterally rotated between 40 and 50 degrees. The cranial third is laterally flared as in all prosimians except lorises, giving the pelvis a sigmoidal shape in ventral view. This trait may allow M. gluteus medius to better act as a medial rotator of the femur during extension, an important function among leapers. The sacro-iliac joint is positioned cranially, but not to the same extent as in the Lorisidae. The anterior inferior iliac spine is a well-developed bump on the lateral surface of the ilium, is routinely separated from the lip of the acetabulum by several millimeters, and provides a stout attachment for M. rectus femoris. Its size seems to be proportional to bodily size within the galagos. The two superior iliac spines are small to moderate in size among the galagos but the posterior superior iliac spine is larger than the anterior. The former is a medio-lateral thickening of the dorsal edge of the iliac crest. The latter is often simply a small bump on the ventral edge of

the iliac crest, but may be a small ridge just caudal to the tip of the iliac crest. Never is it the large, beaked structure seen in many Malagasy prosimians.

Galagos have moderately long pubic rami which provide effective leverage for the adductors of the femur. The ischio-pubic ramus is particularly thin and long. As in lorises, this results in an elongate obturator foramen. Along the cranial margin of the superior pubic ramus can be found one or several pubic tubercles which vary with the bodily size of the individual, and are related to the origin of the adductor musculature along this bone. Unlike lorises, galagos have a long, caudally sloping pubic symphysis, and the pelvic inlet is intermediate in shape between the V-shape seen in lorises and the gentle curve seen in indriids and some other Malagasy taxa.

Galagos have a short but stout ischial ramus capped by an ischial tuberosity that projects slightly dorsally relative to the acetabulum. This dorsal projection is a consequence of the small angle between the blade of the ilium and the ischial ramus, not a result of any dorsal lengthening of the tuberosity itself. The short ischial moment arm for femoral extension is shared by tarsiids, indriids, and lorises. The ischial spine is consistently well-formed, as is the lesser sciatic notch between it and the ischial tuberosity.

The various species of Galago share the same basic pelvic morphology. The main distinctions seem related to differences in bodily size and include characters such as the relative robusticity of the pubic tubercles and of the iliac spines.

4.2.3. Tarsiidae

In many respects the tarsiid ilium closely resembles that of galagos. It is a long and narrow structure with only a very slight expansion of the iliac crest for the attachment of *M. tensor fasciae femoris*. The gluteal surface of the ilium also resembles that of galagos in being only slightly concave and facing mainly laterally. The blade of the ilium is laterally rotated approximately 60 degrees, and its cranial third is laterally flared, giving it a sigmoidal appearance in ventral view and aiding *M. gluteus medius* in medial rotation. The sacro-iliac joint is placed quite cranially in tarsiers, with roughened areas for ligamentous attachments extending to the iliac crest. The anterior inferior iliac spine is a small bump on the lateral surface of the ilium. separated by a few millimeters from the lip of the acetabulum. The anterior superior iliac spine is a small ridge just caudal to the ventral edge of the iliac crest. Among the prosimians, the anterior superior iliac spine is morphologically distinct from the ventral edge of the iliac crest only in tarsiers and some galagos. The posterior superior iliac spine is a

medio-lateral thickening of the dorsal edge of the iliac crest. In tarsiers it is larger than the anterior superior iliac spine.

Tarsiers also resemble galagos among leaping prosimians in the moderate length of the pubic rami, which provides for a fairly long moment arm in femoral adduction, an important postural adaptation of small-bodied vertical clingers. The long and thin superior and inferior pubic rami enclose an elongate, oval, obturator foramen. Pubic tubercles are usually lacking on the superior ramus. The pubic symphysis is moderately long and slopes caudally, while the pelvic inlet is narrow and V-shaped as in lorises.

The tarsier ischium is similar to that found among both galagids and indriids. The ischial ramus is short and stout, with a well-developed ischial spine and tuberosity. The ischial tuberosity faces mainly caudad but also, as a result of the angle between ilium and ischium, projects to a slight degree dorsad to the acetabulum. As in galagos, the ischial tuberosity itself is not prolonged or elongated dorsad to the acetabulum. A short ischial moment arm allows rapid femoral extension and appears to be an important adaptation among saltatorial prosimians.

4.2.4. Tupaiidae

The tupaiid pelvis is quite distinct from that of all prosimians. The ilium is a short bone, narrow but not rodlike, and expanded cranially along the iliac crest. The gluteal surface of the ilium is moderately concave. The blade of the ilium is laterally rotated quite strongly (60 - 70 degrees), and the cranial half is laterally flared, resulting in a sigmoidal appearance in ventral view. The position of the sacro-iliac joint is midway up the ilium. Tupaia has a large anterior inferior iliac spine that somewhat resembles the lemurid condition. It is a laterally projecting flange that arises on the ilium at the cranial edge of the acetabulum and provides a strong attachment to M. rectus femoris. The superior iliac spines are, however, weakly developed. The posterior superior iliac spine is a very slight medio-lateral thickening on the dorsal edge of the iliac crest. The anterior superior iliac spine resembles those of Tarsius and Galago in that it is distinct from the ventral edge of the iliac crest, being a few millimeters caudal to the crest. It is small and variable in expression.

Tree shrews have moderately long pubic rami and a very long, horizontal pubic symphysis. Pubic tubercles mark the origin of the adductor muscles on the superior ramus. Enclosed within the short pubic rami is a fairly rounded obturator foramen. The pelvic inlet is intermediate in

shape, most closely resembling the condition seen in galagos.

The tree shrew ischium is noteworthy for the length of its ischial ramus, which provides a large moment arm for powerful femoral extension. As a result of the great length of the ischium, the well-developed ischial spine and tuberosity are widely separated from each other. In addition, the ischial tuberosity shows a very marked dorsal projection beyond the level of the acetabulum. This latter trait is a very distinctive feature of tupaiids.

4.2.5. Cheirogaleidae

The Cheirogaleidae have long and narrow, rodlike ilia with only a very slight amount of dorso-ventral expansion along the iliac crest. Unlike most prosimians, the gluteal surface of the ilium is not concave, although cranial to the sacro-iliac joint it is laterally flared. The plane of the ilium is laterally rotated approximately 50 degrees from that of the ischio-pubic ramus. The sacro-iliac joint in both Cheirogaleus and Microcebus is placed cranially on the ilium. The superior iliac spines are both rather weakly developed. The anterior superior iliac spine is a tiny bump on the ventral edge of the iliac crest, while the larger posterior superior iliac spine is a medio-lateral thickening of the dorsal edge of the iliac crest. The anterior inferior iliac spine is better developed,

providing origin for M. rectus femoris. It is a small (Microcebus) to moderate sized (Cheirogaleus) laterally facing bump on the ilium, separated from the lip of the acetabulum by a few millimeters.

Cheirogaleus and Microcebus are much less similar in the caudal half of the pelvis than they are in the ilium. Microcebus has very long and thin pubic rami which, in conjunction with a long ischial ramus, give its obturator foramen a decidedly triangular look in lateral view. Cheirogaleus has a short superior and a moderate ischio-pubic ramus, giving it a very different appearance. The pelvic inlets of both genera are V-shaped, but the V is more acutely angled in Microcebus. Cheirogaleus usually has a single pubic tubercle on its superior ramus, while Microcebus may or may not have a very small, similarly positioned tubercle. The pubic symphyses of both Cheirogaleus and Microcebus are short and fairly horizontal, but that of Microcebus seems relatively shorter.

Both genera have long, stout, and straight ischial rami. The long ischial moment arm seems to be a trait common among quadrupedal prosimians, and in direct contrast to the short ischium found among leapers and slow-climbers. The ischial spine and tuberosity are well separated in both Cheirogaleus and Microcebus by a long groove for M. obturator internus. The ischial tuberosity in both projects

dorsad to the acetabulum only very slightly; this seems to be a variable character, especially in Cheirogaleus. In both Microcebus and Cheirogaleus the ischium and the ilium are essentially in line with each other (i.e., there is an 180 degree angle between them).

4.2.6. Lemuridae

The lemurid ilium is long and narrow caudally, but expanded cranially along the iliac crest. The expansion of the iliac crest is mainly anterior, the result of the large and projecting anterior superior iliac spine which is also characteristic of Lepilemuridae and Indriidae. The expanded gluteal surface of the ilium is strongly concave throughout most of its length, and faces mainly dorso-laterally as a result of the moderate lateral rotation (50 - 60 degrees) of the blade of the ilium. In ventral view the lemurid pelvis has a strongly sigmoidal shape as a result of the lateral flare of the cranial part of the ilium. The position of the sacro-iliac joint among lemurids is slightly more than mid way up the ilium. As mentioned above, the anterior superior iliac spine is a well developed, beaklike ridge projecting ventro-laterally. The anterior inferior iliac spine is another powerfully developed flange of bone that projects laterally from the surface of the ilium, beginning at the lip of the acetabulum. It extends laterally beyond the tip of the

acetabulum, but not as far as does the anterior superior iliac spine, and provides a powerful attachment for *M. rectus femoris*. Between the two anterior iliac spines, the ventral border of the ilium is broadly curved, providing origin for the powerful *M. gluteus medius*. The posterior superior iliac spine is a minor medio-lateral thickening along the dorsal edge of the iliac crest.

The lemurid pubis is composed of a short superior ramus, usually with one or several tubercles, and a moderately long and thin ischio-pubic ramus. The symphysis is fairly long and horizontal, while the obturator foramen has an oval shape. The pelvic inlet is gently curved as in Indriids. The ramus of the ischium is stout and moderate in length, with a well developed lesser sciatic notch between the ischial spine and tuberosity. The ischial moment arm is intermediate in length between those of Indriidae and Cheirogaleidae. The large ischial tuberosity has a well developed dorsal projection.

There is a fair amount of interspecific variation in pelvic morphology among the Lemuridae, most noticeably in the ilium. Dorso-ventral expansion of the iliac crest is best developed in Lemur catta, moderately so in L. fulvus, and least developed in Varecia variegata. This is a result of the relative development of the anterior superior iliac spine, which is largest and projects farthest in L. catta. The anterior inferior iliac spine is also significantly

larger in L. catta than in other lemurids. In general, L. catta has the highest degree of lateral rotation of the ilium among the lemurids, resulting in a more dorsally facing gluteal aspect. Finally, V. variegata has a slightly shorter ischial ramus than do members of the genus Lemur.

4.2.7. Indriidae

Several characteristics of the ilium contribute to the very distinctive shape of the indriid pelvis. Among prosimians, indriids have the most expanded iliac crests, mainly as a result of the great development of the anterior superior iliac spine. The gluteal surface is strongly concave for most of its length, and faces dorso-laterally as a result of the strong lateral rotation of the ilium (65 - 70 degrees). The area for attachment of the gluteal musculature along the lateral surface of the ilium is greatly expanded. The pelvis is strongly sigmoidal in ventral view, a consequence of the lateral flare of the cranial region of the ilium. Indriids are unique among prosimian primates for the caudal placement of the sacro-iliac joint. While the anterior superior iliac spine is a large, beaklike structure that strongly projects ventro-laterally, the posterior superior iliac spine is a moderate thickening of the dorsal edge of the iliac crest. The anterior inferior iliac spine is also a large, laterally projecting flange of bone, separated by up to 10

millimeters from the edge of the acetabulum, and it provides effective leverage for the action of *M. rectus femoris* in femoral flexion and tibial extension. The cranial edge of the anterior inferior iliac spine reaches nearly the same height as the caudal edge of the sacroiliac joint, while in other prosimians these points are well separated.

Indriid pelves are characterized by short pubic rami enclosing an oval obturator foramen. The short adductor moment arm is probably a function of the emphasis on flexion and extension of the femur in leaping. Pubic tubercles are usually present on the superior pubic ramus and vary with bodily size. The pelvic inlet is rounded in indriids, and the pubic symphysis is long and slopes caudally. As in the other families of predominantly leaping prosimians, the ischial ramus among the indriids is short and stout, often with a pronounced dorsal curve, and provides for rapid femoral extension. The ischial tuberosity has a strong dorsal projection.

In spite of the large range in bodily size among the indriids, their pelvic morphology is remarkably uniform. There are, however, several major points of intrafamilial variation among Indriidae. In *Avahi*, the smallest genus in the family, the anterior inferior iliac spine is unique. It is neither projected as far laterally, nor is it as clearly demarcated from the ventral border of the ilium as in other

indriids. Rather, it is a sharp, thin ridge on the ventral border of the ilium. Consequently, the ventral curvature of the ilium is less developed in Avahi than in either Indri or Propithecus. Avahi also seems to have a more cranially placed sacro-iliac joint than either of the other indriid genera. In Indri the ventral border of the anterior superior iliac spine is turned laterally at a much greater angle than in the other indriids.

4.2.8. Lepilemuridae

The pelves of Lepilemur and Hapalemur are very similar to each other and to those of the genus Lemur. The ilium is narrow caudally but broadens considerably at the iliac crest. Both genera have a strongly concave gluteal surface that is sharply rotated laterally (60 - 80 degrees) and provides a large attachment area for *M. gluteus medius*. The cranial part of the ilium is flared laterally, giving it the sigmoidal shape noted in other Malagasy prosimians. The sacro-iliac joint is positioned slightly more than midway up the ilium as in lemurids. The iliac spines are also quite similar in shape and size to those seen both in Lemuridae and Indriidae. The anterior superior iliac spine is a ventro-laterally projecting beaklike structure that is responsible for the expansion of the iliac crest and the curvature of the ventral border of the ilium. The anterior inferior iliac spine is a well developed laterally facing

flange of bone, while the posterior superior iliac spine is as described for other Malagasy taxa.

As in other Malagasy taxa, the pubic rami of lepilemurids are short and enclose an oval obturator foramen. A single pubic tubercle is usually present on the cranial third of the superior pubic ramus. The pubic symphysis is long and horizontal, and the pelvic inlet is gently curved as in lemurids. Ischial rami are moderate in length and capped by a large ischial tuberosity that projects dorsally to a variable extent. As in Lemuridae, the ischial moment arm is longer than that of the more specialized leapers (galagos, tarsiers, and indriids), but shorter than those of Cheirogaleidae and Tupaiidae.

There are some interesting differences in pelvic morphology between Hapalemur and Lepilemur. Hapalemur shows a more robust development of the anterior superior and inferior iliac spines, and consequently, a more expanded iliac crest and greater ventral curvature. In addition, the anterior inferior iliac spine arises from the lip of the acetabulum in Hapalemur, while it is separated from the acetabulum by several millimeters in Lepilemur. The lateral rotation of the ilium is greater in Hapalemur, resulting in a more dorsally facing gluteal surface in this genus. Caudally, Hapalemur has a longer superior pubic ramus and a more consistently dorsally projecting ischial tuberosity than does Lepilemur.

4.3. Musculature

In this section I describe the morphology of the pelvic musculature among prosimian primates, including origin, insertion, innervation, and function. A knowledge of muscular attachments is essential to a thorough discussion of bony morphology because of the importance of muscular forces in shaping that morphology. Special emphasis is placed on muscles of importance in positional behaviors. Unless otherwise noted, these descriptions apply to all of the prosimians examined in this study. Published descriptions of prosimian myology used in this compilation include George (1977) on Tupaiidae, Jouffroy (1962) on Lemuriformes, McArdle (1981) on Lorisiformes, Woolard (1925) and Grand and Lorenz (1968) on Tarsiidae, and Stevens et al. (1981) on Galagidae. Stern (1971) and Uhlmann (1968) offer overviews of the pelvic musculature of the entire Order Primates. In addition, my own dissection notes on Galagidae, Tupaiidae, and Tarsiidae were consulted.

4.3.1. *M. gluteus superficialis*

This muscle, the *M. gluteus maximus* of human anatomy, has two variably separated parts among prosimians, the pars anterior and pars posterior. These are separated by the inferior gluteal nerve, which supplies the entire muscle. The pars posterior lies dorsal to the sciatic nerve, and is

the *M. femorococcygeus* of some authors. The pars anterior arises from the gluteal fascia overlying *M. gluteus medius* and/or the caudal fascia overlying *M. abductor caudae medialis*. The pars anterior inserts via its "ascending tendon" (Stern 1971) into the third trochanter. This insertion is in common with that of the *M. tensor fasciae femoris*. The pars posterior of *M. gluteus superficialis* arises from the transverse processes of the first two or three caudal vertebrae and inserts for a variable distance on a line distal to the third trochanter. *M. gluteus superficialis* serves mainly as an extensor of the thigh. Rapid and powerful hip extension is of great importance in leaping behavior.

4.3.2. *M. tensor fasciae femoris*

Situated along the anterior border of the *M. gluteus superficialis* (from which it is often difficult to separate), the *M. tensor fasciae femoris* arises by muscular fibers from part or all of the iliac crest cranial to the origin of *M. gluteus medius*, and also from the gluteal fascia overlying *M. gluteus medius*. It inserts with the ascending tendon from *M. gluteus superficialis* pars anterior into the third trochanter. This muscle is the *M. tensor fasciae femoris* part 2 of Stern (1971), part 1 being absent from all prosimians. It is called *M. tensor fasciae latae* by human anatomists because it inserts into the fascia lata in humans. Innervation is by the superior

gluteal nerve, and its functions are flexion and medial rotation of the leg. These functions are especially important during the recovery phase of the leap. After the leap is initiated, the extended femur must be rapidly flexed (protracted) while the animal is in midair, in preparation for the landing. The length of the moment arm of the M. tensor fasciae femoris is closely approximated by the length of the ilium.

4.3.3. M. gluteus medius

There is little variation in the M. gluteus medius among the prosimians. It arises from much of the gluteal aspect of the ilium (cranial to the gluteal line if present) and inserts into the greater trochanter of the femur. It is the largest and most powerful of the gluteal muscles among prosimians, and is innervated by the superior gluteal nerve. Its origin is especially extensive among the Malagasy families Lemuridae, Lepilemuridae, and especially Indriidae. Its functions are medial rotation and extension of the thigh. Both of these functions come into play in the propulsive phase of the leap. The flexed and laterally rotated femur must be rapidly extended at the hip in order for the leap to occur. Since the M. gluteus medius arises from much of the iliac blade, the length of the ilium approximates the average length of its constituent muscle fibers.

4.3.4. *M. gluteus minimus*

The *M. gluteus minimus* is the deepest layer of gluteal musculature and, like *M. gluteus superficialis*, is often divided into two separate parts. The pars anterior arises from the inferior ventral edge of the ilium, slightly cranial to the acetabulum. This is the "scansorius" muscle of some authors (see Sigmon 1969 for a review). The pars posterior arises from the dorsal edge of the ilium, both dorsal and cranial to the acetabulum. In all primates there is a single insertion into the greater trochanter, and a single innervation by the superior gluteal nerve. Its function is mainly as a medial rotator of the thigh. Stern (1971) states that *G. medius* and *G. minimus* act jointly as a "regulator femoris", assuring the integrity of the hip joint during a wide variety of movements and postures.

4.3.5. *M. ilio-psoas*

As indicated by its name, *M. ilio-psoas* is a compound muscle composed of *M. iliacus* and *M. psoas major*. These important hip flexors vary little among primates. The former arises on the medial surface of the blade of the ilium, while the latter takes its origin from the intervertebral discs, vertebral bodies, and transverse processes of the lumbar vertebrae. The two muscles unite and insert by a common tendon into the lesser trochanter of the femur. Innervation of *M. iliacus* is by the femoral nerve and of *M. psoas major* by a branch of the lumbosacral

plexus. These muscles are important in femoral flexion during the recovery phase of saltatorial locomotion.

4.3.6. M. psoas minor

M. psoas minor is a rather insignificant muscle that runs on the ventral surface of M. psoas major. It arises from intervertebral discs and vertebral bodies in the lumbar region and inserts by a small tendon into the iliopectineal eminence on the pubis. Its innervation is from a branch of the lumbosacral plexus, and it acts to flex the pelvis on the vertebral column.

4.3.7. Mm. obturator externus and internus

These two lateral rotators arise from the external and internal surfaces of the ischial and pubic rami around the obturator foramen and from the obturator membrane. They insert with the Mm. gemelli into the trochanteric fossa, and are innervated by branches from the lumbosacral plexus.

4.3.8. Mm. gemellus superior and inferior

These two muscles are also lateral rotators of the hip joint. They both arise from the ischium, M. gemellus superior from the ischial spine and M. gemellus inferior from the ischial tuberosity. They join M. obturator internus as it crosses the lesser sciatic notch and insert with this muscle into the trochanteric fossa. They are also innervated by branches from the lumbosacral plexus.

4.3.9. *M. quadratus femoris*

Most authors have distinguished two parts of *M. quadratus femoris* with a variable degree of separation or fusion. My treatment of this muscle follows that of McArdle (1981). The dorsal portion of *M. quadratus femoris* arises from the body of the ischium, just anterior to the ischial tuberosity. The ventral portion arises from the ischial part of the ischio-pubic ramus. The insertion, which may be partially fused or double, extends a variable distance distally on the posterior aspect of the femur from the level of the third trochanter. Innervation of both dorsal and ventral portions is by the lumbosacral plexus, while the ventral portion has an additional innervation from the obturator nerve. Stern (1971) and McArdle (1981) follow Uhlmann (1968) in judging those ventral fibers innervated by the obturator nerve as homologs of part of the *M. adductor magnus*. *M. quadratus femoris* is an extensor of the thigh, important in hindlimb propulsion in leaping.

4.3.10. *M. sartorius*

This muscle shows a wide range of variation in its origin, yet is fairly constant in its insertion. In tupaiids it arises from the tendinous caudal border of the external abdominal oblique muscle. In loriforms and tarsiids it arises from the ventral border of the blade of the ilium. Among lemuriforms *M. sartorius* arises from the interspinous ligament connecting the anterior inferior and

anterior superior iliac spines in Lemur, Hapalemur, and the indriids. It arises from the anterior superior iliac spine in Lepilemur, while in the cheirogaleids and in Daubentonia it arises from the cranial part of the ventral border of the ilium. The insertion is into the anterior tibial crest, often in common with the tendons of M. gracilis and M. semitendinosus. This common insertion is the "pes anserinus" of human anatomy. M. sartorius is always innervated by the femoral nerve. Its functions include flexion of the thigh and leg, and medial rotation of the leg. These functions come into play in the recovery phase of leaping.

4.3.11. M. rectus femoris

This muscle is the only part of the quadriceps femoris group to cross both the hip and the knee joints. Its double origin is similar in all primates. The straight or iliac head arises from the anterior inferior iliac spine, and the reflected or acetabular head arises from the ilium just cranial to the acetabulum. An osteological measure of the importance of this muscle is the size of the anterior inferior iliac spine. The muscle inserts via the quadriceps tendon into the patella and via the patellar tendon into the tibial tuberosity. The entire quadriceps group is supplied by the femoral nerve and acts to extend the leg. M. rectus femoris also flexes the femur after the leap.

4.3.12. *M. semitendinosus*

Several prosimian taxa retain two heads of origin for the *M. semitendinosus*; a caudal head arises from the transverse processes of the first few caudal vertebrae, and an ischial head arises from the ischial tuberosity. This condition is retained in tree shrews, lemurids, cheirogaleids, and Daubentonja. The caudal head is lacking among tarsiiids, indriids, and lorisiforms. The insertion of *M. semitendinosus* is usually in common with that of *M. gracilis* and *M. sartorius* into the anterior crest of the tibia. Among the taxa considered in this study, important variation exists in the distal extent of the insertion of *M. semitendinosus*. The flexor femoris nerve, a branch of the sciatic nerve, innervates the entire hamstring group. The functions of *M. semitendinosus* include flexion and medial rotation of the leg, as well as extension of the thigh. Along with the other hamstring muscles (*Mm. semimembranosus*, *flexor cruris lateralis*, *adductor magnus*, and *quadratus femoris*), the *M. semitendinosus* is an important propulsive muscle in leaping. The length of the moment arm of femoral extension by the hamstrings is approximated by the length of the ischium.

4.3.13. *M. semimembranosus*

M. semimembranosus is fairly constant in its morphology among the prosimians. It arises from the ischial tuberosity and sometimes from a variable length of the vertical ramus

of the ischium. It may be inseparable at its origin from M. presemimembranosus, when the latter muscle is present.

Insertion is into the knee joint capsule and by a strong tendon into the medial tibial condyle. M. semimembranosus acts to extend the thigh and to medially rotate the leg.

4.3.14. M. presemimembranosus

According to McArdle (1981), M. presemimembranosus is present in some prosimians although not in lorises, tarsiers, or tree shrews. He does not mention its absence or presence among galagines but suggests that it has become attached to M. adductor magnus among some prosimians. Its functions include extension and adduction of the thigh.

4.3.15. M. flexor cruris lateralis

This muscle is homologous to the long head of the M. biceps femoris of anthropoid primates. In all prosimians it arises from the ischial tuberosity, often in common with the ischial head of M. semitendinosus. It inserts into the lateral tibial condyle and also, to a variable extent, into the crural fascia. This powerful muscle serves as an extensor and lateral rotator of the thigh, and a flexor and lateral rotator of the leg. It is another important propulsive muscle whose moment arm is determined by the length of the ischium.

4.3.16. M. tenuissimus

This muscle, present only in tupaiids, is the homologue of the short head of *M. biceps femoris*. It takes its origin from the dorsal caudalis fascia, deep to the *M. gluteus superficialis*. Its insertion is into the crural fascia, distal to but continuous with the crural insertion of *M. flexor cruris lateralis*. Its functions include flexion and lateral rotation of the leg.

4.3.17. M. caudofemoralis

Among the prosimians, this extensor of the thigh is present in tupaiids, lemurids, cheirogaleids, galagids, and tarsiids and is absent from lorisids, indriids, and Daubentonia. It typically arises from the transverse processes of the first few caudal vertebrae, deep to *M. femorococcygeus*. Cheirogaleids and tarsiids have an ischial origin, while galagids have both an ischial and a vertebral origin. The insertion is into the posterior surface of the distal half of the femoral shaft.

4.3.18. M. gracilis

A relatively uniform muscle among prosimians, *M. gracilis* arises mainly from the symphyseal ramus of the pubis, as well as from a variable part of the adjacent horizontal and vertical pubic rami. Among the lorisids, *M. gracilis* has a very extensive origin from almost the entire pubis. The muscle inserts into the anterior tibial crest, often in common with *M. sartorius* and *M. semitendinosus*. It

is supplied by the obturator nerve, and is mainly an adductor of the thigh. Other functions include flexion and medial rotation of the leg.

4.3.19. M. pectineus

Another very uniform muscle among the prosimians, M. pectineus typically arises from the superior pubic ramus and inserts to a variable extent on the medial and dorsal aspect of the femur, distal to the lesser trochanter. M. pectineus usually has a double innervation, from both the femoral and the obturator nerve. It serves as an adductor and a flexor of the thigh.

4.3.20. Mm. adductores

The adductor group includes Mm. adductor magnus, adductor longus, and adductor brevis (pars longa and pars brevis). See Stern (1971), Uhlmann (1968), and McArdle (1981) for discussions of the distinguishing criteria and characteristics of the adductors. They arise from the pubis and part of the ischium and insert along the dorsal surface of the femur to a variable extent. The entire group is relatively uniform among the prosimians, serving mainly in adduction but also in flexion and sometimes in extension of the thigh. Innervation is always by the obturator nerve. The length of the moment arm of the adductor musculature (including Mm. gracilis and pectineus) is approximated by the length of the superior ramus of the pubis. In

terrestrial saltators, the emphasis on flexion and extension of the hindlimb occurs at the expense of adduction. Hence, these forms characteristically have a very short pubis (Howell 1944). Since prosimian saltators are also vertical clingers, they may require a stronger component of adduction in their hindlimbs.

4.4. Ratios

A series of 20 ratios was computed from the pelvic measurements (Table 11, Appendix A). The relative length of the ischium was analyzed in four different ratios. Ischial length was the numerator in each of these ratios, while the denominators were skeletal trunk length (P1), pelvic length (P2), iliac length (P3), and femoral length (P4). Ischial length, as measured here, is an approximation of the length of the moment arm of a group of femoral extensors including *Mm. quadratus femoris*, *adductor magnus*, *semitendinosus*, *semimembranosus*, and *flexor cruris lateralis*. These powerful extensors of the thigh arise mainly from the ischial ramus and tuberosity to insert onto the tibia and/or femur. In general, quadrupedal taxa tend to have longer ischia than do leapers or slow climbers. At the familial level, tupaiids have by far the longest ischia among the taxa analyzed here, followed by cheirogaleids, and then by lemurids and lepilemurids. The shortest ischia are always found in the indriids, galagids, and tarsiers, as well as in the slow-climbing lorisids. Among the three

families of leapers, the shortest relative ischial length is represented by the tarsiids in two of the ratios (P2 and P3), and in galagids (P1) and indriids (P4) by one ratio each. The four ratios present a remarkably consistent spectrum of increasing ischial length from the predominantly leaping galagos, tarsiers, and indriids, through the active quadrupeds of Madagascar (lemurids and lepilemurids) to the unspecialized quadrupedal cheirogaleids and tupaiids. This trend is most clearly documented in ratio P4, which is an approximation of the mechanical advantage of the hip extensor musculature. The combination of a short ischium and a long femur gives the leaping taxa a much lower mechanical advantage in hip extension than is conferred upon the more quadrupedal taxa by the combination of a long ischium and short femur. Smith and Savage (1956) have shown that a low mechanical advantage is often an adaptation for rapid limb movement.

No consistent pattern is evident in the intergeneric variation within the families Lemuridae, Lepilemuridae, and Indriidae. In Cheirogaleidae, however, Cheirogaleus has a slightly greater ischial length than does Microcebus, as shown in three of the four ratios calculated. Among the Lorisidae, the larger-bodied genera Nycticebus and Perodicticus have consistently longer relative ischial lengths than do their smaller relations Arctocebus and

Loris. Within the genus Galago, there is a consistent spectrum of decreasing relative ischial length from G. crassicaudatus through G. demidovii and G. alleni, to G. senegalensis. This result is consistent with the results at the familial level, that is, the more quadrupedal prosimians tend to have longer relative ischial lengths than do the more specialized leapers.

The relative length of the pubis was also used in four ratios with skeletal trunk length (P5), pelvic length (P6), iliac length (P7), and femoral length (P8) as the denominators. Pubic length is an approximation of the moment arm of the Mm. adductores. This relatively undifferentiated muscle mass arises along much of the pubis among prosimians and inserts into the medial border of the femoral shaft. The Lorisidae have by far the longest relative pubic length among prosimian primates. They are most closely approximated in this trait by the Cheirogaleidae and Tupaiidae. Tarsiers and galagos are intermediate in relative pubic length, while the shortest pubes are found in the Lemuridae, Lepilemuridae, and Indriidae. Among the Malagasy taxa there is a clear spectrum of decreasing pubic length as one proceeds from the generalized quadrupedal Cheirogaleidae, through the active quadrupedal Lemuridae and Lepilemuridae, to the leaping Indriidae. This same trend is seen among the species of Galago. Within this genus there are significant

differences in relative pubic length between the primarily leaping species G. senegalensis and G. alleni, and the more quadrupedal G. demidovii and G. crassicaudatus. In three of the four ratios the leapers show lower values than do the quadrupedal species. The mechanical advantage of the adductor musculature, as calculated in ratio P8, is clearly greater among slow-climbing and unspecialized quadrupedal prosimians than among the leapers and active quadrupedal taxa. At the familial level, relative pubic length does not, however, successfully distinguish between the latter two groups, nor does it link all three families of leapers. Rather, Indriidae appear to have significantly shorter pubes than do Galagidae and Tarsiidae.

Two ratios document the length of the ilium relative to skeletal trunk length (P9) and pelvic length (P10). The length of the ilium approximates the moment arm of the M. tensor fasciae femoris, an important flexor of the femur at the hip joint during the recovery stroke. In addition, it is a good measure of the length of attachment of the M. gluteus medius that arises along much of its lateral surface. Ratios P9 and P10 clearly indicate that leaping taxa have significantly longer ilia than do quadrupedal taxa. In both of these ratios tarsiids have the longest ilia, followed closely by galagids and indriids. The shortest ilia are found among Cheirogaleidae and Tupaiidae.

Among the Malagasy prosimians there is a clear spectrum of increasing relative iliac length from Cheirogaleidae to Lemuridae, Lepilemuridae, and finally Indriidae. The genus Avahi has the longest ilium among Indriidae, while Microcebus has a significantly longer ilium than does its relative Cheirogaleus. The Lorisidae show little intergeneric variation in this trait. As a family they are intermediate between leapers and unspecialized quadrupeds in relative iliac length. There is considerable interspecific variation in iliac length among the species of the genus Galago. Galago senegalensis and G. alleni have significantly longer ilia than do their more quadrupedal relatives G. demidovii and especially, G. crassicaudatus. Since all three predominantly leaping families are characterized by a relatively long ilium, we can hypothesize that increasing the moment arm of M. tensor fasciae femoris in femoral flexion may be an adaptation for leaping among prosimians.

The length of the pubic symphysis was analyzed in two ratios, one with skeletal trunk length (P11), and one with pelvic length (P12) in the denominator. In both of these ratios, the Lorisidae, especially the African genera Arctocebus and Perodicticus, are clearly distinguished from all other prosimian taxa by the possession of extremely short pubic symphyses. Lorisids are most closely approximated in this respect by the Cheirogaleidae,

especially Microcebus. Indriids have significantly longer pubic symphyses than the Lemuridae, Lepilemuridae, or the other leaping families (Galagidae and Tarsiidae). In addition, galagos and tarsiers show little difference from lemurids and lepilemurids in pubic symphysis length. Clearly, factors other than positional behavior influence the length of the prosimian pubic symphysis. Likely factors include bodily size and obstetric requirements. There is little interspecific variation in relative length of the pubic symphysis within the genus Galago.

The dorso-ventral length of the pelvis was also used in two ratios in which skeletal trunk length (P13) and pelvic length (P14) were used as denominators. In general, Malagasy taxa have pelves which are shorter in the dorso-ventral direction than those of non-Malagasy prosimians. Tarsiid and lorisid pelves are the longest dorso-ventrally among prosimians, and are followed by those of galagos and lastly, by tupaiids. While ratio P13 fails to distinguish between the four Malagasy families, ratio P14 indicates a spectrum of increasing dorso-ventral length from Indriidae and Lepilemuridae to Lemuridae and Cheirogaleidae. Again, no clear pattern of interspecific variation can be seen within Galago.

Ratios P15 and P16 are descriptive measures of the length of the ischio-pubic ramus relative to skeletal trunk length and to pelvic length, respectively. Both ratios clearly distinguish the Lemuriformes from the Lorisiformes and Tarsiiformes. Tarsiers, galagos, and lorises have significantly longer ischio-pubic rami than do tupaiids or any of the Malagasy lemuriforms. Both ratios further indicate a progressive decrease in ischio-pubic ramus length from Cheirogaleidae through Lemuridae and Lepilemuridae, to Indriidae. At the generic and specific levels, few interesting patterns emerge from these data. Ratio P16 may indicate a greater ischio-pubic length in Cheirogaleus than in Microcebus, and in Hapalemur compared to Lepilemur. However, these conclusions must remain tentative due to the high variability in these data, as reflected in the large standard deviations and standard errors of the mean. There is no clear pattern of interspecific variation in Galago.

Ratios P17, P18, and P19 document the width of the iliac crest relative to skeletal trunk length, pelvic length, and iliac length, respectively. All three ratios clearly indicate that the indriids possess the widest, and the lorisids and cheirogaleids the narrowest iliac crests among prosimian primates. Lepilemuridae and Lemuridae are consistently intermediate in iliac crest length between the extremes represented by Indriidae and Cheirogaleidae.

Tupaids tend to have a relatively wide iliac crest, while galagos and tarsiers possess fairly narrow iliac crests. The broadened ilium among the Indriidae provides a large area for the attachment of *M. gluteus medius*, one of the powerful hip extensors in this leaping family. The large amount of variability in the data make it difficult to see any meaningful patterns at the generic and specific levels of analysis.

The final pelvic ratio (P20) is a measure of the maximum cranio-caudal length of the pelvis relative to skeletal trunk length. The data clearly demonstrate that leaping prosimians are characterized by relatively longer pelvises than are quadrupeds or slow-climbers. Tarsiers have by far the longest pelvises, followed by indriids, lepilemurids, and galagids. The Malagasy families are neatly arrayed in decreasing relative pelvic length from Indriidae to Lepilemuridae, Lemuridae, and Cheirogaleidae. While all four loroid genera possess short pelvises, this trait is especially prevalent in the smaller genera, Arctocebus and Loris. Among the Malagasy genera, a longer pelvis is found in Lepilemur as compared to Hapalemur, in Lemur as compared to Varecia, and in Microcebus as compared to Cheirogaleus. There is no clear pattern in comparable data from the various species of Galago.

4.5. Discriminant Analysis

4.5.1. Results

Multiple discriminant function analysis was used in the analysis of three different pelvic data sets; the raw data, logarithmically transformed data, and ratios using STL as the denominator. While plots from each of the three runs present essentially the same information for the first two discriminant axes, the amount of overlap between taxonomic groups is greatest in the raw data plots and least in the STL ratio plots. The logged data plots closely resemble the raw data, with perhaps slightly less overlap between and somewhat better cohesion within groups. Consequently, the ratio run will be the main object of discussion below.

Univariate and bivariate plots of family means are presented for each of the first three discriminant axes in each discriminant run (Appendix E). These data are from the SPSS runs, and were plotted on a Macintosh computer using Microsoft Chart software. Only the first three discriminant axes are plotted and discussed because in all cases they account for the overwhelming majority of between-group variance (greater than 90%).

The univariate plots of the first three discriminant axes reveal some interesting patterns on initial examination. Discriminant axis one appears to distinguish between three sets of taxa, with a small degree of overlap between them. Indriidae and Tupaiidae have high values on

axis one, Tarsiidae and Lorisidae have low values, and a central group consists of Lepilemuridae, Lemuridae, Galagidae, and Cheirogaleidae. Discriminant axis two likewise discriminates between three groups of taxa. Indriidae and Tarsiidae have the highest values on this axis, Tupaiidae and Cheirogaleidae have the lowest values, and the central group consists of Lepilemuridae, Lemuridae, Galagidae, and Lorisidae. One difference between the ratio plots and those using raw and logged data can be seen along axis two where, in the latter two plots, Indriidae are alone at the high end of the scale. Also in these plots, Tarsiidae are part of the central group, closely allied with Galagidae. Discriminant axis three clusters to a slight extent the Indriidae, Tarsiidae, and Galagidae at the negative end of the spectrum in the raw data plots. The logged data plot emphasizes, however, the uniqueness of Tarsiidae at the expense of any clustering with Indriidae and Galagidae. Overall, the patterns demonstrated in these plots clearly have nothing to do with bodily size, and we can quickly dismiss the hypothesis that any of these axes are discriminating solely or mainly on the basis of size. The alternative hypothesis would be that these axes are discriminating on the basis of differences in shape that can be related to the original predictor variables.

Table 13. Order of entry of variables into pelvic discriminant analyses.

A. STL Ratio Analysis

1. Ischio-pubic ramus length
2. Ilium length
3. Pubic symphysis length
4. Ischium length
5. Iliac crest length
6. Pubis length
7. Total pelvic length
8. Dorso-ventral pelvic length

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B. Log Analysis

1. Iliac crest length
2. Total pelvic length
3. Skeletal trunk length
4. Pubis length
5. Ischium length
6. Pubic symphysis length
7. Ilium length
8. Dorso-ventral pelvic length

C. Raw Data Analysis

1. Ischium length
2. Ilium length
3. Skeletal trunk length
4. Dorso-ventral pelvic length
5. Iliac crest length
6. Total pelvic length
7. Ischio-pubic ramus length
8. Pubic symphysis length

Table 14. Canonical coefficients and correlations for pelvic discriminant analyses: Axes 1 and 2. *

FIRST DISCRIMINANT AXIS							
VARIABLE	RAW		STL		LOG ¹⁰		
		r		r		r	
1. Ischium l.	1.877	.22	.562	.30	1.811	.13	
2. Pubis l.	-1.214	-.09	-.283	-.40	-.994	-.08	
3. Ilium l.	.298	.14	-.120	-.06	-.566	.05	
4. Symphysis l.	.385	.38	.379	.47	.627	.29	
5. Dorso-ventral l.	-1.044	.02	-.607	-.27	-2.121	-.01	
6. Iliac crest l.	.582	.31	.585	.29	1.498	.18	
7. Pelvic l.	.463	.15	.187	.03	1.280	.07	
8. Ischio-pubic l.	-.770	-.14	-.364	-.53	-1.367	-.11	
Percent Dispersion	53%		62%		52%		
SECOND DISCRIMINANT AXIS							
VARIABLE	RAW		STL		LOG ¹⁰		
		r		r		r	
1. Ischium l.	-1.851	.37	-.774	-.22	-1.940	.22	
2. Pubis l.	-.163	.47	-.314	.13	-.528	.31	
3. Ilium l.	5.852	.58	1.003	.59	7.044	.43	
4. Symphysis l.	-.425	.38	.116	.22	-.091	.27	
5. Dorso-ventral l.	.566	.46	.382	.25	-.076	.31	
6. Iliac crest l.	.624	.54	.525	.44	.914	.40	
7. Pelvic l.	-3.853	.52	-.165	.38	-4.293	.35	
8. Ischio-pubic l.	-.510	.43	-.134	.09	-.397	.30	
Percent Dispersion	28%		24%		32%		
Cumulative Percent	81%		86%		84%		

* See Table 15 for explanation.

Table 15. Canonical coefficients and correlations for pelvic discriminant analyses: Axis 3.

VARIABLE	THIRD DISCRIMINANT AXIS					
	RAW	r	STL	r	LOG	r
1. Ischium 1.	1.513	.54	.076	.31	.942	.41
2. Pubis 1.	-.380	.40	.137	.31	.450	.37
3. Ilium 1.	-.859	.48	-.044	.03	-.498	.39
4. Symphysis 1.	-.976	.21	.821	.82	-1.048	.14
5. Dorso-ventral 1.	-.641	.44	.436	.60	2.316	.33
6. Iliac crest 1.	-.596	.19	-.332	.07	-.105	.30
7. Pelvic 1.	.276	.50	-.366	.13	-5603	.40
8. Ischio-pubic 1.	-.134	.51	.247	.27	-.458	.38
Percent Dispersion		10%		7%		10%
Cumulative Percent		91%		93%		94%

The data in Tables 14 and 15 are from the SPSS DISCRIMINANT analyses of pelvic data. The coefficients presented are the standardized canonical discriminant function coefficients and the r values are pooled, within-group correlations between canonical discriminant functions and discriminating variables. Correlations of .30 or greater are generally considered to be significant. Dispersion and Cumulative Dispersion are the percentages of the total between-group variance that are accounted for by the discriminant axes.

Referring now to specific taxa and to their positions on the bivariate plots of the first three discriminant axes, we can look for patterns that relate to the positional behavior of these groups. The ratio plot of axes one and two distinguishes between the unspecialized quadrupedal Tupaiidae and Cheirogaleidae and their more cursorial or saltatorial relations. In all three runs, the tupaiids are closest to the cheirogaleids, and the separation of these two groups from the rest of the prosimians is mainly effected along axis two. The slow-climbing lorisids are also in a unique position relative to all other prosimians, but this is mainly along axis one. Their unique position is seen to even better effect on the raw and logged data plots of the first two axes. Interestingly, the lorisids are closest in all three plots to the phylogenetically close but functionally very different galagids. In all three plots, the Malagasy taxa are clearly arrayed in a band extending across the plot from upper right side (Indriidae) to lower left (Cheirogaleidae). In all plots, the functionally similar and phylogenetically related Lepilemuridae and Lemuridae show a great deal of overlap with each other, and always bridge the gap between Indriidae and Cheirogaleidae. In addition, Lepilemuridae and Lemuridae are always much closer to the Galagidae than are the Indriidae. The ratio plot is the only plot that

clearly separates Tarsiidae from Galagidae; both the raw and logged data plots align these two families very closely with much overlap. While the ratio plot aligns the tarsiers with the indriids along axis two, on axis one the galagos and tarsiers are consistently much closer to each other than either is to Indriidae. The raw data plots seem to separate the three saltatorial Families (Tarsiidae, Indriidae, and Galagidae) from the rest of the prosimians along axis three. While these results are clearly of interest, it must be noted that the STL and the log plots do not give the same results on the third discriminant axis. The ratio plot separates Tarsiidae and Tupaiidae from the rest of the prosimian taxa, while the log data plot only clearly separates the tarsiers, and to a lesser extent the galagos, from the other groups.

4.5.2. Evaluation of predictor variables

There are two steps involved in the evaluation of the predictor variables undertaken here. The first step is to discover, by the use of the three methods described in Section 3.4., which variables are the important discriminators along each of the first three axes. With one or several key variables noted for each discriminant axis, the pelvic ratio data can be used to try to identify the range of values for a variable that determines its placement along the axis. The first method for discovering the importance of individual variables is examination of

the order of their entry into the discriminant equation. As can be seen in Table 13, there is a substantial degree of variation in the order of entry into the three different discriminant runs. However, four variables are most commonly entered into the equation in the early steps. They are iliac crest length, ischial length, iliac length, and ischio-pubic ramus length. We can tentatively state that these four variables may be significantly contributing to the separation seen in the discriminant analysis.

Unfortunately we cannot, by this method alone, link any of these variables to the separation along any specific discriminant axis. To do that, we must look at the canonical coefficients or loadings of the individual variables on the first three axes, and at the correlations between the variables and the discriminant axes.

Table 14 presents the canonical coefficients and correlations for the SPSS runs. Due to the relatedness of these two evaluative techniques, they will be discussed together for each of the first three discriminant axes. On the first axis there is much variation in the particular variables that were picked as significant by these two methods, and seemingly little agreement between the two methods. For example, in the raw data run, two of the variables with the highest loadings also have the lowest correlations (pubic length and dorso-ventral length).

Similarly, in the ratio and logged data runs, high correlations seem to be linked with low loadings or vice versa. Indeed, no variables are significantly correlated with axis one in the logged data run. Two variables do, however, stand out as having consistently high loadings. These are ischial length and dorso-ventral length. Two variables may be important discriminators along axis one on the basis of correlations on the STL plot. These are pubic symphysis length and ischio-pubic ramus length.

Axis two presents a clearer picture of the contribution of several variables to its discrimination. On all three runs, iliac length has the highest loading among pelvic variables, and it is also very significantly correlated with this axis in each of these runs. Two other variables with a combination of high loadings and significant correlations are pelvic length and ischial length.

Choosing significant contributors to the separation along axis three is made difficult by the large number of variables that have relatively high r values on the SPSS discriminant runs. In addition, the variation in magnitude of the canonical coefficients for given variables between raw, log, and STL runs is enormous. Dorso-ventral length of the pelvis has consistently high loadings. In addition, dorso-ventral length is significantly correlated with axis three. Pubic symphyseal length also has consistently high loadings, especially on the runs using STL ratio data,

where it has the highest correlation seen in this entire study ($r=.82$). Clearly, dorso-ventral length and length of the pubic symphysis are two important contributors to discrimination along axis three. However other variables, for example ischial length, iliac length, and skeletal trunk length may also contribute significantly.

Having identified several variables as having special significance in accounting for the separation of taxa along each of the first three discriminant axes, we can test these claims by referring back to the plots and comparing the alignment of taxa along the discriminant axes with the values of these same variables obtained from the analysis of pelvic ratios. For example, if iliac length is truly the most important discriminator along axis two, we would expect to see forms with short ilia at one end and forms with relatively long ilia at the other end of that axis.

Comparison of the discriminant plots and the relative length of the ischium indicates that ischial length alone cannot satisfactorily explain the separation along axis one. Families with the shortest relative ischial length include Tarsiidae, Galagidae, Indriidae, and Lorisidae. Yet on the discriminant plots, these taxa span almost the entire range of axis one. In addition, Tupaiidae, with the relatively longest ischia, and Indriidae, with relatively very short ischia are both situated at the extreme right

end of axis one. The ratios involving dorso-ventral length agree better with the separation along axis one, but again not completely. The Lorisidae, Galagidae, and Tarsiidae, which are all at the left end of axis one, have the largest values on both dorso-ventral pelvic length ratios.

Tupaiaidae and all the Malagasy taxa have short dorso-ventral pelves and are all placed from the middle to the right along axis one. One variable that shows almost complete agreement between ratio scores and position along axis one of the discriminant plots is ischio-pubic ramus length. Tarsiers and lorises consistently have the longest relative ischio-pubic ramus length, while tupaiaids and indriids have the shortest. The taxa that are centrally located in the discriminant plots are also intermediate in relative ischio-pubic length. The ischio-pubic ramus length was one of the four variables usually entered into the discriminant equation during the early steps, and it also had a very significant correlation with axis one in the STL discriminant analysis, as well as fairly high loadings on axis one on the raw and logged data discriminant runs. It appears to be a good discriminator along axis one.

We have seen that iliac length was unequivocally the most important discriminator along axis two in all discriminant runs both on the basis of loadings and correlations. Both ratios depicting relative iliac length show a clear progression from Indriidae and Tarsiidae,

which have the longest ilia among prosimians, to intermediate forms like the Galagidae, Lepilemuridae, Lemuridae, and Lorisidae, to the taxa with the shortest ilia, Cheirogaleidae and Tupaiidae. This picture agrees perfectly with the separation along axis two of the discriminant analysis, confirming the importance of iliac length in determining this discrimination. Both the ratios and the discriminant analyses show the same progression among the Malagasy taxa from Indriidae, through Lepilemuridae and Lemuridae, to Cheirogaleidae. Two other variables that appear to be of some importance in determining separation along axis two of the discriminant runs are dorso-ventral length and ischial length. Again, good agreement exists between the relative placement of taxa along discriminant axis two and their rank order on the basis of relative length of dorso-ventral pelvis and of the ischium, and it can be stated with confidence that these two variables contribute to the separation along discriminant axis two.

It has proven difficult to relate the separation along axis three to the relative length of the pubic symphysis or the dorso-ventral pelvis. Examination of the ratios involving these two variables indicates that they cannot be used to explain the clustering of Indriidae, Galagidae, and Tarsiidae. That Lemuridae appear to be most distant on axis

three from the saltatorial group is also not easily explained. In most morphological measures, the lemurs are much more similar to leapers than are, for example, Tupaiidae. Perhaps the fact that more than half of the predictor variables are significantly correlated with axis three is a hint that a single variable or two are not overwhelmingly determining the separation along this axis. The most conservative interpretation may be that a complex interaction of variables is affecting the discrimination along axis three. It may be impossible, given the present data set, to answer this question with greater precision.

4.6. Functional Anatomy

4.6.1. Biomechanics

A consideration of the basics of biomechanics, the application of Newtonian physics to problems involving animal and human movement, is a necessary prerequisite to the following functional analysis. The main emphasis of this section is on the often stated view that bone-muscle systems in animals are adapted for the production of either powerful or rapid movements. The speed vs. power dichotomy can be traced back at least to Gregory (1912), and has been accepted by many other authors, including Elftman (1929), Waterman (1929), Howell, (1932, 1944), Smith and Savage (1956), Walker (1967), Stern (1974), and McArdle (1981). The general theory accepted by almost all of these authors is that short muscular moment arms are optimally designed

to provide rapid movements, while long moment arms sacrifice speed for powerful contractions. A moment arm can be defined as the perpendicular distance from the line of action of a force to the axis of rotation. Some authors call muscular moment arms "lever arms", and load or resistance moment arms "load arms" (the distance from the axis of rotation to the point of application of the load). Thus, Smith and Savage (1956) calculate the "mechanical advantage" of a bone-muscle system as the ratio of lever arm to load arm. Large mechanical advantages are said to characterize systems that rely on power at the expense of speed, while low mechanical advantages can be found in joints that are specialized for rapid movements.

Stern (1974) very cogently demonstrated that the speed-power dichotomy is more complex than recognized by most previous authors. He used a mathematical model that relied on recent advances in muscle physiology to perform computer simulations of the effects of changed sites of muscular attachment on the dynamic characteristics of bone-muscle systems. Comparing physiologically identical muscles (same length of contractile tissues, same cross-sectional areas, same rate of contraction, same angle of fibers), Stern found that in general it is true that muscles that attach close to joints (and hence have small moment arms) allow greater velocity and less power than muscles that attach at

a greater distance from the joint. However these results were qualified in several important ways. First, Stern discovered that there is an optimum moment arm length for physiologically identical muscles such that either increasing or decreasing it will result in lessened dynamic performance. Therefore, while it is true that shorter moment arms in general yield faster movements, it is not true that reduction of muscular moment arms will always produce greater velocity. Second, Stern found that

"a muscle ideally suited to produce high velocity of movement at a certain position of the limb is not best designed to bring the limb to this position most quickly" (Stern 1974:422).

His results indicate that larger moment arms will bring the limb to a given position in the shortest time due to the greater initial acceleration attained, while smaller moment arms produce greater velocities at a given point in the limb movement. Third, Stern concludes

"that these muscles which are ideally suited for producing high velocity at some determined position retain their ability to supply further torque at this point whereas those muscles designed to bring the limb to the same position most quickly are forced to contract so rapidly when the position is reached that they can no longer exert force" (Stern 1974:422).

With this background in theory, we can now look at the results of the pelvic analysis with an eye toward the functional differences exhibited by prosimians of differing positional regimes.

4.6.2. Ischium

As a result of the origin of the hip extensor muscles (Mm. flexor cruris lateralis, semitendinosus, semimembranosus, adductor magnus, quadratus femoris) from its ramus and tuberosity, the length of the ischium is widely accepted as a good osteological approximation of the moment arm of these muscles (Walker 1967, 1974; Smith and Savage 1956; McArdle 1981; Howell 1932, 1944). Among some non-primates, the simple speed vs. power dichotomy appears to accurately explain relative ischial length. Smith and Savage (1956) note the long ischium in powerful aquatic mammals like Phoca, and the short ischium found among cursorial Equiidae. Since bipedal saltators, like cursors, require great accelerations in hip extension, we can expect to find a short ischium among these taxa. Indeed, Walker (1967) first noted the uniquely short ischium among prosimian saltators. Zuckerman et al. (1973) further noted that a short ischium distinguished Lorisiformes (both Galagidae and Lorisidae) from all other primate taxa in their study. These results have since been confirmed by Godfrey (ms.), McArdle (1981), and myself. Interestingly, non-primate terrestrial saltators, both marsupial (Elftman 1929) and placental (Howell 1932), have long ischia compared to their quadrupedal relatives.

One obvious, if somewhat facile, explanation for the difference in ischial length between arboreal primate and terrestrial non-primate saltators is that the animals are doing entirely different things, in spite of the fact that we label both "leapers". The importance of the large "counterbalancing" tail in marsupial (Elftman 1929) and rodent (Howell 1932; Bartholomew and Caswell 1951) saltation is well known. Howell (1944:47) has gone so far as to state that "saltation in mammals requires a heavy tail as a counterbalance". Yet a tail does not appear to be an important element in prosimian leaping, and is, indeed, totally lacking in Indri (Tattersall 1982). Additionally, in light of Stern's (1974) findings, we can hypothesize that the two groups are maximizing different kinds of velocity, resulting in different optimal moment arm lengths. While acknowledging the significant behavioral differences between primate and non-primate leapers, Godfrey (ms.) suggests that the shortened ischium among primates may be associated with habitual femoral extension at the hip, and not specifically with leaping. In this way she explains the similarly short ischium of both bipedal Homo and of the specialized hanger Paleopropithecus. McArdle (1981) notes that the prosimian leapers are also characterized by proximal insertions of the hamstrings muscles into the tibia. This would seem to be another adaptation for rapid extension at the hip (Gregory 1912;

Stern 1974). It seems safest to state that the short ischium among prosimian leapers is an adaptation that allows a very rapid extension of the hip with little loss of power. It is unclear why the Lorisidae are also characterized by a very short ischium.

4.6.3. Ilium

As noted above, the length of the ilium is greatest among the leaping prosimians and least among unspecialized quadrupeds (e.g., Tupaiidae and Cheirogaleidae). Several important muscles of the hip and thigh arise along the ilium, both the gluteal group of extensors and a number of important hip flexors (e.g., Mm. tensor fasciae femoris, sartorius, rectus femoris, and iliacus). The length of the ilium affects the dynamic characteristics of these muscles in a number of ways. Since the M. gluteus medius, a powerful femoral extensor, arises along much of the length of the lateral surface of the iliac blade, lengthening of the ilium increases the area of origin and the average length of the fibers of this muscle. Since all skeletal muscle fibers contract approximately one third of their length, longer fibers contract an absolutely greater distance, and thus bring the distal end of a bone through a greater distance. Since similar muscle fibers, short or long, contract at a uniform rate, longer fibers confer greater velocity than do physiologically similar short

muscle fibers (Gowitzke and Milner 1980). With respect to the femoral flexors, it is clear that an increase in length of the iliac blade increases the length of the moment arm of the M. tensor fasciae femoris which arises from the iliac crest and inserts into the femoral fascia. The moment arms of the other femoral flexors would probably also increase with a longer ilium, but not to the same degree as that of M. tensor fasciae femoris. An increase in iliac length, then, would appear to have two different effects: namely an increase in the velocity of gluteal extension of the femur, and increased power of femoral flexion with the added benefit (according to Stern 1974) of flexing the extended femur during the recovery stroke of locomotion in a shorter time.

A survey of the relative length of the ilium among non-primates yields some interesting results. Gregory (1912) and Smith and Savage (1956) argue that long and narrow ilia are characteristic of cursorial quadrupedal mammals, while graviportal mammals tend to have short and broad iliac blades. Smith and Savage (1956) go on to hypothesize that two different muscle groups can be functionally differentiated in femoral extension at the hip among mammals. The gluteal group, with short moment arms but extensive origins along the iliac blade are the "fast" extensors that provide a late burst of acceleration, while the ischial group, arising from a longer ischial moment

arm, provide the power needed in early stages of leaping or running to overcome inertia. Howell (1932) found that the saltatorial rodents that he investigated were characterized by short ilia, especially in the distal part of the ilium, between the sacral articulation and the acetabulum. Again, we can only note the apparent contradiction between terrestrial, non-primate saltators and the arboreal, prosimian leapers in this trait and assume that the significant biomechanical differences in leaping must explain this seeming paradox. Howell later disagreed with Gregory (1912) and stated that the

"length of the ilium...is not a cursorial character, although a long ilium is frequently found present in cursorial species" (Howell 1944:167).

Rather, Howell (1944) argued that a long ilium is a cushioning mechanism acting by means of the attachment of ligaments and back muscles along its length for transmitting stresses from the femur incurred during locomotion. While cursorial and saltatorial animals certainly incur large stresses during locomotion, other, mainly large-bodied quadrupeds, would also be expected to have long ilia if Howell (1944) were correct.

Stern (1974) and Waterman (1929) both suggest that the functional significance of the long ilium in cursorial mammals and, by extension, in saltatorial prosimians, lies in its effect on the moment arm for flexion of the femur on

the hip. Femoral flexion mainly comes into play during the recovery stroke of mammalian locomotion, after the extensors have provided the main propulsion. Both cursorial quadrupeds and bipedal saltators need to protract the extended hindlimb in the shortest possible time: cursors, in preparation for the next propulsive stage, and saltators in preparation for landing. As a result, we would expect a greater moment arm for femoral flexion than for extension. Indeed, Stern (1974) states that the moment arm of the M. tensor fasciae femoris, an important femoral flexor, is the longest in the hindlimb. The long ilial moment arm (flexion) in combination with the short ischial moment arm (extension) appear to be equally well adapted for rapid running on all fours (Stern 1974) and for rapid bipedal leaping in the trees.

In his original diagnosis of the morphology of vertical clingers and leapers, Walker stated that a narrow, bladelike ilium was characteristic of indriids, tarsiids, and galagids (Walker 1967; Napier and Walker 1967). The results presented here agree with respect to Tarsiidae and Galagidae. These latter families are joined by Lorisidae and Cheirogaleidae in having very narrow iliac blades. Contrary to Walker, however, indriids are distinguished from all other prosimians by virtue of their very broad ilia (Tattersall 1982; Godfrey ms.). Lemuridae,

Lepilemuridae, and Tupaiidae also have broad ilia, although consistently less wide than those of Indriidae. Both Tattersall (1982) and Godfrey (ms.) state that the function of the broadened indriid ilium is to provide a broad area of attachment for the large Mm. gluteus medius and iliacus, which arise from its lateral and medial surfaces, respectively. Howell (1944:166) adds the effects of abdominal muscles and "ligamentous factors, which are hard to evaluate" in determining the breadth of the ilium. The powerful Mm. erector spinae in saltatorial macropodids (Elftman 1929) and in indriids (Tattersal 1982) may also affect the width of the ilium. These intrinsic muscles of the back are important in hyperextension of the vertebral column during leaping, and arise above the proximal ilium, along the lumbar and sacral vertebrae.

4.6.4. Pubis

Few authors have discussed or presented data on the relative length of the pubis among mammals. The pubis provides attachment for the adductor musculature of the hindlimb, and pubic length can be considered an approximation of the length of the adductor moment arm. Howell (1944) states that pubic length is shortest among taxa that confine their hindlimb movements to the parasagittal plane of flexion and extension, and thus deemphasize the importance of adduction. Quadrupedal cursorial animals would be expected to have short pubes, as

would terrestrial bipedal saltators. Prosimian saltators, while they strongly emphasize flexion-extension in locomotion, also rely on femoral adduction while clinging in vertical postures to trunks or branches. There must, therefore, be a compromise in the length of their adductor moment arm. Among prosimian primates, the longest pubis is found among the slow-climbing Lorisidae, followed closely by the unspecialized quadrupedal Cheirogaleidae and Tupaiidae. The small-bodied leapers (Galagidae and Tarsiidae) have intermediate pubic lengths, while the Malagasy taxa have the shortest pubes in the suborder. My predictions are partially realized in this matter, in that the taxa with few or no cursorial habits retain the longest pubes. Pubic length also clearly distinguishes galagos and tarsiers from indriids. The significant difference in pubic length between these groups may be related to differences in bodily size and associated differences in clinging behavior.

Other aspects of pubic morphology in this analysis include pubic symphyseal length, ischio-pubic ramus length, and dorso-ventral length of the pelvis. Pubic symphyseal length is clearly more closely related to parturition than to locomotion (Howell 1944), and is thus not easily analyzed in a study of this sort. Both ischio-pubic ramus length and dorso-ventral pelvic length are compound

measures which include aspects of both pubic and ischial size and shape. Neither is easily related to discussion of locomotion.

4.7. Summary

To summarize, we can return to Walker's original diagnosis of the pelvis among vertical clingers and leapers. Walker (1967, 1974; Napier and Walker 1967) suggested that a short ischium and a long ilium with prominent iliac spines and a blade that widens with increasing bodily size were the pelvic traits that linked Galagidae, Tarsiidae, and Indriidae. The results presented here support only a part of these conclusions.

With respect to the length of the ilium and of the ischium, my results completely agree with Walker's. Both the analysis of the pelvic ratios and the discriminant analysis indicate the presence of a short ischium in combination with a long ilium among leaping prosimians. The functional analysis presented here explains the short ischium as a means of lowering the mechanical advantage of femoral extension by the ischio-pubic musculature, resulting in rapid extension with no loss of power. The long ilium has a twofold effect on muscular function at the hip. First, it increases the moment arm of M. tensor fasciae femoris, thus allowing this important femoral flexor to rapidly prepare the hindlimb for landing after a leap. Second, it increases the area and length of origin of

M. gluteus medius, one of the femoral extensors that plays an important role in the propulsive stage of the leap. In addition, we noted the paradox that non-primate mammalian saltators are characterized by the exact opposite set of pelvic traits, namely, a long ischium and a short ilium.

On the other hand, leaping prosimians do not appear to cluster on the basis of either prominent iliac spines or of iliac width. Both of these traits, in fact, link the "hindlimb-dominant" Malagasy taxa (Lemuridae, Lepilemuridae, Indriidae), but distinguish these from Tarsiidae and Galagidae. Godfrey (ms.) has convincingly refuted Walker's (1967) argument concerning allometry and the width of the ilium. She argues that since the width of the ilium is greater among all Malagasy taxa (leapers and quadrupeds) than among tarsiers and galagos, one can just as easily argue that there is an "allometric" relationship that links galagos, tarsiers, and lemurs. In addition, examination of the ilium in the approximately equal-sized Avahi laniger and Galago crassicaudatus shows by how much the indriid ilium differs from the galagid.

While this study failed to discover any other pelvic traits that clearly link all vertical clinging and leaping prosimians, several traits did appear to link Galagidae and Tarsiidae to the exclusion of Indriidae. Relative to pelvic length, the former families possess a longer pubis and a

longer ischio-pubic ramus than Indriidae, while the relative length of the pubic symphysis is greater in Indriidae. The great similarity in pelvic morphology between Galagidae and Tarsiidae is also revealed by examination of the discriminant plots. These plots also indicate the essential pelvic similarity of Indriidae, Lepilemuridae, and Lemuridae. Indeed, the four Malagasy families form a linear array in most of the discriminant plots in which Indriidae are consistently closer to Lepilemuridae and Lemuridae than they are to either Galagidae or Tarsiidae. In many ways the pelvic morphology of the indriids appears to be an exaggeration of a pattern common to all of the Malagasy families, rather than a "leaping" morphology distinct from that of non-leaping Malagasy taxa and similar to that of non-Malagasy leapers. Thus, the VCL hypothesis is not strongly supported by the data on pelvic structure.

Chapter 5. The Prosimian Tarsus

5.1. Introduction to Chapter 5

The mammalian foot skeleton may be divided into three anatomical regions: tarsus, metatarsus, and phalanges. Jouffroy (1975) and Schultz (1963a, 1963b) have presented quantitative data on the length of the various parts of the pedal skeleton among prosimians, while Szalay and Decker (1974) and Decker and Szalay (1974), building on the work of Schaeffer (1947), Barnett (1955, 1970; Barnett and Napier 1952) and Manter (1941), have discussed the tarsal joints and their axes of rotation among extant and extinct prosimian primates. My interest here is the highly specialized condition of tarsal elongation found among some prosimian taxa, and in its effect on the leverage involved in plantarflexion by the *Mm. triceps surae*. The bones routinely involved in tarsal elongation among prosimians are the calcaneus and navicular, and this condition seems to be limited to the non-Malagasy leaping families, namely Galagidae and Tarsiidae.

While the presence of tarsal elongation among Galagidae and Tarsiidae has been noted for over 100 years (Murie and Mivart 1872; Mivart 1873), the functional or biomechanical significance of this trait has been ignored or misunderstood for much of this time. In addition, there have been no studies presenting comparative data on tarsal

length from a large number of prosimian taxa, each with a reasonably large sample size. After describing the morphology of the tarsal bones and extrinsic muscles of prosimian feet, I present a series of ratios which clearly indicates the nature and extent of tarsal elongation among prosimian primates (Table 10 and Appendix B). Finally, I discuss the history of the study of tarsal elongation and present a functional analysis of the significance of this characteristic to the leaping behavior of some prosimians. Due to the uniquely specialized pedal morphology of the Lorisidae, this family has not been included in the analysis that follows.

5.2. Osteology

In this section I briefly describe the morphology of the tarsal bones among prosimian primates. Important anatomical landmarks that mark either the attachment areas of muscles or the course of their tendons are noted. The major joints of the tarsus are described in terms of their articular facets and the movements allowed therein. Of the seven tarsal bones, my interest is mainly on the talus, calcaneus, navicular, and cuboid. In general, these bones form the joints that allow plantarflexion, dorsiflexion, inversion, and eversion of the pedal skeleton. The calcaneus and navicular bones are subject to extreme elongation among some of the leaping families of

prosimians, and this is indeed, the main subject of analysis in the discussion of the tarsal ratios.

The calcaneus is involved in two important joints of the foot, the subtalar and the calcaneo-cuboid joints. Both of these joints allow rotation of the distal foot around its long axis in the movements of inversion (supination) and eversion (pronation). The subtalar joint is actually a compound joint which includes the talocalcaneal and the talocalcaneonavicular joints (Barnett 1970). There are two major facets on the dorsal aspect of the calcaneus that take part in the subtalar joint. Medially, the sustentaculum tali is a flat, oval articular area which accommodates the inferior surface of the talar neck. Postero-laterally, the posterior talar facet is a convexly arched surface which articulates with the concave posterior calcaneal facet of the talus. The thin, non-articular area separating the sustentaculum tali from the posterior talar facet is the calcaneal sulcus. Together with the talar sulcus, it forms the tarsal sinus. An interosseous ligament runs between these two sulci to attach calcaneus and talus.

The calcaneocuboid joint is also important in inversion and eversion of the foot. In fact, Szalay and Decker (1974:255) have stated that short of the opposability of the hallux, the calcaneocuboid "pivot" joint is "probably the most significant pedal adaptation of primates to the arboreal substrate". The cuboid facet of the calcaneus is a

semilunar articular surface with a depressed notch medially. A small projection from the proximal surface of the cuboid inserts into this depression, allowing medial and lateral rotation of the entire foot distal to this articulation. While not restricted to primates (a similar condition is found among arboreal marsupials), the calcaneocuboid pivot joint is an adaptation that allows the foot the postural versatility needed for support in a discontinuous and unpredictable arboreal environment (Decker and Szalay 1974). In addition, a small synovial joint is present between the shafts of the calcaneus and navicular bones among the Galagidae (Hall-Craggs 1966b) who, along with Tarsiidae, are characterized by extreme elongation of these two bones.

Posteriorly, the calcaneus bears the tuber calcanei for insertion of the calcaneal tendon. This powerful tendon is formed of the fusion of the tendons of *M. soleus* and of the lateral and medial heads of *M. gastrocnemius*. These muscles are the major plantarflexors of the foot about the talocrural joint, and are of crucial importance in leaping animals. Other noteworthy anatomical points on the body of the calcaneus are the groove for the tendon of *M. flexor digitorum fibularis* and the lateral tubercle. The *M. flexor digitorum fibularis* tendon runs anteriorly across the calcaneus inferior to the sustentaculum tali on the medial

aspect of the bone, and leaves a variably developed groove there. The lateral tubercle, which may or may not be homologous to the peroneal tubercle of fossil primates (Decker and Szalay 1974), is a small bump on the lateral aspect of the calcaneus near the anterior margin of the posterior talar facet. The tendon of *M. peroneus longus* runs just inferior to this bump, sometimes leaving a faint groove in the bone. The peroneal retinaculum, a ligamentous binding that keeps the peroneal tendons close to the calcaneus, also attaches on this tubercle.

As the tarsal member of the talocrural joint, the talus transmits the weight of the entire body to the foot. In addition to the talocrural joint, the talus is involved in the subtalar joint. The talocrural joint is a simple hinge joint that allows dorsiflexion and plantarflexion, while the subtalar joint is involved in inversion and eversion of the foot. The talus can be divided into a proximal body, a medially directed neck, and the distal head. The talar head bears a spherical articular surface for the navicular. This articular surface is prolonged onto the plantar surface of both head and neck for articulation with the sustentaculum tali of the calcaneus, forming the anterior calcaneal facet. A narrow non-articular area (the talar sinus) separates the anterior from the posterior calcaneal facet, the other component of the subtalar joint. The posterior calcaneal facet is sharply arched concavely for

articulation with the convex posterior talar facet of the calcaneus. Dorsally, the talar body forms the trochlea for articulation with the distal tibia and fibula. The trochlea is deep and bounded by sharp lateral and medial crests with a midline groove running proximo-distally. On the steeply sloping lateral and medial surfaces of the trochlea can be found the articular facets for the malleoli of both tibia and fibula. The lateral facet (for articulation with the fibular malleolus) is prolonged into a lateral talar process. Proximally, the body ends in a small talar shelf. The midline groove in the talar shelf is bounded by lateral and medial tubercles, and allows passage of the tendon of *M. flexor digitorum fibularis*.

The navicular articulates with the talus proximally and with the three cuneiform bones of the tarsus distally. The talar facet is ovoid and concave, with a slight extension on the medial aspect for articulation with the talar head and attachment of the plantar calcaneonavicular ligament ("spring ligament"). This important ligament provides support for the talar head. The navicular is one of the tarsal bones that is typically greatly elongated in *Tarsiidae* and *Galagidae*.

The cuboid is a short, rectangular bone which articulates with the navicular and the lateral cuneiform medially, the calcaneus proximally, and with metatarsals 4

and 5 distally. The calcaneal facet is curved and bears a small projection that fits into a complementary depression on the articular facet of the calcaneus. This calcaneocuboid "pivot" joint accomodates the distal, grasping foot to uneven arboreal surfaces by allowing inversion of the normally everted foot (Decker and Szalay 1974). On the plantar surface of the cuboid can be found the groove left by the tendon of M. peroneus longus as it crosses the tarsus to insert on the first metatarsal. The cuneiforms are three small and irregularly shaped bones of the tarsus which articulate with the first three metatarsals distally and the navicular proximally. In addition, the lateral cuneiform bears a small articular facet for the cuboid.

5.3. Musculature

In this section I describe the extrinsic musculature of the foot among prosimians. Origins, insertions, innervations and functions are detailed for all of the muscles arising from the hindlimb to insert on the foot. In addition to my dissections of galagos, tarsiers, and tree shrews, several published sources were referred to, including George (1977) on Tupaiidae, Stevens et al. (1972) on Galagidae, Grand (1967) on Lorisidae, Woolard (1925) on Tarsiidae, Murie and Mivart (1872) on Lemuridae and Galagidae, and Jouffroy (1962, 1975) on all of the Lemuriformes. The major functions that are discussed

include dorsiflexion (extension) and plantarflexion (flexion) around the talocrural joint, and eversion (pronation) and inversion (supination) around the oblique axes of the subtalar and calcaneocuboid joints. While the latter functions are important to all arboreal primates, powerful plantarflexion at the ankle is the sine qua non of prosimian leaping. The discussion follows the organization of the muscles themselves, beginning with the anterior muscular compartment and moving to the lateral and posterior compartments.

The anterior compartment is composed of the Mm. tibialis anterior, extensor digitorum longus, and extensor hallucis longus. M. tibialis anterior arises from a variable portion of the proximal tibia, interosseous membrane and, among Tupaiidae, from the fibula as well. It inserts into the medial cuneiform and is a dorsiflexor and invertor of the foot. Both the Mm. extensor digitorum longus and extensor hallucis longus arise from the proximal tibia and interosseous membrane, and send tendons to the distal phalanges of each digit. Like M. tibialis anterior, these muscles are both dorsiflexors and invertors of the foot. M. extensor hallus longus is also an abductor of the hallux. Each of these muscles is innervated by the deep peroneal nerve.

The lateral or peroneal compartment is composed of the Mm. peroneus longus, peroneus brevis, and peronei digiti quarti et quinti. While the M. peroneus longus usually takes origin from the proximal shaft of both tibia and fibula, the other peroneal muscles arise from the shaft of the fibula only. M. peroneus longus inserts on the base of metatarsal 1 while M. peroneus brevis inserts onto metatarsal 5. Mm. peronei digiti quarti et quinti are variably expressed but, when present, insert onto the distal phalanges of digits 4 and/or 5. While the main function of these muscles is eversion of the foot, they also assist in plantarflexion. They are all innervated by the superficial peroneal nerve.

Finally, the posterior compartment contains the Mm. gastrocnemius, soleus, plantaris, flexor digitorum fibularis, flexor digitorum tibialis, and tibialis posterior. These muscles are the powerful plantarflexors of the foot brought into play during leaping behavior. M. gastrocnemius arises from lateral and medial heads of origin which attach just proximal to the lateral and medial femoral condyles. Mm. gastrocnemius and plantaris are the only two-joint muscles inserting on the foot. Several studies have indicated the predominance of M. gastrocnemius among the talocrural plantarflexor musculature in vertical clinging and leaping taxa (Jolly and Gorton 1974; Hall-Craggs 1974; Anemone 1982). M. soleus arises from the head

and proximal shaft of the fibula, and its tendon merges with that of the *M. gastrocnemius* to form the powerful calcaneal tendon which is inserted into the tuber calcanei. Among leapers, *M. soleus* is a small and relatively insignificant part of the plantarflexors. Among lorisids, however, it is normally larger than *M. gastrocnemius* (Grand 1967; Jolly and Gorton 1974). *M. plantaris* arises in common with the lateral head of the *M. gastrocnemius* and inserts into the plantar fascia of the foot. It is much larger among leapers than among lorisids. While *M. flexor digitorum tibialis* usually arises solely from the tibial shaft, the more powerful *M. flexor digitorum fibularis* often arises from both tibia and fibula, and the intervening interosseous membrane. The tendons of these two muscles usually fuse before sending slips to the distal phalanges of the digits. Among lorisids, *M. flexor digitorum tibialis* is the largest muscle in the posterior compartment (Grand 1967; Jolly and Gorton 1974). *M. tibialis posterior* arises from the proximal shaft of the fibula and the interosseous membrane and inserts into the navicular and, sometimes, into the medial cuneiform as well. These muscles are all involved in plantarflexion, while the latter three also serve as inverters of the foot. The innervation of all posterior compartment muscles is uniformly from the tibial nerve.

5.4. Ratios

The five tarsal ratios presented in this analysis (Table 10 and Appendix B) share a double purpose: to gauge the nature of tarsal elongation among leaping prosimians, and to compare the relative length of tarsal elements among leapers and less specialized prosimians. The length of the calcaneus, cuboid and navicular bones relative to skeletal trunk length is measured in ratios T3, T4, and T5. Ratios T1 and T2 are attempts to quantify the leverage (i.e., mechanical advantage) of the M. triceps surae in plantarflexion of the foot at the talocrural joint. The moment arm of this muscle is closely approximated by the length of the posterior calcaneus as defined here, while its load arm is equal to the combined length of the anterior calcaneus and cuboid (Hall-Craggs 1965a, 1965b). Thus, ratio T2 is the more accurate measure of the mechanical advantage of M. triceps surae. Ratio T1, however, is valuable in that it allows a close approximation of this parameter to be measured in the absence of the cuboid bone, a common occurrence in paleontological studies. As a comparison of ratios T1 and T2 indicates, the calcaneal index is an accurate predictor of the mechanical advantage of the pedal plantarflexors. In addition, since calcaneal elongation among prosimians always occurs in the anterior calcaneus, the calcaneal index is a measure of the degree of calcaneal elongation.

Since they attempt to measure the same aspect of tarsal function, and because their results are so similar, ratios T1 and T2 are discussed together. In fact, these two ratios, the calcaneal index and the mechanical advantage in plantarflexion, present almost identical pictures in all respects. In both ratios the Galagidae and Tarsiidae have the lowest values while the Tupaiidae have the highest. Low values for these ratios indicate an elongate anterior calcaneus or load arm, while high values show a lack of elongation of the calcaneus. Closely following the tupaiids in both ratios are the Indriidae, with the highest mechanical advantage among all Malagasy taxa. The lowest mechanical advantage and, consequently, the longest calcaneus among the Malagasy taxa, is found in the Cheirogaleidae. An examination of the ratios by genus indicates that this position is mainly due to the length of the calcaneus in Microcebus, and not so much that of Cheirogaleus. In fact, of all the Malagasy taxa, Microcebus most nearly approaches the Galagidae in all measures of tarsal elongation. At the generic level, the results show that the lemurid and lepilemurid genera have uniformly high values for these two ratios, while Varecia is closer to the Indriidae than to Lemur or the Lepilemuridae in both ratios. Among the species of Galago, there is a clear separation of the mainly quadrupedal G. crassicaudatus and

the specialized leaper G. senegalensis, with the latter exhibiting lower values for both ratios. The greatest calcaneal elongation among Galagidae appears to occur in G. demidovii, the smallest of the galagos, while G. alleni is closest to G. senegalensis in both ratios.

Ratio T3, relative calcaneal length, indicates that relative to body size (as approximated by skeletal trunk length), the calcaneus is somewhat longer in Tarsiidae than in Galagidae. Again, the unspecialized quadrupedal Tupaiidae have the shortest calcanei, followed closely by the Lemuridae, and then the other Malagasy taxa. Among Malagasy prosimians, Microcebus and Lepilemur are distinguished by possession of the longest calcanei, which are nonetheless, always much shorter than those of even the most quadrupedal of the Galagidae. Relative to STL, calcaneal length again distinguishes between the primarily leaping (G. senegalensis) and the mainly quadrupedal (G. crassicaudatus) species of the genus Galago. Galago demidovii, while mainly quadrupedal in habits, again appears to contradict the general trend by having a very long calcaneus. McArdle (1981) has speculated that this may be related to the extremely small body size of G. demidovii. This point is treated at greater length in the discussion below.

Ratios T4 and T5 detail the lengths of the cuboid and navicular bones relative to skeletal trunk length. Ratio T4

clearly indicates the lack of any significant elongation of the cuboid bone among prosimians. Although galagos have a slightly longer cuboid than all other prosimians, the lack of any significant variation among other taxa coupled with the lack of any differences between the species of Galago in this trait imply that this difference is not significant. Ratio T5, on the other hand, clearly shows the extreme elongation of the navicular bone that is found among Galagidae and Tarsiidae. These two families are again most closely approximated among the Malagasy taxa by the genus Microcebus. The shortest navicular is that of Tupaia, closely followed by those of Indriidae and Lemuridae. Among the species of Galago, the longest navicular is found in G. senegalensis and the shortest in G. crassicaudatus. The navicular of G. demidovii is intermediate in length between these two extremes, but is closer to that of G. senegalensis than one would predict solely on the basis of locomotor behavior.

5.5. Previous Studies

Early studies in which tarsal elongation among the Galagidae and/or Tarsiidae was noted but not analysed in any functional or biomechanical sense include Murie and Mivart (1872), Mivart (1873), and Woolard (1925). Murie and Mivart (1872:4) stated:

"As is well known, certain genera (e.g. Galago and Tarsius) present an elongation of the tarsal part of the leg which is altogether peculiar, and no approximation to which is possessed by any other order of the vertebrate subkingdom."

In a footnote, they mentioned a letter from a Mr. Bartlett, Superintendent of the Zoological Society's Gardens, in which the saltatory habits of a captive Galago crassicaudatus were noted (Murie and Mivart 1872). Thus, they associated tarsal elongation with leaping behavior, but in no way did they attempt to discover the functional or biomechanical significance of this trait. Mivart (1873) presented some quantitative osteometric data that clearly indicate the fact of tarsal elongation among the Galagidae and Tarsiidae. Woolard (1925) similarly noted the presence of an elongate calcaneus and navicular in Tarsius, but carried the analysis no further.

The first investigator who attempted to both quantify tarsal elongation and to understand its functional significance was Schultz (1963a, 1963b). Working with sample sizes of 200 (40 prosimians, Schultz 1963a) and 238 (45 prosimians, Schultz 1963b), Schultz devised a series of ratios to document metric variability in the primate pedal skeleton. One ratio of particular interest related the length of the "power arm" (lever arm) to that of the load arm of the plantarflexors. This ratio is essentially the same as my tarsal ratio T2 in that it is a measure of the mechanical advantage of the plantarflexor musculature.

The values for this ratio are puzzling in that there is scarcely any discrimination between genera with tarsal regions of totally different proportions. For example, measurements of Tupaia, Propithecus, and Galago all yield the same value for this ratio (Schultz 1963a:201). Closer examination of Schultz's "load arm" indicates the problem in these data. In both papers, Schultz (1963a, 1963b) incorrectly measured the load arm of plantarflexion by adding the length of metatarsal 3 to that of the anterior tarsals. In effect, Schultz assumed that the point of resistance against the ground in the prosimian foot was at the metatarsal-phalangeal joints, as it is among humans and other higher primates. In fact, Hall-Craggs (1964, 1965a, 1965b) has shown cinematographically and Jouffroy and coworkers have shown cineradiographically (Jouffroy and Gasc 1974; Jouffroy et al. 1973; Jouffroy et al. 1974) that galagos push off the ground at the tarso-metatarsal joint. Therefore, the correct load arm does not include the length of metatarsal 3, but is restricted to that of the anterior calcaneus and cuboid. As Morton (1924) realized, the need for small prosimian leapers to maintain a grasping pes has channelled elongation of the load arm to the anterior tarsal region, not the metatarsal region as in non-primate saltators (Howell 1932, 1944). This results in the "tarsi-fulcrumating" pes of the prosimians, in distinction to the

"metatarsi-fulcrumating" foot of higher primates and non-primate saltators. Schultz (1963a) was, however, on the right track in his analysis of the significance of an increase in the length of the load arm of plantarflexion. He clearly stated that a decreased mechanical advantage, as seen in taxa with elongated tarsal regions, requires greater power in muscular contraction, but also yields movement through a greater distance and with a greater velocity. I return to the question of the functional significance of the lessened mechanical advantage in plantarflexion in the following section.

Walker's original diagnosis of the morphology of vertical clingers and leapers includes discussion of the length and morphology of the pedal skeleton (Walker 1967, 1974; Napier and Walker 1967). Certain qualitative traits of pedal morphology, such as the presence of a powerful abductable hallux with large peroneal tubercle (for insertion of *M. peroneus longus*) and the overall dominance of the lateral border of the foot, are easily verified. Concerning tarsal elongation, and reminiscent of his argument concerning the width of the ilium, Walker again pleads "allometry" to explain the obvious differences in the tarsus of Galagidae and Tarsiidae and that of Malagasy leapers. Careful reading of the three cited works indicates a subtle shift in his argument concerning tarsal elongation. In one paper (Napier and Walker 1967), it is

claimed that only the small-bodied vertical clingers and leapers possess elongated tarsals, while in his dissertation (Walker 1967) and in a later review article, Walker (1974) states that tarsal elongation is found in both leapers and arboreal quadrupeds, although to a greater extent in the former group, and is governed by "allometry" in both cases. Compare the following quotations:

"The calcaneus and navicular are elongated in small vertical clingers such as Galago and Tarsius but are short in the bigger forms such as Indri" (Napier and Walker 1967:210).

"In the foot, the development of an elongated tarsus is seen in both vertical clingers and leapers and arboreal quadrupeds. This development appears to be governed by allometric factors, but the observed regression lines for the two locomotor groups are of different gradients. For a given size, a vertical clinging and leaping form has a relatively longer calcaneal load arm than an active quadruped" (Walker 1974:361).

It is perhaps of interest to speculate that the reason for this shift in Walker's thinking was a realization of the intermediate position, with respect to tarsal elongation, of Microcebus in the gap separating the Galagidae and Tarsiidae from the rest of the Malagasy prosimians. In any event, the data presented here clearly indicate that the tarsus of arboreal quadrupeds are not elongated. In fact, an elongated tarsus is restricted among prosimians to the two families of non-Malagasy leapers, the Galagidae and Tarsiidae. The tarsus is moderately lengthened in Microcebus, the smallest of the Malagasy

taxa, and quite short in the remaining prosimians from the Malagasy Republic.

In his study of the hip and thigh of Lorisiformes (Galagidae and Lorisidae), McArdle (1981) addressed the question of tarsal elongation among leaping prosimians. Although he measured the lever arm in a slightly different manner than I, he calculated a calcaneal index that was identical to ratio T1 of this study, and came up with essentially the same results. In his discussion of these results, McArdle (1981:110) concluded that

"comparisons of the calcaneal index suggest a complex relationship between elongation of the load-arm of the calcaneus, body size and locomotor behavior".

While agreeing that the longest calcanei among prosimians are found in specialized leapers, McArdle also notes that within these groups, the longest calcanei are always found in the smallest animals. Within the Galagidae, this bodily size effect is especially noticable in G. demidovii. Although a predominantly quadrupedal form, it has the relatively longest calcaneus in its family. McArdle suggests that this may be a function of its very small bodily size. It is also clear that, among the Malagasy taxa, the form with the longest calcaneus is also the smallest, Microcebus. McArdle suggests that there is a limit, set by bodily size, on elongation of the tarsus in leaping among mammals, possibly due to the great bending

moments applied to the tarsus during leaping. As a result, larger animals either do not leap as frequently as smaller animals (e.g., G. crassicaudatus as opposed to G. senegalensis), or they rely on either a lengthening of the proximal hindlimb only (e.g., Indriids), or elongation and fusion of metatarsals (e.g., Macropodids and Dipododids) as adaptations for leaping.

The worker who has probably contributed most to our understanding of the significance of tarsal elongation among prosimians is E.C.B. Hall-Craggs. In a series of articles, Hall-Craggs (1964, 1965a, 1965b, 1966a, 1966b, 1974) used a wide range of innovative approaches to the study of tarsal elongation among Galagidae including high speed cinematography, gross dissection and histological analysis of muscles, ligaments and joints, physiological and histochemical analyses of muscle tissue, and biomechanical analysis. Hall-Craggs clearly understood that tarsal elongation is a means of increasing the length of the load arm while maintaining a "clinging grasp" (Morton 1924), and that the resultant lessening of mechanical advantage could be seen as an adaptation for speed (Smith and Savage 1956). However he went beyond this interpretation to find an additional rationale for this condition. Hall-Craggs (1965b) showed that the poor mechanical advantage in the galagid foot allows full distal

excursion, while requiring only a minimal departure from the resting length of the *M. gastrocnemius*. This, in turn, allows the muscles to operate in the most favorable region of the length/tension curve (i.e., close to resting length), where nearly maximal forces can be generated. The bipennate arrangement of muscle fibers in *M. gastrocnemius* was seen as an integral part of this adaptation (Hall-Craggs 1966a, 1974), serving to greatly increase the cross-sectional area of the muscle and hence, its maximum force (Gans and Bock 1965). Hall-Craggs clearly understood that the galagid tarsal region represents an elegant compromise between conflicting biomechanical demands. The poor mechanical advantage brought on by distal elongation of the tarsus requires large muscular forces from the plantarflexors. These muscular forces are realized by greatly increasing the size and cross-sectional area of the bipennate *M. gastrocnemius*, and by allowing it to generate near maximal tensions by remaining close to its resting length during most contractions. The small mechanical advantage in turn allows rapid plantarflexion through a great arc of motion. The result is the extremely adept leaping behavior of the Galagidae and, by analogy, the Tarsiidae.

5.6. Functional Anatomy

The following discussion is a functional analysis of the significance of tarsal elongation among leaping

prosimian primates of the galago-tarsier type. This discussion relies on basic principles of biomechanical analysis as presented by Gowitzke and Milner (1980). Some of the ideas discussed here have been touched upon previously by other students of prosimian pedal morphology, notably Schultz (1963a), McArdle (1981), and Hall-Craggs (1965a, 1965b, 1974).

The talocrural joint is a hinge joint that allows dorsiflexion (flexion) and plantarflexion (extension) of the pes upon the crus, and can be considered to act as a lever of the first class in plantarflexion. In the accompanying figure (Figure 3), the force is that exerted on the tuber calcanei by contraction of *M. triceps surae*, the fulcrum is the center of rotation of the talocrural joint, and the resistance occurs at the tarsometatarsal joints, where the body's weight is applied to the ground during locomotion. The lever arm is the distance from fulcrum to force, and the load arm is the distance from fulcrum to resistance. The moment of the muscular force is equal to the force of muscular contraction multiplied by the length of the lever arm, while the moment of resistance is equal to the load (body weight) multiplied by the length of the load arm. At equilibrium, all moments about the talocrural joint must sum to zero. Thus, the moment of force must equal the moment of resistance. This

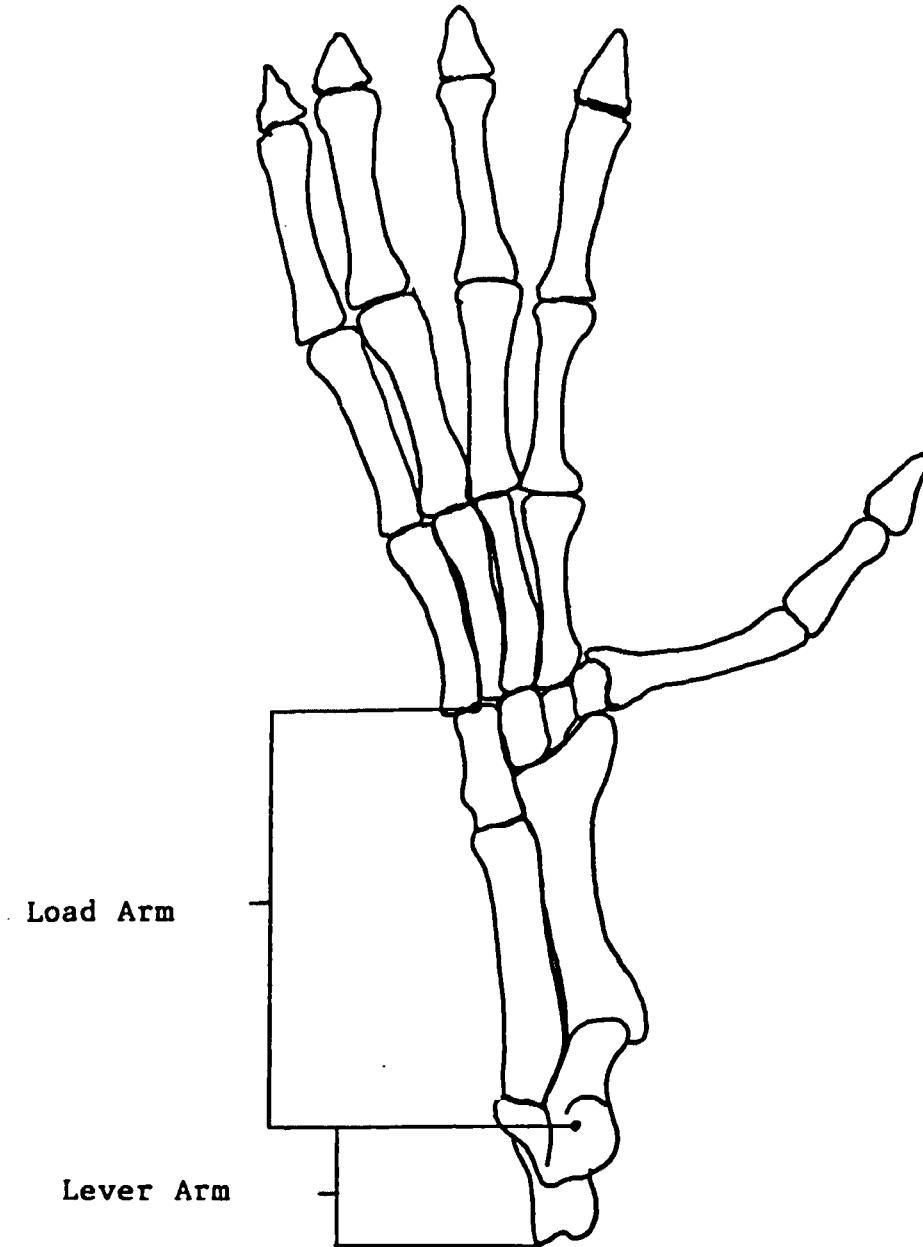


Figure 3. Biomechanics of the prosimian foot.

relationship can be expressed algebraically as follows.

force x lever arm = load x load arm, therefore

force = load x load arm/lever arm

Since the quantity load arm/lever arm is the inverse of mechanical advantage, the effect of a changed mechanical advantage on muscular forces can be predicted. If the mechanical advantage is large, little effort is required to balance a large load. However, since the ratio of distance moved by the load and by the force is inversely proportional to the mechanical advantage, a joint characterized by a large mechanical advantage can move the load through a small arc of motion per unit of arc moved by the force. Conversely, a poor mechanical advantage requires the generation of large muscular forces in order to balance the load, but moves the load through a greater arc of motion relative to a given muscular contraction. The figure illustrates these effects of changing mechanical advantage on speed and muscular force.

5.7. Summary

In summary, I conclude that the poor mechanical advantage of the talocrural joint in plantarflexion is a distinct advantage to small bipedal leapers like the Galagidae and Tarsiidae. While requiring large muscular forces, mainly provided by *M. gastrocnemius*, it allows large distal excursions at great velocity. The distance to which an animal can leap is directly related to the

velocity it can attain at take-off.

"The take-off velocity, upon which so much depends, is attained by the animal while it is in contact with the ground and is related to the force applied to its centre of gravity either during this time or over the distance travelled by the animal during this time" (Hall-Craggs 1974:830).

A lengthened hindlimb allows muscular force to be applied to the ground and, hence, against the animal's centre of gravity, for a longer time (or over a greater distance) during the propulsive effort of the leap, and results in a greater take-off velocity. Hall-Craggs (1965a) also notes that, in addition to lengthening the load arm, tarsal elongation functionally increases the length of the entire hindlimb, again a clear saltatorial adaptation. Finally, Hall-Craggs (1965a, 1965b, 1974) suggests that tarsal elongation allows *M. triceps surae* to operate close to its resting length and thus at the optimum region of its length/tension curve.

As to the distribution of tarsal elongation among prosimians, the data presented here clearly indicate that extreme tarsal elongation is found only among Galagidae and Tarsiidae, while moderate lengthening of the tarsus is found among the smallest of the Malagasy prosimians, namely Microcebus and perhaps Cheirogaleus medius and Phaner furcifer (McArdle, 1981). The Indriidae are clearly distinguished from both Galagidae and Tarsiidae on the

basis of tarsal metrics, and it is clear that all prosimian vertical clingers and leapers do not possess an elongated tarsus. Distinctly different adaptations in the intrinsic musculature and joints of the feet of Galagidae-Tarsiidae and Malagasy Lemuriformes have come to light in Gebo's (1985) recent study of the grasping mechanism in the prosimian foot. Gebo (1985) characterizes the "I-II adductor grasp" of Lemuridae and Indriidae as a derived trait among prosimians that allows the utilization of vertical supports in these large-bodied lemurs. He considers the "I-V opposable grasp" of tarsiers, galagos, lorises, cheirogaleids and Daubentonia as the primitive condition for all prosimians allowing small-bodied prosimians to cling to vertical supports. Gebo's (1985) results corroborate the conclusions reached here as to the entirely distinct nature of the foot among Malagasy and non-Malagasy vertical clingers and leapers, and offer no support to the VCL hypothesis.

Within the genus Galago, the species representing the behavioral extremes of leaping (G. senegalensis) and of quadrupedalism (G. crassicaudatus) are clearly distinguished on the basis of degree of tarsal elongation, while the position of G. demidovii points up the complicating factor of body size. The smallest and one of the more quadrupedal species of the genus, G. demidovii possesses a calcaneus and navicular that are relatively as

long as those of G. senegalensis, the most specialized leaper in the genus. Additional evidence for the influence of bodily size on tarsal elongation may be seen in the fact that among the Malagasy taxa, only the smallest species show moderate tarsal elongation. McArdle's (1981) suggestion that high stresses encountered during saltatorial locomotion render tarsal elongation alone a feasible mechanical solution in the smallest mammals must be admitted.

Chapter 6. The Prosimian Femur

6.1. Introduction to Chapter 6

The femur has been a focus of attempts to ascertain the morphological adaptations to vertical clinging and leaping among prosimian primates. Some of the features that have been suggested as being functionally related to habitual leaping include the following (Walker 1967, 1974; Napier and Walker 1967):

1. long and straight femoral shaft with thick neck set perpendicular to shaft;
2. posterior expansion of the articular surface of the femoral head onto the neck;
3. greater trochanter overhanging the ventral aspect of the shaft;
4. narrow patellar groove with prominent lateral margin;
5. ventrodorsally deep femoral condyles with tibial articular surfaces facing posteriorly.

This chapter presents a comparative analysis of femoral morphology that aims to test the validity of this proposed suite of characteristics of leaping prosimians, and to explain the functional significance of the observed morphological patterns. I begin with a discussion of qualitative aspects of femoral osteology and myology and their functional significance. Since most of the muscles acting on the femur arise from the pelvis and were described in the previous chapter, the treatment of myology is quite brief, comprising a review of the muscular

insertions on the femur, and a description of the origin of the three vasti muscles and M. popliteus from the femur. Next appear the results of bivariate and multivariate statistical analyses of the femoral measurements. Seven ratios were calculated from the femoral data to aid in the interpretation of the biomechanics of hindlimb form and function (Table 11 and Appendix C). The results of multiple discriminant function analysis of the femur are next reported and discussed (Tables 16 - 19 and Appendix F). In the summary I review the results, evaluate the VCL hypothesis with respect to the femoral evidence, and offer alternative explanations of the observed morphology of the prosimian femur.

6.2. Osteology

Among prosimian primates, the femur is the largest of the long bones. Two of the measurements used in this study, maximum length and midshaft diameter of the shaft (femoral measurements 1 and 8) provide information on the overall size and robusticity of the femur. Important landmarks on the proximal epiphysis include the femoral head, neck, and trochanters. The head is spherical to cylindrical in shape and, forming part of the hip joint, bears the articular surface for the acetabulum. The cranio-caudal and dorso-ventral dimensions of the head were measured (femoral measurements 2 and 3), and the degree of posterior expansion of its articular surface onto the neck was

carefully noted. The head faces medially and is connected to the femoral shaft by the neck. The cranio-caudal dimension of the neck was also measured (femoral measurement 6). On its medial end is a small pit, the fovea capitis femoris, for attachment of the ligament of the femoral head. The trochanters are bony ridges and rugosities resulting from the pull of certain muscles attaching to the proximal femur. Laterally, the greater trochanter may extend higher (i.e., more cranial) than the femoral head. The greater trochanter bears the insertion of the Mm. gluteus medius and gluteus minimus and the origin of M. vastus lateralis. On the distal aspect of the greater trochanter lies the trochanteric fossa, a small recess for attachment of the lateral rotators of the femur (Mm. gemelli and obturators). Also on the lateral aspect of the femur, but distal to the greater trochanter, lies the third trochanter. Both the Mm. gluteus superficialis (pars anterior) and tensor fasciae femoris insert onto the third trochanter. The lesser trochanter is on the medial aspect of the proximal femur and bears the insertion of M. iliopsoas. While the greater and lesser trochanters are found among all primates, the third trochanter is absent from some lorisisids and all anthropoid primates. The distance between the hip joint and the most distal points on the lesser and third trochanters were measured

(measurements 4 and 5). These measurements give an indication of the distal prolongation of the insertions of important hindlimb muscles, and are related to moment arms and moments of inertia of hindlimb bone-muscle systems. Similarly, the maximum distance from the center of the hip joint to the most lateral point on the greater trochanter (measurements 7 and 12) is an approximation of the moment arm of the gluteal muscles that run from the ilium to the greater trochanter.

Although it provides surface area for muscular attachments along much of its length, the femoral shaft has little in the way of distinctive morphology. The distal epiphysis of the femur, however, contains the articular areas for both the tibia and the patella. The patellar surface is a midline groove on the ventral aspect of the epiphysis on which the patella slides during flexion and extension at the knee. The width, length, and depth of this groove vary among prosimians, but it is always bounded by lateral and medial ridges. Distally and posteriorly are the femoral condyles, which articulate with the tibial condyles in the knee joint. On the distal aspect, the femoral condyles are separated by the intercondylar fossa, where the cruciate ligaments of the knee attach. The collateral ligaments of the knee attach on the lateral and medial epicondyles, immediately adjacent to the condyles. The mediolateral and dorsoventral dimensions of the femoral

condyles (measurements 10 and 11) were measured in order to gain a quantitative picture of the size of the "pulley" (Walker 1967) around which the quadriceps tendon pulls in knee extension.

6.2.1. Lorisidae

Both proximally and distally, the lorid femur is a very distinctive bone. Minor differences between lorid genera are mainly due to the greater robusticity of Nycticebus and Perodicticus, compared to their more slender, long-limbed relations Arctocebus and especially Loris. The femur is moderate in length with a shaft that is anteriorly bowed. The head is large and bears a large fovea. There is a moderate degree of posterior expansion of the articular surface onto the neck. Both in the shape of the head and in the degree of posterior expansion of the articular surface, the lorids are morphologically intermediate between the Lemuriformes and the Galagidae. The neck is short and thick, and meets the shaft at a fairly obtuse angle. The head and greater trochanter extend cranially about the same height, while the greater trochanter is less broad laterally than in other prosimians. The dorsoventral width of the greater trochanter is uniform for its entire length in lorids, while it tapers distally in all other prosimians. The third trochanter is small or absent, but when present, as in

Perodicticus, it is a small bump on the distal end of the greater trochanter. The lesser trochanter is very prominent. It is cranio-caudally long, and protrudes medially almost as far as the medial edge of the head. Dorsally, the trochanteric fossa is, as in Galagidae and Tarsiidae, very small.

The distal epiphysis is the most distinctive part of the lorisid femur. Unlike the condition found in most other prosimians, the femoral condyles are very shallow, being wider (medio-laterally) than deep (dorso-ventrally). The patellar groove is wide and shallow, and extends through a short arc cranio-caudally. The patellar ridges are not especially prominent, and only among the lorisids is the medial ridge higher than the lateral. As in other prosimians, the tibial articular surface faces posteriorly.

6.2.2. Galagidae

The femur among the Galagidae is long, straight, and slender. The head is cylindrical with a flattened medial end, and is set on a short and thick neck which is nearly perpendicular to the shaft. The cylindrical shape of the head is a result of the extreme degree of posterior expansion of its articular surface onto the dorsal aspect of the neck. This characteristic is best developed among Galagidae and Tarsiidae, and is in direct contrast to the condition seen among the Lemuriformes. The greater trochanter is well developed, its highest point being at

the same level as that of the head. Anteriorly, the greater trochanter overhangs the ventral aspect of the femoral shaft. Its widest point is proximal, and it tapers in width distally. On its dorsal aspect, the trochanteric fossa is moderate in size. The third trochanter is small to moderate in size and situated on the distal edge of the greater trochanter. Medially, the large lesser trochanter protrudes as far as the medial edge of the head. Distally, the femoral condyles are very deep, and the tibial articular surface points posteriorly. The patellar groove is narrow and deep, with a large arc that implies extreme flexion and extension at the knee. The patellar surface is raised above the level of the ventral shaft, further increasing the moment arm of the M. quadriceps femoris in extension. Both patellar ridges are prominent, but the lateral is especially pronounced.

6.2.3. Tarsiidae

Tarsiers most closely resemble galagos in femoral morphology. The shaft is again long, straight, and slender and lacks muscular ridges along its length. The femoral head is cylindrical, bears a large fovea, and is set on a short, thick, perpendicular neck. The posterior expansion of the articular surface is very extensive, although perhaps slightly less so than in Galagidae. The trochanters are essentially identical to those of the galagos. The

greater trochanter is moderate in size and extends no higher than the head. It overhangs the ventral aspect of the shaft, and tapers in width distally. The third trochanter lies a short distance beyond the distal end of the greater trochanter, and is quite small. The lesser trochanter is again prominent, although more circular in section than its cranio-caudally elongated counterpart in Galagidae. Distally, the trochanteric fossa is moderate in size. The femoral condyles are again deeper than wide, and the tibial articular surfaces face posteriorly. The patellar groove is raised above the ventral level of the shaft, and is narrow and deep with a large arc of curvature. The lateral patellar ridge is sharper and more prominent than the medial.

6.2.4. Tupaiidae

The tupaiid femur is easily distinguished from that of all prosimians. Its shaft is short, straight, and robust. The femoral head is large and spherical, with no evidence of any posterior expansion of its articular surface onto the neck. The fovea is small, and the head is set on a short neck at an obtuse angle to the shaft. The greater trochanter extends higher than the head, and projects somewhat medially over the neck. The width of the greater trochanter tapers distally, and it does not overhang the ventral shaft as it does among Lemuriformes, Tarsiidae, and Galagidae. On its dorsal aspect, the trochanteric fossa is

deep and extensive. The third trochanter is very prominent among tree shrews. It begins at the distal end of the greater trochanter and is a thin, cranio-caudally elongate structure that points to the functional importance of *Mm. gluteus superficialis* and *tensor fasciae femoris*. The lesser trochanter is also a very prominent structure, extending as far medially as the femoral head. Unlike most prosimians, the femoral condyles are wider than deep, while the tibial articular surface faces posteriorly. The patellar groove is moderately wide and shallow, and the patellar ridges are not particularly prominent. The arc of the patellar articular surface is clearly smaller than that seen in galagos, tarsiers, and lemurs.

6.2.5. Lemuridae

The femora of all of the Malagasy Lemuriformes are fairly uniform in overall morphology. Among the Lemuridae, the femoral shaft is long, straight, and moderately robust. The head is spherical, bears a small fovea, and is set on a short, thick neck which meets the shaft at an obtuse angle. There is a very slight posterior expansion of the articular surface onto the neck. The greater trochanter is prominent and, as in Indriidae, overhangs the ventral aspect of the shaft. Unlike the indriid greater trochanter, that of lemurids is wide proximally and tapers distally to form a "trochanteric ridge" which runs obliquely to terminate on

the third trochanter. At its proximal end, the greater trochanter extends medially over the neck, giving this region a notched appearance. On the dorsal surface of the greater trochanter lies the deep and extensive trochanteric fossa. The third trochanter is more prominent in lemurids than in leaping prosimians, and is elongated in its cranio-caudal dimension. The lesser trochanter is thin but elongate. It never protrudes as far medially as the femoral head. Distally, the femoral condyles are both broad and deep, with posteriorly-facing tibial articular surfaces. The patellar groove is narrow and deep with prominent medial and, especially, lateral ridges. While it is not raised above the ventral aspect of the shaft as it is in Indriidae, Galagidae, and Tarsiidae, the patellar surface extends through a substantial arc of curvature.

6.2.6. Indriidae

Indriid femora are, in general, as straight as but longer and more slender than those of the Lemuridae. The head is equally spherical, with a very slight posterior extension of its articular surface onto the neck. The neck is similarly short and thick and set at an obtuse angle to the shaft, but the fovea is much larger among indriids than lemurids. The greater trochanter has a different shape and is more restricted proximally among Indriidae, where it is semi-rectangular, with a straight horizontal distal edge that is clearly separated from the small third trochanter.

Proximally, the greater trochanter extends over the neck, giving the same "notched" appearance noted among lemurs. Ventrally, the greater trochanter hangs over the anterior aspect of the shaft. Dorsally, the trochanteric fossa is deep, but it is much smaller among indriids than lemurids. The lesser trochanter is similar to that seen in lemurids, never protruding as far medially as the head. The femoral condyles are deeper than wide among all indriids, and the tibial articular surface faces posteriorly. The patellar groove is narrow and deep, and raised above the ventral aspect of the shaft. The lateral patellar ridge is higher and sharper than the medial, and the patellar articular surface extends through a very large arc of curvature.

6.2.7. Lepilemuridae

The Lepilemuridae very closely resemble Lemuridae in all aspects of femoral morphology. Although slightly smaller than the smallest of the lemurs (L. coronatus), Hapalemur griseus is essentially indistinguishable from lemurs on the basis of femoral morphology. Lepilemur appears to be intermediate, however, between Indriidae and Lemuridae in some aspects of femoral shape. Both Lepilemur and Hapalemur have spherical femoral heads with only a slight degree of posterior expansion of articular surface onto the neck. Proximally, the traits that link Lepilemur and Indriidae include the large size of the fovea capitis femoris and the

size and shape of the greater and third trochanters. The greater trochanter is proximally restricted and lacks the distally running "trochanteric ridge" seen in Lemuridae. The third trochanter is very small and is situated, as in Indriidae, on the distal edge of the greater trochanter. Distally, the femoral condyles resemble those of all other Lemuriformes in being deeper than wide and facing posteriorly for articulation with the tibia. The patellar groove is narrow and deep, has a prominent lateral ridge, and like that of Indriidae, is raised ventral to the level of the femoral shaft.

6.2.8. Cheirogaleidae

Cheirogaleidae also closely resemble the rest of the Lemuriformes in femoral morphology. The femoral shaft is moderate in length, but straight and slender. The head is always spherical, with a slight posterior expansion of its articular surface onto the neck. The fovea is small and the neck is short, thick, and set at an obtuse angle to the shaft. The morphology of the trochanters is essentially similar to the pattern seen in the Lemuridae. Distally, the femoral condyles are deeper than they are wide, and the articular surface for the tibia faces posteriorly. The patellar groove is narrow and deep, and the lateral patellar ridge is especially prominent. Unlike the condition seen in Indriidae and Lepilemur, the patellar articular surface is not raised above the ventral shaft.

6.3. Functional Osteology

An examination of the distribution of the described femoral traits among prosimians can help to explain the significance of these traits in positional behavior. Lorisids have a unique distal femoral morphology that includes condyles which are wider than deep, and a wide and shallow patellar groove with low margins. Clearly, neither rapid nor powerful flexion and extension of the leg are high priorities among these animals. It is equally clear, however, that few femoral traits link all of the specialized leaping taxa. Galagids, indriids, tarsiids, and Lepilemur do, however, appear to share the following traits: raised ventral surface of patellar groove, reduced third trochanter, large fovea capitis femoris, and moderate to small trochanteric fossa. Galagidae and Tarsiidae are linked by several traits related to the morphology of the proximal femoral epiphysis. In both families, the head is cylindrical with a large degree of posterior expansion of the articular surface onto the neck. Additionally, the neck is short, thick, and set nearly perpendicular to the shaft. The greater trochanter extends no higher than the femoral head, and the lesser trochanter is especially prominent among these two families. On the other hand, all of the Tarsiidae, Galagidae, and Malagasy Lemuriformes, share the following suite of femoral traits:

1. femoral condyles deeper than wide,
2. straight femur, of moderate to long length,
3. greater trochanter overhangs ventral aspect of shaft,
4. narrow and deep patellar groove,
5. prominent lateral patellar ridge,
6. tibial articular surfaces face posteriorly.

Finally, both quadrupedal and saltatorial Malagasy Lemuriformes can be distinguished from galagos and tarsiers by the possession of a spherical femoral head with a slight degree of posterior expansion of articular surface, and a greater trochanter that extends medially over the neck to impart a characteristic "notched" appearance. This survey of femoral osteology among prosimian primates reveals a much more complicated series of morphological relations than indicated by earlier work (Walker 1967, 1974; Napier and Walker 1967). These morphological patterns can, for the most part, be explicated on the basis of hindlimb function during locomotor and postural activities.

In the distal femur, a suite of traits appears to be linked to powerful and efficient extension of the leg at the knee by M. quadriceps femoris. These traits include femoral condyles that are deeper dorsoventrally than mediolaterally wide, a ventrally raised patellar articular surface, a narrow and deep patellar groove bordered by a prominent lateral patellar ridge, and posteriorly-facing tibial articular surfaces. As Walker (1967) first noted, deep femoral condyles and a raised patellar surface are two means of increasing the size of the "pulley" over which the

quadriceps tendon acts, and hence, of increasing the moment arm of *M. quadriceps femoris*. This is best interpreted as an adaptation for maximizing the power of extension at the knee, perhaps at the expense of speed. However, the ubiquity of this condition among prosimians casts doubt on its supposed unique relationship with leaping behaviors (Walker 1967, 1974; Napier and Walker 1967). While the raised patellar articular surface is found only among the most specialized prosimian leapers (Galagidae, Tarsiidae, Indriidae, and Lepilemur), all prosimians except Lorisidae and Tupaiidae have femoral condyles that are deeper than wide (this pattern is confirmed by the metric results of the Condylar Index, ratio F4, discussed in section 4.3). Thus I conclude that, while powerful leg extension is important to both quadrupedal and saltatorial prosimians, attendant morphological specializations are best developed among the latter. Other traits of distal femoral anatomy are similarly related to extension of the leg by *M. quadriceps femoris*. The prominent lateral patellar ridge counteracts the pull of the hypertrophied *M. vastus lateralis*, thus guarding against patellar dislocation during contraction of that muscle. The narrow and deep patellar groove with a large arc of curvature is a further indication of the emphasis on flexion-extension at the knee (Tardieu 1980). These traits, and the posteriorly-facing tibial articular surfaces, are common to both quadrupedal

(except Tupaiidae) and saltatorial prosimians. While they are in sharp contrast to the condition seen in the specialized slow-climbing Lorisidae, these characteristics do not successfully distinguish between quadrupedal and leaping prosimians.

Distinctive traits of the proximal femur of some prosimians include a cylindrical head with large posterior expansion of its articular surface onto a thick and short neck which is nearly perpendicular to the shaft. These traits appear to be related and allow easy separation of Galagidae and Tarsiidae (and to a lesser extent, Lorisidae) from all Malagasy prosimians and Tupaiidae. The crucial trait in this suite of characteristics is the posterior expansion of the articular surface onto the neck; it is this trait that gives the head a cylindrical shape and makes the neck appear short, thick, and perpendicular. The proximal femoral anatomy among Malagasy taxa includes a spherical femoral head with little or no posterior expansion of articular surface onto the neck, and is shared by all Lemuriformes.

I interpret the articular expansion seen in galagos and tarsiers as a postural adaptation of importance during vertical clinging behavior in small-bodied prosimians. While vertically clinging to an arboreal support, the femora are strongly flexed, abducted, and laterally

rotated. In this position, the posterior expansion of articular surface comes into contact with the distal articular region of the acetabulum, allowing the necessary posture preparatory to leaping. Jenkins and Camazine (1977) similarly related the degree of expansion of the articular surface of the femoral head onto the neck among carnivores to the relative importance of the use of the femur in abducted postures. The absence of this trait among Indriidae may be the result of subtle differences in clinging behavior of these larger animals (Godfrey ms.). Other traits that may be shared to some extent by all leaping prosimians include a large fovea capitis femoris, a small to moderately sized trochanteric fossa, and a reduced third trochanter. While the significance of the first two of these traits is unclear, the presence of a large and powerful third trochanter is a cursorial adaptation linked to the powerful development of *Mm. gluteus superficialis* and *tensor fasciae femoris*. The leaping taxa are again joined by the hindlimb-dominant Malagasy quadrupeds in possessing greater trochanters that overhang the ventral aspect of the shaft. The significance of this trait appears to be related to the direction of pull or leverage of the *M. vastus lateralis*, which arises from the ventral aspect of the greater trochanter. In any event, the morphology of the proximal femur can not be interpreted to support the VCL hypothesis (contra Walker 1967, 1974; Napier and Walker

1967). Rather, the available evidence strongly suggests two very different morphological patterns adapted for leaping among prosimian primates.

6.4. Musculature

Many of the muscles of the hip and thigh arise on the pelvic girdle to insert onto the femur and have been described in chapter 4. Their insertions on the femur will be briefly reviewed in this chapter. Of the muscles that gain origin from the femur, *Mm. gastrocnemius* and *plantaris* are plantarflexors of the foot, and have been described in detail in chapter 5. My interest in this section will be on the very important *vasti* muscles, part of *M. quadriceps femoris*, which arise from the femur and insert via the patella and patellar tendon into the anterior tibia. Sources on the myology of the prosimian thigh that have been used in this review include George (1977) on *Tupaiaidae*, Stevens et al. (1972) on *Galagidae*, Woolard (1925) on *Tarsiidae*, McArdle (1981) on *Galagidae* and *Lorisidae*, Jungers et al. (1980) on *Lemuridae*, and Jouffroy (1962, 1975), whose main interest is *Lemuriformes* but who also supplies comparative notes on most prosimian taxa. In addition, my own dissections of the hindlimb of *Galagidae*, *Tarsiidae*, and *Tupaiaidae* have been used to verify details from the literature.

Of the muscles that arise from the pelvic girdle, several insert into the proximal part of the femur. Two of the extensors of the thigh, *Mm. gluteus medius* and *minimus*, insert onto the greater trochanter of the femur. *M. iliopsoas*, an important flexor of the thigh, inserts into the lesser trochanter. The *Mm. gemelli*, *obturator internus*, and *obturator externus* all insert into the trochanteric fossa on the dorsal aspect of the greater trochanter and serve as lateral rotators of the femur. The third trochanter is the site of attachment of the ascending tendon of pars anterior of *M. gluteus superficialis* and of *M. tensor fasciae femoris*. *M. gluteus superficialis* is mainly an extensor of the thigh, while *M. tensor fasciae femoris* is a flexor. The dorsal surface of the femoral shaft also provides attachment to the *Mm. quadratus femoris*, *pectineus*, and *adductores*. Distally, the lateral and medial heads of *M. gastrocnemius* arise by tendons from fabellae situated just proximal to the femoral condyles on the dorsal aspect of the shaft. *M. plantaris* arises in common with the lateral head of *M. gastrocnemius*. Both of these muscles, but especially *M. gastrocnemius*, are important plantarflexors of the foot. *M. popliteus* also arises from the lateral epicondyle of the femur. This short, fleshy muscle crosses the knee joint to insert high on the medial aspect of the dorsal tibia. It aids in flexion and especially medial rotation of the leg and is

supplied by the tibial nerve.

The three vasti muscles, *Mm. vastus lateralis*, *vastus medialis*, and *vastus intermedius*, along with *M. rectus femoris* form the *M. quadriceps femoris*. This four-headed muscle is the major extensor of the leg at the knee joint in primates. *M. rectus femoris* arises by two distinct tendons of origin from the anterior inferior iliac spine and the cranial margin of the acetabulum. This two-joint muscle has the added function of flexion of the thigh, in addition to extension of the leg. All four parts of the quadriceps fuse above the knee to form the quadriceps tendon, which inserts into the patella. Distally, the patellar tendon runs from the patella to insert into the tibial tuberosity. The *M. quadriceps femoris* is innervated by branches from the femoral nerve.

The deepest and usually the smallest member of the quadriceps group is the *M. vastus intermedius*. This muscle arises by short muscle fibers which insert into a tendon running longitudinally along its superficial aspect. It arises for a variable distance from the ventral aspect of the femoral shaft. Among *Tupauidae* and *Lorisidae* it arises from approximately the middle two thirds of the shaft. Among Malagasy taxa, *M. vastus intermedius* arises from the proximal one half of the shaft, while *Galagidae* and *Tarsiidae* have origins from the entire length of the shaft

of the femur. The origin is longitudinally divided into a lateral and a medial part among tarsiers, while it is single in galagos. Among Galagidae, Tarsiidae, and all of the Malagasy prosimians, the tendon of *M. vastus intermedius* has a separate superior patella proximal to the true patella (Retterer and Vallois 1912). Only in Lorisidae and Tupaiidae among the prosimians is this fibrocartilaginous sesamoid absent.

M. vastus medialis is a large muscle whose origin is restricted to the proximal femur among most prosimians. It arises from along the ventral aspect of the neck of the femur, never extending distally beyond the level of the lesser trochanter. *M. vastus lateralis* is the largest and most powerful of the vasti in most prosimians, often covering both the lateral and anterior aspects of the thigh. Its origin is similarly restricted to the proximal femur, arising from along the anterior crest of the greater trochanter. Only among the Lorisidae is this pattern changed. Within this family, the origins of both *M. vastus lateralis* and *vastus medialis* are prolonged distally for a significant distance along the femoral shaft, and neither muscle is as large and powerful as it is among other prosimians. In addition, it is only among the Lorisidae that the *M. rectus femoris* appears superficial to the vasti. In all other prosimians the greatly enlarged *M. vastus lateralis* completely covers *M. rectus femoris*.

6.5. Functional Myology

Gross dissection of the *M. quadriceps femoris* reveals two specializations that have been interpreted by some authors as adaptations to leaping. These are the presence of a large and powerful *M. vastus lateralis* (Murie and Mivart, 1872; Alezais 1900; Jouffroy 1962, 1975; Stern 1971) and the presence of a fibrocartilaginous superior patella in the tendon of *M. vastus intermedius* (Retterer and Vallois 1912; Jouffroy 1962, 1975).

The *M. vastus lateralis* is hypertrophied among all Malagasy prosimians, and Jouffroy (1962, 1975) suggests that this is a critical adaptation that allows all Lemuriformes some degree of proficiency in arboreal leaping. My own dissections of the *M. quadriceps femoris* among Galagidae (*G. senegalensis*, *G. demidovii*, and *G. crassicaudatus*) and Tarsiidae reveal that *M. vastus lateralis* routinely comprises more than 60% of the total quadriceps mass, with *M. vastus medialis* accounting for an additional 20% to 30%. Hypertrophy of *M. vastus lateralis* among saltatorial mammals has been confirmed by McArdle (1981) for Galagidae, Woolard (1925) for Tarsiidae, Stern (1971) and Plaghki et al. (1981) for Cebidae, Alezais (1900) for Rodentia and Hopwood and Butterfield (1976) for Macropodidae. In addition to its large size, the origin of *M. vastus lateralis* is restricted to the proximal femur among both

non-primate (Alezais 1900; Hopwood and Butterfield 1976) and primate leapers (McArdle 1981; Jouffroy 1962, 1975; Woolard 1925; Plaghki et al. 1981; Stern 1971). This proximally restricted origin is seen also in *M. vastus medialis*, and appears to be correlated with the possession of long and parallel muscle fibers among Lemuridae (Jungers et al. 1980), Galagidae and Tarsiidae (Anemone 1983). In fact, prosimian leapers appear to be maximizing both the physiological cross-section of *M. vastus lateralis* (and *M. vastus medialis*) and the length of the constituent muscle fibers.

Stern (1971) has shown that the combination of a large cross-sectional area and long fiber length allows a muscle to develop maximal force generation at high velocities of contraction, and would appear to be well-adapted to the needs of leaping animals. Jungers et al. (1980) have confirmed the importance of *M. vastus lateralis* in the leap of Lemur fulvus by the technique of telemetered electromyography. Their results indicate that *M. vastus lateralis* consistently reaches maximal burst levels as it initiates the leap in this taxon. They further suggest that the amount of force generated by this muscle is enhanced by active stretching (i.e., eccentric contraction) when the femur is hyperflexed in the crouch that typically precedes the leap. Stern's (1971) theoretical work and the experimental results of Jungers et al. (1980) clearly

confirm the suggestions of many gross anatomists as to the importance of *M. vastus lateralis* in the leaping of prosimian primates. Rather than characterizing only vertical clinging and leaping prosimians, however, the described morphology of *M. vastus lateralis* appears to link both quadrupedal and saltatorial Lemuriformes with Tarsiidae and Galagidae.

A functional relationship between the morphology of *M. vastus intermedius*, the presence of a superior patella within its tendon, and leaping behavior (Retterer and Vallois 1912; Jouffroy 1962, 1975) among primates has recently been questioned (Stern 1971; Jungers et al. 1980). The internal architecture of *M. vastus intermedius* appears to be relatively uniform among prosimians. It is mainly composed of short, fleshy fibers arising from much of the ventral femoral shaft to insert into a tendon running superficially along the length of the muscle. Stern (1971:244) suggests that

"The only advantage associated with short-fibered vasti is that they probably manage to maintain some superiority in the number of fibers and, therefore, are able to produce more powerful extension at slow velocities of contraction."

This morphology appears better suited to slow postural activities and maintenance of the integrity of the knee joint than for the propulsive necessities of leaping. Jungers et al. (1980) have confirmed electromyographically

the primary postural activity of *M. vastus intermedius* in Lemur fulvus. Their results indicate that, in L. fulvus, *M. vastus intermedius* undergoes no force enhancement through active stretching prior to the leap, fails to show increased electrical activity during the leap, and is the only part of the quadriceps that is electrically active during resting postures with flexion at the knee.

Stern (1971) found a superior patella in the tendon of *M. vastus intermedius* in a number of cebid genera, including Cebus and Alouatta. Since these two genera leap most and least frequently, respectively, among the Cebidae, Stern (1971) denied any special relationship between the superior patella and leaping (contra Retterer and Vallois 1912; Jouffroy 1962, 1975). Among prosimian primates, a superior patella is found in Lemuriformes (Jouffroy 1962, 1975), Galagidae, and Tarsiidae (Anemone 1983), and is absent in Tupaiidae. It is unclear whether the Lorisidae possess a superior patella; Jouffroy (1962) states that it is lacking, while McArdle (1981) claims that it is present in all four genera. Since it only articulates with the patellar surface of the femur during extreme flexion at the knee, Jungers et al. (1980:287) suggest that

"The existence of a fibrocartilaginous superior patella in the tendon of *vastus intermedius*, is most plausibly related to the complex tensile and compressive stresses generated in the tendon during the completely hyperflexed phase of leaping."

In any event, the presence of the superior patella again does not link the vertical clinging and leaping prosimians to the exclusion of the hindlimb-dominant quadrupeds of the Malagasy Republic.

6.6. Ratios

Most of the seven ratios calculated from the femoral measurements (Table 11 and Appendix C) concern the leverage of various muscles that act on the femur during locomotion. The first ratio (Relative Femoral Length, F1) is a measure of the length of the femur relative to skeletal trunk length. Since elongation of the hindlimb is such a common saltatorial and cursorial trait (Howell 1944), I predict that the specialized leapers would possess the longest femora among the prosimians. McArdle (1981:114) states with regard to this adaptation,

"Elongation of the hindlimb is characteristic of all leaping animals. Since the force required for a particular leap is inversely proportional to the distance (and time) over which the force is applied, longer hindlimbs allow animals of similar size either to decrease the force required to leap a specific distance or to increase the distance leaped with a particular set of musculature."

Additionally, I expect that the shortest femora would be found among those relatively unspecialized quadrupeds, the Cheirogaleidae and Tupaiidae. Indeed, the data do confirm these two predictions in broad outline. The four families that leap the most effectively and most frequently possess femora that are more than half as long as their skeletal

trunk lengths (i.e., Tarsiidae, Indriidae, Galagidae, and Lepilemuridae). Galagidae have significantly shorter femora than do Tarsiidae and Indriidae. In fact, in the latter two families, femoral length is more than seventy percent of skeletal trunk length. Cheirogaleidae and Tupaiidae are both characterized by relatively short femora, while Lemuridae and Lorisidae have relative femoral lengths intermediate between those of the leapers and of the unspecialized quadrupeds.

Much additional information concerning relative femoral length can be gleaned by an examination of the data at the generic and specific taxonomic levels. Among the Lorisidae, it is seen that Loris has by far the longest femur. McArdle (1981) also found this to be the case for this genus. Among the Lemuridae and Lepilemuridae, Varecia has by far the shortest femur, while that of Lemur is not substantially shorter than those of Lepilemur or Hapalemur. The interspecific variation within the genus Galago closely mirrors the range in locomotor behavior among these species. The relatively longest femur is found in the specialized leaper G. senegalensis, while the two quadrupedal species (G. crassicaudatus and G. demidovii) have the shortest femora in the genus. These results clearly indicate that, as predicted on biomechanical grounds, a long femur is advantageous for saltatorial

primates. However, they also show that the degree of femoral elongation varies considerably among leaping prosimians, and that Indriidae and Tarsiidae are far more similar to each other in this respect than either is to Galagidae.

Ratio F2, the Hip Flexor Index, is a measure of the distal extent of the lesser trochanter relative to overall femoral length. The lesser trochanter is an important femoral landmark because it is the site of attachment of the M. iliopsoas, along with M. tensor fasciae femoris, an important flexor of the thigh. Thus the distal extent of the lesser trochanter marks the distal extent of the insertion of M. iliopsoas. Although this measurement is not an approximation of the moment arm of this muscle, it is correlated with it because the moment arm will increase as the insertion is prolonged distally on the shaft (McArdle 1981; Stern 1974). Thus, a proximally positioned lesser trochanter may be a means of shortening the moment arm of hip flexion and, hence, maximizing speed. An additional adaptive rationale for proximal placement of muscle insertions on long bones is a reduction in the moment of inertia of the limb. Gowitzke and Milner (1980:78) describe the moment of inertia as the rotational equivalent of mass in linear motion, and define it as,

"the measure of the resistance of a body at rest to rotatory motion, or, if rotating, to a change in its state of rotation."

In his analysis of the functional anatomy of Megaladapis, an extinct Malagasy subfossil lemur, Jungers (1976:513) states:

"The greater I_o (moment of inertia) becomes, the greater the force needed to produce a given angular velocity. Conversely, the rate at which a limb may be rotated, or the cadence, is dependent not only upon the total mass of the limb, but upon the distribution of this mass as well."

In the work cited above, Jungers (1976) calculated a hip flexor index and a gluteal index that are essentially identical to the similarly named ratios of this study (F2 and F3). He interpreted these ratios both in terms of their relationship to the muscular lever arms involved (and, hence, mechanical advantage), and to the moment of inertia of the hindlimb. In both its effect on the length of the flexor moment arm, and on the moment of inertia of the hindlimb as a whole, a more proximal position of the lesser trochanter can be seen as an adaptation likely to be found in leaping prosimians.

Again the prediction is confirmed in broad outline. Indriidae and Tarsiidae show the most proximally placed lesser trochanters, followed by Lepilemuridae and Galagidae. The most distally positioned lesser trochanters are to be found in Tupaiidae, Cheirogaleidae, and Lorisidae. The Malagasy taxa span almost the entire range of values for this ratio from Indriidae through Lepilemuridae and Lemuridae to Cheirogaleidae. Varecia and

Cheirogaleus have significantly more distally placed lesser trochanters than do their relatives Lemur and Microcebus, while Loris is distinguished from the other lorisisds by its more proximally placed lesser trochanter. A similar intertaxonal spectrum is clearly shown in the genus Galago. The most proximal lesser trochanter is once again seen in the predominantly leaping G. senegalensis. Whether as a result of a shortened moment arm, reduced moment of inertia, or both, these results indicate that a proximally positioned lesser trochanter is advantageous to leaping among prosimian primates. However, they again point up the variation in the degree of expression of this trait among apparently similarly specialized saltatorial animals.

Ratio F3, the Gluteal Index, measures the distal extent of the third trochanter relative to total femoral length. This bony landmark is the attachment site for the tendons of pars anterior of *M. gluteus superficialis* and *M. tensor fasciae femoris*. The much-debated function of *M. gluteus superficialis* (see Stern 1971, 1972 for excellent reviews) must include some components of both abduction and extension of the hip, while *M. tensor fasciae femoris* is an important hip flexor. Distal prolongation of the third trochanter has the double effect of increasing the moment arms of these two muscles, and of increasing the mass moment of inertia of the hindlimb as a whole. As for the

lesser trochanter, I predict a proximal placement of the third trochanter among leapers, and a more distal position among less specialized quadrupedal prosimians.

Again the prediction is confirmed, as the three families with the most proximally position third trochanter are Tarsiidae, Galagidae, and Indriidae. Among the Malagasy genera, Lepilemur and Microcebus are most similar to the three leaping families, as might be predicted on the basis of the large leaping component of locomotor behavior within these two genera. Tupaiidae are most clearly distinguished from all other prosimians on the basis of the extremely distal position of the third trochanter. Among the galagos, G. senegalensis diverges from G. crassicaudatus in the direction of Tarsiidae and Indriidae, while both G. alleni and G. demidovii are intermediate.

The Condylar Index (Ratio F4) is a ratio of the anterior-posterior dimension of the femoral condyles to their medio-lateral dimension. One of the original morphological traits of vertical clingers and leapers noted by Walker (1967, 1974; Napier and Walker 1967) was the deep antero-posterior dimension of the femoral condyles. Femoral condyles with a large antero-posterior diameter were thought to increase the leverage (i.e., mechanical advantage) of knee extension by the M. quadriceps femoris. By increasing the distance from the quadriceps tendon to the center of rotation of the knee joint, the moment arm of

this powerful extensor is increased, allowing a more powerful action. The Condylar Index was calculated to directly test the claim that vertical clingers and leapers are distinguished from other prosimians on the basis of this trait.

The data presented here do not confirm Walker's predictions concerning the antero-posterior dimension of the femoral condyles. The only separation effected by the Condylar Index is between the Lorisidae and Tupaiidae and all other prosimians. There is no clear separation between Malagasy taxa and the non-Malagasy leapers; all 6 of these families have values slightly greater than 100. Only the slow-climbing lorisisds and the unspecialized quadrupedal tree shrews have femoral condyles that are wider (medio-laterally) than deep (dorso-ventrally). Both the quadrupeds and leapers of the Malagasy Republic, and the African and Asian leapers have femoral condyles that are only slightly deeper than wide. While Walkers's functional analysis of the femoral condyles acting as a "pulley" for the action of M. quadriceps femoris in knee extension is certainly correct, this trait does not distinguish between quadrupedal prosimians (e.g., Lemuridae, Hapalemur, and Cheirogaleidae) and leapers (Indriidae, Tarsiidae, Galagidae, and Lepilemur).

Another proposed femoral characteristics of vertical clingers and leapers is the possession among the smaller leapers of a "cylindrical" femoral head, and of a more "spherical" head among the larger-bodied leapers (Walker 1967, 1974; Napier and Walker 1967). Ratio F5, the Femoral Head Index, is an attempt to quantify variability in the shape of the femoral head. The results indicate a very slight difference between, on the one hand, tarsiids and galagids and, on the other, all of the Malagasy taxa and Tupaiidae. In all prosimians, however, the femoral head is slightly larger in its dorso-ventral dimension than in its cranio-caudal dimension. The real significance of Walker's observation is better understood by a qualitative examination of the femoral head and especially the posterior expansion of its articular surface onto the neck among Tarsiidae and Galagidae that appears to be related to the habitually flexed, abducted, and laterally rotated position of the femora in vertical clinging postures (Anemone 1983). This trait, and its absence among all Malagasy taxa, better explains the shape difference between the femoral head of large and small leapers (see discussion in Section 6.3.). However, the essential identity of Indriidae, Lepilemuridae, Lemuridae, and Cheirogaleidae in this trait make it useless as a discriminator between leaping and quadrupedal prosimians.

The two Greater Trochanter Indices (Ratios F6 and F7) are measures of the distance from the hip joint to the lateral edge of the greater trochanter relative to femoral length. Since *Mm. gluteus medius* and *minimus* insert into this region of the greater trochanter, these measures are approximations of the moment arms of these muscles in extension of the thigh. Due to the importance of rapid hip extension in leaping, I predict that the leapers would have lower values for these ratios than would quadrupedal taxa. In general this prediction is confirmed by the data, although it must be noted that the differences between taxa are slight. In both ratios, the taxa with the smallest values are Tarsiidae, Galagidae, and Indriidae. Conversely, those taxa with relatively large values, and hence longer moment arms, are the quadrupedal Tupaiidae, Cheirogaleidae, Lemuridae, and Lorisidae. Among the Malagasy taxa, there is a clear spectrum from the leaping Indriidae with the lowest values, through the progressively less saltatorial Lepilemuridae, Lemuridae, and Cheirogaleidae. Both ratios also indicate minor differences between the leaping and quadrupedal species of Galago, but always in the predicted direction (i.e., smaller values for G. senegalensis than for G. crassicaudatus).

In his study of the hip and thigh of Lorisiformes, McArdle (1981) calculated similar ratios to some of those used here. While his results are essentially similar to

mine, he offered the caveat that the use of femoral length as the denominator in these ratios may have skewed the results, since taxa with apparently more proximally situated trochanters usually have the longest femora. There is, however, every reason to believe that, if it were adaptive, a lineage could increase the length of the femur and maintain high mechanical advantage in the muscles crossing the hip joint. Therefore, the fact that some prosimian taxa (i.e., most leapers) have reduced their muscular moment arms in conjunction with an increased functional length of the hindlimb is certainly significant. The fact that femoral elongation appears to have taken place distal to the level of the trochanters is of functional importance, and should not be ignored.

In summary, analysis of these femoral ratios indicates a suite of traits that are advantageous to an arboreal leaping mode of progression. These include a long femur, proximally located muscle insertions with the resultant reduced mechanical advantage and moment of inertia, and a deep distal femur providing a large mechanical advantage in knee extension. However, these traits are variably expressed among the most specialized prosimian leapers, and often do not allow clear discrimination between these animals and hindlimb dominant quadrupedal Lemuriformes. Since the functional significance of these traits for

leaping appears to be well-established both among primates (McArdle 1981; Stern 1971; Jungers 1976; Fleagle 1976, 1977) and other mammals (Camp and Borell 1937; Howell 1932, 1944; Smith and Savage 1956), perhaps the explanation for this seeming paradox lies in the ability of almost all prosimians to do some leaping. Speaking just of the Malagasy taxa, Jouffroy (1975:149) states,

"Certainly there are other primates which are equally good or even better jumpers, but this propensity is so general among the Lemuriformes that it can be considered as characteristic of the group as a whole."

In any event, these data do not support the hypothesis of a single morphological adaptation to vertical clinging and leaping among prosimian primates.

6.7. Discriminant Analysis

Multiple discriminant function analysis was used in the analysis of three sets of femoral data; raw data, logarithmically transformed data, and ratios using skeletal trunk length as the denominator. Both the BMDP and SPSS statistical packages were used, but since the results were identical in all respects, only the SPSS results are discussed here. Only the first three discriminant axes are plotted and discussed since in all cases they account for approximately 90% of the total between-group variance. As in the pelvic analysis, the results are presented as univariate and bivariate plots of the mean family values for the first three discriminant axes (Appendix F). The

Table 16. Order of entry of variables into femoral discriminant analyses.

A. STL Ratio Analysis

1. Femur length
2. Distal extent of third trochanter
3. Head-greater trochanter length (1)
4. Distal extent of lesser trochanter
5. Dorsoventral length of femoral condyles
6. Height of femoral head
7. Breadth of femoral head
8. Diameter of femoral neck
9. Width of greater trochanter
10. Head-greater trochanter length (2)

10

B. Log Analysis

1. Femur length
2. Breadth of femoral head
3. Width of greater trochanter
4. Mediolateral length of femoral condyles
5. Dorsoventral length of femoral condyles
6. Distal extent of lesser trochanter
7. Distal extent of third trochanter
8. Head-greater trochanter length (1)
9. Height of femoral head
10. Diameter of femoral neck

C. Raw Data Analysis

1. Head-greater trochanter length (1)
2. Mediolateral length of femoral condyles
3. Dorsoventral length of femoral condyles
4. Head-greater trochanter length (2)
5. Width of greater trochanter
6. Femur length
7. Distal extent of third trochanter
8. Distal extent of lesser trochanter
9. Diameter of femoral shaft
10. Height of femoral head

Table 17. Canonical coefficients and correlations for femoral discriminant analyses: Axes 1 and 2. *

VARIABLE	FIRST DISCRIMINANT AXIS					
	RAW	r	STL	r	LOG ¹⁰	r
1. Femur l.	1.16	.61	.91	.65	2.41	.45
2. Head height	1.53	.49	.56	.48	-.07	.30
3. Head breadth	-2.26	.47	-.16	.49	-2.31	.32
4. Third tro.	-1.06	.38	-.60	-.13	-2.25	.14
5. Lesser tro.	-.48	.39	.44	.34	.95	.28
6. Neck diameter	-.42	.41	.11	.33	.78	.33
7. Head-Gr. tro. (1)	2.31	.55	.32	.57	2.05	.35
8. Shaft diameter	-1.06	.50	-.24	.32	-1.31	.33
9. D-V condyles	2.24	.59	-.22	.43	1.30	.39
10. M-L condyles	-1.73	.48	-.41	.36	-1.68	.30
11. Width of Gr. tro.	.55	.56	.27	.48	.45	.36
Percent Dispersion		56%		55%		55%

VARIABLE	SECOND DISCRIMINANT AXIS					
	RAW	r	STL	r	LOG ¹⁰	r
1. Femur l.	-2.28	.15	-.03	.15	-.88	.41
2. Head height	3.04	.24	.76	.34	2.21	.40
3. Head breadth	-1.32	.20	-.26	.18	-2.37	.36
4. Third tro.	2.04	.41	.81	.62	1.82	.49
5. Lesser tro.	-2.40	.15	-.78	-.07	-3.09	.29
6. Neck diameter	-.88	.12	-.46	-.10	-1.18	.29
7. Head-Gr. tro. (1)	.99	.26	.35	.38	2.62	.43
8. Shaft diameter	-.30	.18	-.13	.04	-.25	.36
9. D-V condyles	.40	.18	.42	.07	2.06	.40
10. M-L condyles	.24	.22	-.38	.12	-.96	.38
11. Width of Gr. tro.	-.03	.26	.17	.35	.42	.44
Percent Dispersion		24%		25%		26%
Cumulative Percent		80%		80%		81%

* See Table 18 for explanation.

Table 18. Canonical Coefficients and Correlations for Femoral Discriminant Analyses: Axis 3.

VARIABLE	THIRD DISCRIMINANT AXIS					
	RAW	r	STL	r	LOG ¹⁰	r
1. Femur l.	-2.18	-.16	.61	.42	2.06	.56
2. Head height	-3.08	.12	-.46	.12	-.21	.49
3. Head breadth	-3.69	-.12	.63	.34	5.04	.52
4. Third tro.	-.16	-.16	.63	.57	.29	.50
5. Lesser tro.	.95	-.03	.33	.41	-.58	.45
6. Neck diameter	1.53	.03	.21	.26	-.63	.43
7. Head-Gr. tro. (1)	3.43	-.04	-.87	.14	-2.97	.45
8. Shaft diameter	.01	-.05	.14	.30	.13	.46
9. D-V condyles	1.99	.01	-.30	.25	-3.01	.41
10. M-L condyles	.42	.05	.36	.33	1.43	.47
11. Width of Gr. tro.	-.21	-.05	-.38	-.10	-1.13	.39
Percent Dispersion		8%		11%		8%
Cumulative Percent		89%		91%		90%

The data in Tables 17 and 18 are from the SPSS DISCRIMINANT analyses of femoral data. The coefficients presented are the standardized canonical discriminant function coefficients and the r values are pooled, within-group correlations between canonical discriminant functions and discriminating variables. Correlations of .30 or greater are generally considered to be significant. Dispersion and Cumulative Dispersion are the percentages of the total between-group variance that are accounted for by the discriminant axes.

relative importance of individual variables in explaining the overall discrimination along the various axes is evaluated by the order of variable entry into the stepwise analysis, the magnitude of the canonical coefficients, and the correlations between the variables and the discriminant axes themselves (Tables 16 - 18).

Univariate plots of the first discriminant axis indicate a slight separation of those prosimians whose locomotor repertoire contains a significant proportion of leaping (Indriidae, Lepilemuridae, Lemuridae, Galagidae, and Tarsiidae) from those that rarely (Cheirogaleidae) or never (Lorisidae, Tupaiidae) leap. In the raw and logged data plots, Indriidae are alone at the high end of the spectrum, while they are joined by Tarsiidae in the ratio plot. In all three plots, Tupaiidae have the lowest values on axis one, most closely approximated by Cheirogaleidae and Lorisidae. Looking at the Lemuriformes as a group, a pattern that will become increasingly familiar is seen in which the Indriidae are highest, Lemuridae and Lepilemuridae are intermediate, and Cheirogaleidae have the lowest value. The second discriminant axis is not easily interpreted in terms of the known locomotor behavior of the animals. Indriidae and Tupaiidae have the highest values, clearly separated from Galagidae, Cheirogaleidae, Lorisidae, and Tarsiidae which have the lowest values on this axis. Lemuridae and Lepilemuridae are again

intermediate between the high values of Indriidae and the low values of Cheirogaleidae. On the raw data plot, Tupaiidae are uniquely separate from all other prosimian taxa along axis two. Discriminant axis three is also difficult to interpret solely in terms of locomotor behavior. The logged plot and the raw data plot clearly separate the Lorisidae from all other taxa. The ratio plot presents a different picture, with no really uniquely positioned taxon. On this plot, Tupaiidae have the highest value but are closely approximated by Galagidae, Tarsiidae, and Lorisidae. The Malagasy taxa are again arrayed from Indriidae through Lepilemuridae and Lemuridae and finally to Cheirogaleidae, which has the lowest value for all taxa.

Several of the patterns noticed in the univariate plots are clearly represented in the bivariate plots of the first three discriminant axes. The bivariate plots of the first two discriminant axes clearly reveal the unique position of Tupaiidae among prosimian primates. Indriidae are to a lesser extent uniquely positioned. In all three plots, Lemuridae and Lepilemuridae are situated very closely to each other and between Indriidae and Cheirogaleidae. Lorisidae are usually situated closest to the unspecialized quadrupedal Cheirogaleidae, while Galagidae and Tarsiidae are quite close to each other and distinct from Indriidae in both the raw and logged data plots. The bivariate plot

of the first two discriminant axes does not provide any support for the VCL hypothesis.

The plots of axes one and three reinforce the unique position of Tupaiidae and Indriidae along the first axis, and add to this the clear separation of Lorisidae from all other prosimians along axis three. Both the ratio and the logged data plots again demonstrate the intermediate nature of Lepilemuridae and Lemuridae between Indriidae and Cheirogaleidae. The plots of discriminant axes two and three provide no additional information not already noted in the other plots.

6.7.1. Evaluation of predictor variables

In this section, the relative importance of individual variables to the discrimination along the first three axes is discussed. As mentioned above, three different methods are used to answer these questions. Since stepwise discriminant analysis adds variables into the discriminant function in the order in which the variables add the most to the between-group separation, the order of variable entry provides a rough estimate of the relative importance of each variable in the overall discrimination achieved. While there is significant variation in the order of variable entry in the three discriminant runs (Table 16), the variables that are most commonly entered early in the analysis, and hence those that significantly contribute to the separation of groups, are femoral length, head-greater

trochanter length (1), and dorsoventral condylar length. A group of variables of slightly less importance includes the distal extent of the lesser and third trochanters, and the width of the greater trochanter. The order of variable entry provides information on the importance of variables to the overall discrimination. In order to explore the importance of individual variables to discrimination along particular axes, the canonical coefficients and correlations between variables and discriminant axes must be examined (Tables 17 - 18).

For axis one, both the canonical coefficients and the correlations indicate the importance of many of the same femoral variables in providing separation of groups. Seven variables have significant correlations with axis one in all three discriminant runs, and three of these seven (femoral length, head-greater trochanter length (1), dorsoventral condylar length) also have consistently high loadings on axis one. It should be noted that these three variables are also those most frequently entered in the earliest steps of the stepwise analysis. Other variables that may be of some importance in the discrimination along axis one include the distal extent of the lesser and third trochanters, and mediolateral condylar length. Axis two presents a simpler picture with fewer variables contributing to its discrimination and good agreement

between the different methods of evaluation of the relative contribution of individual variables. Variables with consistently high correlations with axis two include the distal extent of the third trochanter, head-greater trochanter length (1), width of greater trochanter, and the height of the femoral head. Three of these four variables (distal extent of third trochanter, head-greater trochanter length (1), and head height) and also the distal extent of the lesser trochanter have the highest canonical coefficients on axis two. Additionally, the order of variable entry listing cites the importance of head-greater trochanter length (1), width of the greater trochanter, and the distal extent of the lesser and third trochanters to the overall discrimination.

Some of these same variables appear to be important to the discrimination along axis three. The length of the femur and the breadth of the femoral head have both high coefficients and high correlations with axis three, and are probably the two variables that contribute the most to discrimination along this axis. Other variables with significant correlations include the distal extent of the third and lesser trochanters, and the mediolateral length of the femoral condyles. On the basis of canonical coefficients, head-greater-trochanter length (1) and dorsoventral condylar length are also important variables on axis three.

In summary the three methods of evaluation indicate that the most important variables for discrimination along axis one appear to be femoral length, head-greater trochanter length (1), and dorsoventral condylar length; for axis two, distal extent of third trochanter, head-greater trochanter length (1), and head height; and for axis three, femoral length and head breadth. Several other variables appear to be of considerable, but lesser importance for the discrimination provided in these analyses. In addition, a caveat must be stated concerning these results. The distribution of significant correlations between variables and discriminant axes is curious in several respects. Specifically, all variables are significantly correlated with axis one in the raw data analysis, as are all variables on axis three in the logged data analysis. Conversely, all of the raw variables have very low correlations with axis three, as do all but one of the raw variables with axis two. This apparently random distribution of significant correlations recalls the difficulties of Oxnard, German and McArdle (1981) in ascertaining the importance of individual variables in their discriminant function analysis of McArdle's (1981) prosimian hip and thigh data. These authors stated that:

"In this study, each axis is a melange of variables which as a whole produce significant separations among genera" (Oxnard, German and McArdle 1981:481).

While this is clearly an unsatisfactory state of affairs, perhaps it is a sometimes necessary result of our inadequate understanding of the internal workings of multivariate analyses on biological data (Kowalski 1972).

Having identified several key variables for discrimination along each of the first three discriminant axes, we can now refer back to the plots and attempt to relate the distribution of groups to the femoral ratios involving these variables. Concordance between the distribution of families along the discriminant axes and their relative positions in the ratio analysis will allow greater confidence in the interpretation of the discriminant analysis. Since femoral length, head-greater trochanter length (1), and dorsoventral length of the condyles appear to account for much of the discrimination along axis one, the appropriate ratios to examine are Relative femoral length (ratio F1), Greater trochanter index (1) (ratio F6), and Condylar index (ratio F4). Relative femoral length appears to satisfactorily explain much of the discrimination along axis one. The Tupaiidae, with the shortest femora among prosimians, are clearly distinguished at one end of axis one, while Indriidae and Tarsiidae with the longest femora in the suborder are at the other end of axis one. Lorisidae and Cheirogaleidae are partially separated from Lemuridae, Lepilemuridae, and

Galagidae along axis one, and indeed have shorter femora than do the latter families. The Condylar index results also appear to be explainable in terms of the separation of groups along discriminant axis one. Again, Indriidae and Tarsiidae are at one extreme in both the ratios and along the discriminant axis, while there is a good deal of overlap between Galagidae, Lemuridae, and Lepilemuridae. The Condylar index does not, however, explain the unique position of Tupaiidae along axis one, since their value on this ratio is intermediate between Lorisidae and the rest of the taxa. Nor is the Greater trochanter index (1) easily explainable in terms of locomotor groupings or in terms of the separation along axis one.

The key variables along axis two are distal extent of the third trochanter, head-greater trochanter length (1), and height of the femoral head. Thus, the ratios to be considered are the Gluteal index (ratio F3), Greater trochanter index (1) (ratio F6), and Femoral head index (ratio F5). The Gluteal index can only partially explain the discrimination along axis two. Tupaiidae are again clearly distinguished in both the ratio and the discriminant analysis by their large value in this variable. However, the taxon that is closest to Tupaiidae in the discriminant plot (Indriidae) is nearly the furthest from them on the basis of the ratio results. In addition, the taxa that are furthest from Tupaiidae along axis two

(Cheirogaleidae, Lorisidae, and Galagidae) are clearly intermediate in Gluteal index value. The Greater trochanter index (1) is again poorly correlated with the results of the discriminant plot. This ratio neither establishes the unique position of Tupaiidae, nor the distribution of the other taxa that is seen along axis two. Similarly, the Femoral head index only partly corresponds to the distribution along axis two. While Lorisidae, Galagidae, and Tarsiidae are at the low range in both ratio and discriminant plot, Cheirogaleidae have the highest values on the ratio, yet are positioned near the bottom of axis two along with the Lorisiformes and Tarsiidae. The other taxa with high values on the Femoral head index are arrayed at the high end of axis two. These include Tupaiidae, Indriidae, Lemuridae, and Lepilemuridae. Since these taxa span almost the entire range of prosimian locomotor behavior, this axis is not easily explained in terms of behavior.

The most important variables for discrimination along axis three are femoral length and femoral head breadth, and the corresponding ratios are Relative femoral length (ratio F1) and Femoral head index (ratio F5). Axis three, especially in the raw and logged data discriminant runs, mainly distinguishes between the morphologically unique Lorisidae and the rest of the prosimians. However, Relative

femoral length is not one of the traits that clearly distinguishes Lorisidae. They are, in fact, intermediate in femoral length between the short-limbed quadrupeds (Tupauidae and Cheirogaleidae), and the longer-limbed Lemuriformes, Galagidae, and Tarsiidae. Similarly, the Femoral head index reveals an intermediate position of Lorisidae between Galagidae and the Lemuriformes. Only the Condylar index clearly separates the Lorisidae from all other prosimians, and I suggest that the mediolateral and dorsoventral dimensions of the femoral condyles are the variables most responsible for the unique position of Lorisidae along axis three. In addition to being one of the first variables entered into the discriminant runs, dorsoventral condylar length also has high loadings on axis three, while mediolateral length has significant correlations with this axis.

To summarize the results of the discriminant analysis, the correspondence between the variables noted as significant contributors to discrimination along the first three axes and the results of the femoral ratios leaves much to be desired. Perhaps the discriminant results can not be related explicitly to particular variables, but rather reflect an overall contribution to discrimination by many or all of the variables similar to that noted by Oxnard, German and McArdle (1981). In any event, many of the variables that may be important in the discriminant

analysis (e.g., femoral length, head-greater trochanter length, length of femoral condyles, distal extent of third and lesser trochanters) are of clear functional significance in the positional behaviors of prosimians.

6.8. Summary

It should be clear from the evidence presented in this chapter that the existence of a single morphological solution to the demands of vertical clinging and leaping among prosimians can not be supported on the basis of femoral anatomy. While all of the traits mentioned by Walker (1967, 1974; Napier and Walker 1967) are found among at least some saltatorial prosimians, none are found exclusively among all leapers, and many do not readily distinguish between leapers and hindlimb-dominant quadrupeds. In addition, the metric results presented here indicate other femoral traits that appear to be functionally linked to positional behavior among at least some leaping taxa. As with the pelvis, the femoral results indicate a much closer affinity between Indriidae and the rest of the Malagasy Lemuriformes than between the Indriidae and the non-Malagasy leapers (Galagidae and Tarsiidae). In addition, the anatomical adaptations to leaping found among galagos and tarsiers appear to be in marked contrast to those of the Malagasy leapers.

Of the proximal femoral traits thought by Walker (op. cit.) to characterize leaping prosimians, I have shown that one (posterior expansion of articular surface of head onto neck) is found only in galagos and tarsiers, while the other (greater trochanter that overhangs the ventral shaft) is found among leapers and most quadrupeds. The first of these traits is best interpreted as a postural adaptation to vertical clinging among smaller leaping prosimians, while the second increases the leverage of *M. vastus lateralis* in knee extension in most prosimians. However, all prosimian leapers appear to be linked by the possession of a reduced third trochanter, and relatively proximally located lesser and third trochanters. I have shown that proximally restricted muscle insertions on the femur have the double effect of both reducing the moment arm and reducing the moment of inertia, both adaptations for speed that are characteristic of cursorial and saltatorial animals.

The morphology of the distal femur played a large role in the original diagnosis of the vertical clinger and leaper morphology (Walker 1967; Napier and Walker 1967). Traits thought to characterize only leapers include deep femoral condyles with posteriorly facing articular surfaces for the tibia, and a narrow and deep patellar groove with a prominent lateral margin. My results again indicate that these traits are found in both leapers and quadrupedal

Lemuriformes, and thus cannot be used to define vertical clingers and leapers. These traits appear to be part of a functional complex related to the powerful action of *M. vastus lateralis* (and the other parts of *M. quadriceps femoris*) in extension of the leg at the knee. While this function may be related to a general propensity for leaping among all Lemuriformes (Jouffroy 1975), and indeed may be best developed among specialized leapers, these traits are, nevertheless, poor discriminators between taxa classified as vertical clingers and leapers and most quadrupeds. The traits that do appear to link leaping prosimians separately from quadrupeds are the raised ventral surface of the patellar groove which increases the size of the quadriceps "pulley", and the extreme lengthening of the femoral shaft.

As in the pelvic discriminant analysis, there is little support for the VCL hypothesis in the results of discriminant function analysis of the femoral measurements. Galagidae and Tarsiidae are generally linked to a great degree, while Indriidae are usually quite separate from these families and closely approximated to the rest of the Lemuriformes. This result is confirmed by qualitative examination of the femoral morphology of the animals, and by the quantitative results seen in the femoral ratios. All of the femoral evidence appears to refute the hypothesis that there is one morphological solution to the demands of

vertical clinging and leaping among prosimians. Again, Galagidae and Tarsiidae appear to possess similar adaptations, while Indriidae are most similar to other lemuriform taxa that leap much less frequently and spectacularly than they do.

Chapter 7. Skeletal Proportions And Allometry

7.1. Introduction to Chapter 7

Attempts to correlate limb proportions with positional behavior have a long history in primatology. Mollison (1911), Schultz (1969), Erikson (1963) and Napier and Napier (1967) are just a few of the workers who have attempted to organize data on primate skeletal proportions on the basis of differing patterns of positional behavior. As might be expected, Walker (1967, 1974) and Napier and Walker (1967) included skeletal proportions as part of their diagnosis of the morphology of vertical clingers and leapers. Following Schultz (1929) and Erikson (1963), Walker (1967, 1974) relied on standard appendicular indices (e.g., brachial, crural, intermembral) to argue that skeletal traits shared by leaping prosimians include long hindlimbs, short forelimbs, and a longer radius than humerus.

Since the publication of the VCL hypothesis in 1967, several workers have published additional data on prosimian limb proportions (Jungers 1979; McArdle 1981; Oxnard, German, Jouffroy and Lessertisseur 1981; Jouffroy and Lessertisseur 1979; Godfrey ms.). In this chapter, I review all the published information, and present my own findings on this subject. In addition to the standard appendicular indices, I have calculated the length of the forelimb and the hindlimb, and of the proximal and distal

bony elements of the forelimb and hindlimb, relative to skeletal trunk length (STL). These indices (Table 12 and Appendix D) provide a good measure of the elongation of limbs and limb segments relative to the body size of the individual animal, and are similar to ratios calculated by McArdle (1981). Rather than using skeletal trunk length as a bodily size variable, McArdle (1981) used the trunk height of Schultz (1929). Finally, in order to more fully understand the ratio results, least squares regressions of hindlimb and forelimb length against skeletal trunk length were performed. The slopes for these allometric equations are presented in Tables 19 and 20 and the patterns of hindlimb scaling are examined in light of the information gleaned from the appendicular indices and other ratios, and in terms of patterns of positional behavior. The chapter ends with a discussion of the relevance of limb proportions and skeletal allometry among prosimian primates to the VCL hypothesis.

7.2. Limb Proportions

The intermembral index (ratio LP1) is a measure of forelimb or hindlimb dominance in overall limb proportions. It is the single best discriminator of prosimian locomotor groups according to Walker's (1967) data, and also looms large in the data presented by McArdle (1981) and Jouffroy and Lessertisseur (1979). Walker's (1967) leaping genera

had values of between 49.2 and 67.4, active quadrupeds were between 67.7 and 74.2, and the slow-climbing lorisisds had values ranging from 83.5 to 94.3 (Walker 1967:139). Godfrey (ms.) questioned the separation of vertical clingers and leapers from active quadrupeds on the basis of intermembral index. While my results confirm Walker's conclusion that leapers are the most hindlimb dominant of all prosimians, they also establish a greater degree of overlap between leapers and active quadrupeds than noted by Walker (1967, 1974).

At the family level, the specialized leapers (Galagidae, Tarsiidae, and Indriidae) have the lowest intermembral indices. They are joined by the Lepilemuridae, the most adept Malagasy leapers after the Indriidae. The taxa with the highest intermembral indices, and hence the least hindlimb dominant, are the Lorisidae, followed by Tupaiidae, Cheirogaleidae, and Lemuridae. The fact that these animals leap least frequently among Prosimii supports the argument for the significance of a low intermembral index among prosimian leapers. Within the Indriidae intermembral index increases as bodily size increases, from Avahi to Indri. This point will be returned to in the skeletal allometry section of this chapter. Among the Lepilemuridae, the genus Lepilemur has a significantly lower intermembral index than does Hapalemur. Similarly, Lemur has a lower intermembral index than does Varecia.

These results are exactly what would be predicted on the basis of the greater proportion of leaping in the daily locomotor repertoire of Lepilemur and Lemur. Among the species of Galago, there is a very clear spectrum, first noted by McArdle (1981), of increasing intermembral index between the predominantly leaping G. senegalensis and the mainly quadrupedal G. demidovii and G. crassicaudatus. While the general picture presented by the intermembral index data appears to satisfactorily distinguish between leapers and quadrupeds, the intermediate position of several genera makes clear separation difficult. Specifically, the fact that the mainly quadrupedal Hapalemur has a lower intermembral index than Indri, G. demidovii, and G. crassicaudatus leads me to conclude that the intermembral index alone does not always distinguish between leapers and active quadrupeds among prosimians (contra Walker 1967, 1974).

While the crural index (ratio LP2) provides no discrimination between prosimians on the basis of locomotor preferences, it does contain interesting information on different patterns of hindlimb elongation among the leaping taxa. For instance, the relative amount of elongation in the femur and the tibia is essentially equal in Tarsiidae, nearly equal in Galagidae, and much greater in the femur than the tibia in Indriidae. This conclusion is confirmed

by the results of the relative tibial and relative femoral length ratios (ratio LP3 and ratio F1). These ratios also show that, relative to body size, femoral and tibial elongation is greatest in Tarsiidae. In both of these measures, Indriidae are closer to Tarsiidae than are Galagidae. The relative hindlimb length (ratio LP4) confirms that, among all prosimians, the longest hindlimb is found among the leapers, and that among the leapers, the longest hindlimb is found among Tarsiidae. With respect to all of these measures (relative femoral, tibial, and hindlimb length), the lowest values are found among animals that rarely or never leap; Lorisidae, Tupaiidae and Cheirogaleidae. In all ratios, Lepilemuridae and Lemuridae are intermediate between Indriidae and Cheirogaleidae. It is interesting to note that Lepilemur and Hapalemur show an almost identical pattern of hindlimb elongation. Thus, differences between these two genera in intermembral index must be explained on the basis of differences in forelimb, not hindlimb length. On the other hand, Lemur and Microcebus have longer hindlimbs than Varecia and Cheirogaleus. Conversely, the extremely minor differences in intermembral index between these pairs of genera must similarly be attributable to differences in forelimb length.

In summary, ratios concerning the relative length of the hindlimb and of its segments clearly point to the

importance of a relatively long hindlimb for animals with saltatorial habits. As discussed earlier, a long hindlimb allows muscular forces to propel the animal's center of gravity through a greater distance (or for a longer time) while still in contact with the ground. This increases the take-off velocity that can be attained, and thus, increases the maximum height to which the animal can leap.

Interspecific variation in the genus Galago reflects this same principle in relative hindlimb, femoral and tibial length. This is not to say, however, that on the basis of any one of these ratios one can unequivocally predict whether an individual or a taxon is a leaper or a quadruped. This difficulty appears to concern those animals that are clearly capable of vertical clinging and leaping, but who, for one reason or another, rarely seem to engage in this kind of locomotion (e.g., Hapalemur, G. crassicaudatus, G. demidovii). In purely metric terms, Tarsiidae are more similar to Indriidae than to Galagidae in degree of hindlimb elongation.

Relative forelimb length (ratio LP6) clearly shows that, in spite of low intermembral indices, leaping prosimians actually possess long forelimbs relative to body size (contra Walker 1967, 1974). Their low values on the intermembral index are simply a result of much greater elongation in the hindlimb than the forelimb, not the

combination of long hindlimbs and short forelimbs. Tarsiidae have the longest forelimbs in the suborder, followed by Indriidae, Lorisidae, Galagidae, and Lepilemuridae. The shortest forelimbs, like the shortest hindlimbs, are found in the unspecialized quadrupedal Tupaiidae and Cheirogaleidae. The correlation of long forelimbs with leaping among prosimians is, however, much less compelling when one examines the data at the generic and specific levels. Hapalemur and Lepilemur have shorter forelimbs than Lemur, in spite of the fact that the former genera leap substantially more than does the latter. In addition, the most proficient leaper among the Galagidae (G. senegalensis) has the shortest forelimbs in the genus. In fact, the relatively short forelimb in G. senegalensis and in Lepilemur is in large part responsible for the extremely low intermembral indices of these genera. Among the indriid genera relative forelimb length increases with bodily size, resulting in the trend towards a higher intermembral index with increasing bodily size. The slow-climbing Lorisidae parallel the leapers in possessing a relatively long forelimb, but for a very different adaptive reason. These animals often need to "bridge" small gaps in the forest canopy, and are able to accomplish this more successfully with relatively long limbs (McArdle 1981; Jungers 1979).

The brachial index (ratio LP5), a measure of the relative contribution of radius and humerus to forelimb length, completely fails to distinguish between prosimians of different locomotor abilities (contra Walker 1967, 1974). While Tarsius has the highest brachial index (and hence, the longest radius relative to length of the humerus) while all of the other taxa except Tupaiidae have a radius that is barely longer than the humerus. With respect to relative humeral (ratio LP7) and radial (ratio LP8) lengths, I note a tendency for the leaping taxa to have longer segments than unspecialized quadrupeds. There is, however, a substantial degree of overlap in both measures between some leapers and some of the active quadrupeds of the Malagasy Republic. Tarsiidae again have the relatively longest humerus and radius, followed in both cases by Indriidae and Lorisidae. An intermediate group contains Galagidae, Lepilemuridae, and Lemuridae, and the shortest forelimb segments are found in Tupaiidae and Cheirogaleidae. Patterns at the generic and specific levels of analysis mirror the results of the interfamilial comparisons for relative forelimb length.

In summary, and contrary to the expectations of the VCL hypothesis (Walker 1967, 1974; Napier and Walker 1967), the families of leaping prosimians are characterized by relatively long forelimbs. Tarsiidae have the relatively longest forelimb, humerus, and radius, and are most closely

approximated in these respects by Indriidae. Galagidae also have long forelimbs, but are much closer to Lepilemuridae and Lemuridae than to the other vertical clinging and leaping taxa (Tarsiidae and Indriidae). With brachial indices slightly over 100, most prosimians (except Tupaiidae) have radii that are very slightly longer than humeri: the brachial index is thus of little use in distinguishing between prosimians of different locomotor habits. Ratios of relative forelimb, humeral, and radial length are better at separating leapers from unspecialized quadrupeds (Tupaiidae and Cheirogaleidae), but do not successfully distinguish between leapers and the active quadrupedal Lepilemuridae and Lemuridae. The significance of long forelimbs among animals that vertically cling to arboreal supports is best explained in terms of Cartmill's (1974) "vertical support model" (Jungers 1976a, 1976b) for large clawless mammals. These animals must rely on forces of adduction generated by their limbs and the resultant friction between these limbs and the support surfaces to remain on a vertical support. Possession of long forelimbs allows a vertically clinging prosimian to subtend a larger central angle and to thus remain on vertical supports of large diameter. As Jungers (1976a, 1976b) argues, this is especially important for the larger vertical clingers, the Indriidae, and thus explains the correlated increase in

forelimb length and bodily size in this family which results in larger intermembral indices in the larger indriids. The retention of long forelimbs in arboreal prosimian saltators provides a major contrast with the very short forelimbs found among bipedal, terrestrial saltators (e.g., dipododid rodents, Howell 1936, 1944) and should be interpreted as a postural, not a locomotor adaptation that allows clinging to vertical supports of varying diameter in the arboreal environment.

7.3. Skeletal Allometry

In addition to the ratios described above, I have utilized least squares regressions to investigate skeletal allometry among prosimian taxa. Jungers (1979) recognized the value of postcranial scaling as an adjunct to the information derived from limb proportion ratios. In this landmark study, he performed regressions of the length of forelimb, hindlimb, femur, tibia, humerus, and radius against skeletal trunk length, and related the patterns observed to locomotor and postural adaptations among the taxa studied (Indriidae, Lemuridae, and Lorisidae). In addition to these three families, the present study includes Galagidae and Cheirogaleidae. The slopes and sample sizes for each regression equation are listed in Tables 19 and 20. As in Jungers's (1979) study, the genus Hapalemur was treated as a member of the Lemuridae, while Lepilemur was excluded from both Jungers's and the present

Table 19. Skeletal allometry of the prosimian hindlimb:
Slopes and sample sizes.

Taxa	Femur	Tibia	Hindlimb
Indriidae	.98 (24)	.98 (24)	.98 (24)
Lemuridae *	.80 (78)	.75 (75)	.78 (75)
Cheirogaleidae	.86 (27)	.71 (27)	.79 (27)
Galagidae	.89 (63)	.90 (69)	.95 (63)
Lorisidae	.59 (54)	.59 (51)	.59 (51)

Table 20. Skeletal allometry of the prosimian forelimb:
Slopes and sample sizes.

Taxa	Humerus	Radius	Forelimb
Indriidae	1.21 (24)	1.12 (24)	1.16 (24)
Lemuridae *	1.13 (72)	1.02 (70)	1.08 (70)
Cheirogaleidae	.86 (27)	.71 (27)	.79 (27)
Galagidae	1.09 (62)	1.09 (61)	1.09 (61)
Lorisidae	.63 (54)	.44 (51)	.54 (51)

* Lemuridae includes Lemur, Varecia, and Hapalemur.
Slopes are from Least Squares Regression Analysis of
limb segments and skeletal trunk length (STL).
Numbers in parentheses are sample sizes.

study. In the following discussion, the term isometry refers to the condition where the slope of a regression equation is not significantly different from 1.00, implying geometric scaling of a limb or limb segment relative to body size. Positive and negative allometry refer to situations where the slope is, respectively, greater than or less than 1.00, indicating an increase or decrease in limb length relative to body size.

For Indriidae, my results confirm Jungers's (1979) in indicating a pattern of hindlimb isometry coupled with positive forelimb allometry. This pattern leads to relatively longer forelimbs, and hence higher intermembral indices in the larger members of this family. As mentioned above, Jungers (1979) has interpreted this trend as a confirmation of Cartmill's (1974) vertical support model, allowing large clawless mammals to effectively grasp vertical supports of large diameter. My results for Galagidae indicate a similar, although not identical pattern of skeletal allometry. In this family, a very slight positive forelimb allometry is coupled with very slight hindlimb negative allometry. Thus in Galagidae also, larger taxa will have relatively longer forelimbs and higher intermembral indices, and will retain the ability to cling to vertical supports. In addition, the slightly negative scaling of femur and tibia lengths is a reflection of the decreased emphasis on leaping in the largest of the

galagids, G. crassicaudatus. While this pattern is quite similar to that seen in Indriidae, the slopes and the differences between hindlimb and forelimb slopes within Galagidae are of lesser magnitude than those of Indriidae.

Lemuridae, including Hapalemur, are characterized by the combination of very slight positive forelimb allometry with strong negative hindlimb allometry. This pattern again conforms to the predictions of Cartmill's (1974) vertical support model, resulting in relatively longer forelimbs and higher intermembral indices in larger taxa. A slight difference between my data and that of Jungers (1979) appears in these regressions. While Jungers (1979) found a significantly lower slope in the scaling of the hindlimb than the forelimb, both scaled negatively according to his data. In any event, the strongly negative allometry of the lemurid hindlimb effectively restricts leaping, which requires long hindlimbs, to the smallest taxa. Accordingly, V. variegata, the largest of the lemurids, is an able vertical climber but not a leaper. Cheirogaleidae are unique among Malagasy prosimians in showing strong negative allometry in both forelimb and hindlimb, especially in the distal limb segments (i.e., tibia and radius). The relatively short limbs of subequal length in this family may be an adaptation to lowering the center of gravity, an advantageous trait in animals that travel above horizontal

arboreal supports (Fleagle 1977). With regards to Lorisidae, my results confirm Jungers's (1979) in demonstrating that these specialized slow-climbers have the strongest negative allometry in both forelimb and hindlimb among the prosimians studied. The result of this pattern is the possession of relatively much longer limbs (forelimbs and hindlimbs) among the two small lorid genera, Arctocebus and especially Loris. Jungers (1979) explains this as an adaptation that allows "bridging" between discontinuous but adjacent arboreal supports.

7.4. Summary

As stated in the introduction to this chapter, the traits considered to be a part of the VCL adaptation among prosimian primates include short forelimbs and long hindlimbs (reflected in low intermembral index), and a longer radius than humerus (reflected in a high brachial index) (Walker 1967, 1974; Napier and Walker 1967). Through a combination of standard appendicular indices, ratios of limb and segment length relative to skeletal trunk length, and regression analysis of postcranial scaling, this study has clarified the patterns of limb proportions found among prosimians. In most respects, the traits mentioned by Walker do not appear to successfully separate leapers from all quadrupeds. An alternative set of traits is suggested that offers better, but far from perfect discrimination between locomotor groups of prosimians.

As can be seen by examination of several ratios (relative hindlimb, femoral, and tibial length), leaping prosimians clearly possess relatively longer hindlimbs than do most other prosimians. This characteristic is confirmed in the data of McArdle (1981) and Jouffroy and Lessertisseur (1979). High values on these ratios, combined with the low intermembral indices mentioned by Walker (op. cit.), consistently and completely separate vertical clingers and leapers from both the slow-climbing Lorisidae and the unspecialized quadrupedal Tupaiidae and Cheirogaleidae. There is a substantial amount of overlap, however, in all of these ratios between the leapers and the Lepilemuridae and Lemuridae. Metrically and behaviorally intermediate taxa include the more quadrupedal species of Galago (G. crassicaudatus and G. demidovii), Lepilemur, and Hapalemur. These latter two genera are usually intermediate between the leaping Indriidae and the more quadrupedal Lemuridae. Tarsiidae consistently have the longest hindlimb, femur, and tibia among leaping prosimians, and are most closely approximated in this respect by Indriidae, and then by Galagidae. Within the genus Galago there is a noticeable spectrum in hindlimb length that correlates well with interspecific differences in locomotor behavior. The most specialized leaper, G. senegalensis, has the longest hindlimb, while the mainly quadrupedal species (G.

crassicaudatus and G. demidovii) have the shortest hindlimbs. As discussed previously, the functional significance of long hindlimbs is clearly related to leaping behavior, and the attainment of accelerations that enable a high take-off velocity. However, long limbs are of value to all cursorial animals (Howell 1944) in increasing stride length. It is thus not surprising to find elongate hindlimbs in the rapid quadrupeds of the Malagasy Republic, especially in light of the fact that some of these animals do have the ability to leap (Tattersall 1982).

The results presented here are equally clear in indicating that, rather than having short forelimbs relative to body size (Walker 1967, 1974; Napier and Walker 1967), leaping prosimians are characterized by the longest forelimbs in the entire suborder. Walker was obviously misled by the low intermembral indices of leapers into assuming that their forelimbs were relatively short. While short forelimbs are very common among non-primate, terrestrial saltators (Howell 1944), the ratios presented here (relative forelimb, humeral, and radial length) clearly show that leaping prosimians are unique in having very long forelimbs relative to body size. Their low intermembral indices result from the combination of extremely long hindlimbs and moderately long forelimbs. The ratios of relative forelimb length clearly separate leapers from Cheirogaleidae and Tupaiidae, but again show much

overlap with Lemuridae and Lepilemuridae. While Lorisidae are quite similar to vertical clingers and leapers in possessing long forelimbs, the adaptive significance of this trait is quite different in these two groups. While allowing lorisisids (especially the smaller genera) to bridge the gaps between discontinuous but adjacent branches, long forelimbs appear to be a postural adaptation among vertical clingers and leapers that allow them to cling to vertical supports of large diameter, as first noted by Cartmill (1974). Of the specialized leapers, Tarsiidae have the longest forelimbs. They are most closely approximated again by Indriidae, while Galagidae are again closer to Lemuridae and Lepilemuridae than they are to Tarsiidae in the degree of forelimb lengthening. Within the genus Galago and among the Lepilemuridae, the best leapers (G. senegalensis and Lepilemur) have the shortest forelimbs. This appears to contradict the trend towards long forelimbs noted at the familial level of analysis. It is also related, among Galagidae at least, to the fact that the best leaper is also one of the smaller species. Since the forelimb among Galagidae is characterized by slight positive allometry, smaller species would tend to have shorter forelimbs than larger species. Thus, although it is true to say that leaping prosimians possess longer forelimbs than their non-leaping relatives, this pattern may be significantly

different among different taxa.

With respect to the brachial and crural indices, my results clearly show that these standard indices do not allow any segregation of leapers from other prosimians. I suggest that the relative lengths of limb segments is better measured by the ratios involving skeletal trunk length as the denominator. These ratios provide easily interpretable information on the length of limb segments relative to a bodily size variable (e.g., skeletal trunk length).

The results of the regression analysis of postcranial scaling add valuable information to that derived from ratios of limb proportions. For example, in spite of the fact that Lorisidae are indistinguishable from vertical clingers and leapers on the basis of measures of relative forelimb length, they are unique among all prosimians by virtue of their extremely low scaling coefficients of both forelimb and hindlimb scaling. We have discussed how the extremely negative allometry of forelimbs and hindlimbs among Lorisidae leads to long-limbed small genera (Arctocebus and Loris), and short-limbed larger genera (Nycticebus and Perodicticus), and the functional significance of this pattern. Turning to the leaping and active quadrupedal taxa, Indriidae, Lemuridae, and Galagidae all appear to conform to the "vertical support model" of Cartmill (1974) in having higher scaling

coefficients in the forelimb than the hindlimb. In all measures, Indriidae have the highest slopes while Lemuridae have the lowest. In spite of interlimb differences in scaling, the largest taxa in all three families have relatively longer forelimbs than the smaller, allowing them to effectively grasp vertical supports of large diameter. In the hindlimb, Indriidae and Galagidae have significantly higher slopes than do Lemuridae. Since leapers require long hindlimbs, this pattern allows leaping behavior in large indriids and galagids, but restricts it to smaller lemurids. While galagids and indriids display similarities in both hindlimb and forelimb scaling, they are each unique and the similarities can easily be considered convergent solutions to a similar adaptive problem.

On the basis of the results presented here, I suggest four traits, the possession of which may characterize the limb proportions and allometric scaling patterns of prosimian leapers:

1. long hindlimbs relative to body size,
2. long forelimbs relative to body size,
3. isometry in hindlimb scaling,
4. positive allometry in forelimb scaling.

This suite of traits does not, however, produce perfect segregation of leapers from active quadrupeds. The best separation is again between leapers, unspecialized quadrupeds, and slow-climbers. In addition, the subtle differences between the various leaping families in each of

these traits imply that the similarities are convergent adaptations to similar adaptive problems in similar animals. Each family of leaping prosimian shows a unique combination of these traits, perhaps suggesting independent acquisition of many of them from a less specialized quadrupedal ancestor. While the general trends among leaping prosimians are clearly towards elongation in the forelimb and especially the hindlimb, there is little in the data on limb proportions to support a strict adherence to the VCL hypothesis.

Chapter 8. Conclusions and Discussion

8.1. Introduction to Chapter 8

As discussed in detail in Chapter 1, the Vertical Clinging and Leaping hypothesis of Napier and Walker (1967) comprises three major aspects that can be labeled behavioral, morphological, and evolutionary. The behavioral aspect refers to the proposed existence of a group of extant prosimians sharing a mode of positional behavior that can be called vertical clinging and leaping. The morphological aspect refers to the possession by this group of a common suite of specialized adaptations that make vertical clinging and leaping possible. Finally, the evolutionary aspect of the VCL hypothesis is the speculation that the same morphological pattern found among extant practitioners of vertical clinging and leaping was present among all known Eocene primates. As a result, Napier and Walker (1967) conclude that vertical clinging and leaping may have been the ancestral locomotor pattern among primates, and hence preadaptive to some or all of the present patterns of primate locomotion.

My approach to testing the validity of the VCL hypothesis has been to examine the hindlimb morphology (including myology, arthrology, and osteology) of most genera of extant prosimians in light of known patterns of positional behavior. The obvious intent of this

morphological survey has been to determine whether or not there exists among extant leaping prosimians a single, coherent, morphological adaptive complex. The decision to investigate the morphological aspect of the VCL hypothesis was made for several reasons, not the least of which was the previous lack of a comprehensive survey of the hindlimb morphology of prosimian primates. The most important reason was to gain a better understanding of the functional significance of morphological traits found among leaping prosimians. This aspect of my work should be of value to students attempting to reconstruct the positional behavior of extinct prosimians. Finally, the morphological question was seen as central to acceptance of the VCL hypothesis. If more than one pattern of hindlimb morphology were found to exist among extant prosimians classified as vertical clingers and leapers, the VCL hypothesis, and especially its relevance to the evolution of positional behavior among primates, would need to be reevaluated.

The methods of data collection that I relied on in this work are the traditional tools of the physical anthropologist: observation, dissection, and osteological measurement. The osteometric data were analyzed in terms of insights derived from functional biomechanics through both bivariate (i.e., ratios and regressions) and multivariate (i.e., discriminant function) analyses. The use of discriminant analysis, although certainly warranted by the

nature of this study, proved to be of little help in the analysis of the femoral and pelvic data. Although the plots generated by the discriminant analyses often made sense given the positional behaviors and morphologies of the taxa involved, it proved difficult to relate these plots back to the actual variables. Without this essential link to the morphology of the animals, the value of multivariate analysis to a functional study is questionable.

8.2. Ecology and Behavior

As is demonstrated in Chapter 2, the prosimians generally classified as vertical clingers and leapers show no simple patterns ecological preferences relating to diet and habitat usage. Dietary diversity among leaping prosimians runs the gamut from the exclusive carnivory of Tarsiidae through the herbivory of Indriidae to the specialized folivory of Lepilemur. Among the Galagidae alone, the range of dietary preferences includes, in varying proportions, insects and small vertebrates, gums, fruits, and flowers. While, as Fleagle (1984) notes, all specialized primate feeders on tree exudates practice some degree of vertical clinging and leaping, one cannot generalize as to the dietary preferences of all or most prosimian leapers.

Prosimian leapers appear to have equally eclectic tastes in their habitat preferences. While G. alleni and G. demidovii are usually found in the dense undergrowth of tropical forests, Lepilemur and the indriids move and feed in the terminal branches of the forest canopy. In southern Africa, G. senegalensis inhabits the lower reaches of Acacia thornveld, while G. crassicaudatus is found higher in the canopy of wetter, riparian and montane forests. With respect to bodily size, prosimian leapers similarly defy easy categorization. While Napier and Walker (1967) stated that leaping prosimians tend to be small, their actual sizes range from some of the smallest (G. demidovii and Tarsius sp.) to the largest (Indri and Propithecus) taxa in the suborder.

8.3. The Morphology of Leaping Prosimians

In their original diagnosis of the morphology of leaping prosimians, Napier and Walker (1967; Walker 1967) suggested the following list of traits as adaptations to vertical clinging and leaping habits:

1. Small to medium bodily size and a long tail.
2. Long hindlimbs with an extreme range of flexion and extension.
3. Long, straight femora with cylindrical heads marked by a posterior expansion of articular area.
4. Femoral condyles projecting posteriorly.
5. Narrow patellar groove projecting anteriorly to shaft of femur and having prominent lateral margins.
6. Femoral condyles more deep than wide.
7. Short forelimbs with the radius longer than the humerus.
8. Pelvis with a long ilium and short ischium,
9. Iliac width is positively allometric (i.e., wider among

- larger taxa) and the ilium bears prominent iliac spines.
10. Calcaneus and navicular are negatively allometric (i.e., long in small forms, short in large forms).

The major goal of this thesis has been to examine the morphological status of the extant animals classified as vertical clingers and leapers, and in so doing, to test the validity of this aspect of the VCL hypothesis. It should be noted here that I am mainly concerned with those traits that serve to distinguish between leaping prosimians and active quadrupedal ones; the slow-climbing lorisisids present a unique hindlimb morphology which is easily distinguished from that of both quadrupedal and saltatory forms.

My results clearly indicate a much more complicated situation than suggested by the authors of the VCL hypothesis. While confirming the presence of some traits among all leaping prosimians, the data presented here convincingly demonstrate the presence of two very different morphological adaptations to leaping among prosimian primates. In most qualitative and quantitative measures, Galagidae and Tarsiidae share a similar morphological adaptation to a saltatorial existence which is easily distinguished from that of Indriidae and Lepilemur. Contrary to the findings of Napier and Walker (1967; Walker 1967, 1974, 1979), I conclude that modern leaping prosimians do not share a single morphological adaptation to the requirements of an arboreal, saltatory lifestyle.

As mentioned above, all extant leaping prosimians do, in fact, share some morphological traits that appear to be adaptations to a saltatory existence. As suggested by Napier and Walker (1967), all leaping prosimians possess a long hindlimb and a long femur, and a pelvis with a short ischium and a long ilium. Similarly, leaping prosimians share proximally positioned femoral trochanters with the resultant reduced moment arms and moments of inertia, and a raised patellar articular surface on the distal femur. The functional significance of these traits in vertical clinging and leaping has been discussed in detail in previous chapters and will not be repeated here.

Several of the VCL traits mentioned by Napier and Walker (1967) are, in fact, shared by both leaping and active quadrupedal taxa (mainly Lemuriformes). These include femoral condyles which project posteriorly, a narrow patellar groove with a prominent lateral margin, and femoral condyles which are deeper than they are wide. As a result, these traits are of no use in defining leaping prosimians, except in so much as they characterize a low level of leaping which is practiced by nearly all prosimians except the slow-climbing Lorisidae (Jouffroy 1975). Alternatively, these traits may be cursorial adaptations of benefit to both saltators and to active quadrupedal prosimians.

My results indicate that several of the traits included by Napier and Walker (1967) simply do not have any relationship to or even correlation with vertical clinging and leaping. These traits include the possession of a long tail and small to medium bodily size, a short forelimb with a longer radius than humerus, and allometric functions relating to the width of the ilium and the length of the tarsus. As mentioned in Section 8.2., bodily size among leaping prosimians varies enormously, ranging from some of the smallest to the largest prosimian taxa. While a long tail is possessed by many leaping (as well as by many non-leaping) prosimians, the only prosimian lacking a tail is also a vertical clinger and leaper (Indri). My results also indicate that leaping prosimians possess the relatively longest forelimbs among prosimians, and that their low intermembral indices are the result of extremely long hindlimbs in combination with long forelimbs. Also contrary to Napier and Walker (1967), the brachial index does not serve to distinguish between leapers and quadrupeds; both groups have radii and humeri of essentially equal length (i.e., brachial indices near 100). Finally, rather than ascribing the apparent differences in width of the iliac crest and tarsal elongation to allometry, I conclude that the differences between leaping prosimians with respect to these traits are functionally significant and not simply related to differences in bodily size. Tarsal elongation

is, in fact, one of the major differences between the galago-tarsier and the indriid-Lepilemur morphological adaptations to vertical clinging and leaping. Likewise, differences in the shape of the ilium and the iliac crest between, on the one hand, galagos and tarsiers and, on the other, indriids and Lepilemur, are not convincingly explained as simply size-related (Godfrey ms.).

Morphological traits that bind galagos and tarsiers in distinction to indriids and Lepilemur, and that lead to the conclusion that two very different adaptations to leaping exist among prosimians, are present in every anatomical region studied in this research. Beginning with the pelvis, the major distinctions between the two groups are found in the shape of the ilium and the relative size of the iliac spines, and in the length of the pubic rami and symphysis. Galagos and tarsiers have narrow, rodlike ilia and only moderately developed iliac spines. Malagasy leapers have an ilium that is broadened significantly in its cranial third and is bounded by a wide iliac crest that terminates anteriorly in a large and projecting anterior superior iliac spine. Both the pubic rami and the pubic symphysis are longer among galagos and tarsiers than they are among indriids and Lepilemur. All prosimian leapers do, however, share two functionally important pelvic traits: the longest ilia and the shortest ischia among prosimians.

The femur shows an interesting distribution of traits among leaping prosimians in that its proximal, but not its distal, end is clearly different in the two groups. Traits of the proximal femur that distinguish between the two leaping adaptations include the shape of the femoral head, neck, and greater trochanter. A cylindrical head set on a short and thick neck with a large posterior expansion of articular surface characterizes the proximal femur of Galagidae and Tarsiidae. In sharp contrast to this is the condition seen among Malagasy forms, in which the femoral head is spherical and contains only a very small expansion of its articular surface onto the neck. In addition, the greater trochanter of the latter group extends higher than the femoral head, extends medially toward the head, and imparts a characteristic "notched" appearance to the proximal femur, which is in marked distinction to the condition seen among galagos and tarsiers. In the distal femur, leaping prosimians alone share a ventrally raised patellar articular surface, while they share with the active quadrupeds of Madagascar posteriorly facing femoral condyles which are deeper than wide, and a narrow and deep patellar groove with a prominent lateral margin.

Probably the most significant morphological difference between the two leaping adaptations is the elongation of the tarsal region, which is so important to the leaping of galagos and tarsiers, but which is not found among the

specialized leapers of the Malagasy Republic. Contrary to the arguments of Napier and Walker (1967; Walker 1967, 1974), the lack of elongation of the calcaneus and navicular bones of Indriidae and Lepilemur can not be satisfactorily explained as an allometric extension of the condition seen in the smaller Galagidae and Tarsiidae. While it is clearly advantageous to all leapers to maximize the length of the hindlimb, Malagasy leapers rely on elongation of the long bones of the hindlimb, while the non-Malagasy leapers have added elongation of the tarsus to that already documented in the femur and tibia. As McArdle (1981) argues, body size may play a role in limiting the availability of tarsal elongation to small prosimians because of the large bending forces engendered in this adaptation. In any event, there is no mistaking the morphological and mechanical differences in the tarsus of the two groups of leaping prosimians.

Finally, the analysis of limb proportions and skeletal allometry among prosimian primates provides further information concerning the specific details of limb and limb segment lengths among leapers. Napier and Walker (1967) suggested that the intermembral index and, secondarily, the brachial index were the best discriminators of leaping and quadrupedal prosimians. My results clearly indicate, as does a close examination of

Walker's (1967) own data, that a great deal of overlap in intermembral index exists between quadrupeds and leapers. Neither does the brachial index clearly distinguish between leapers and quadrupeds; both groups cluster around 100, indicating radii and humeri of approximately equal length. Rather than demonstrating the presence of a short forelimb, and contrary to the conclusions of Napier and Walker (1967), my results indicate that leaping prosimians possess the relatively longest forelimbs in the suborder. This result accords well with the "vertical support model" of Cartmill (1974b) and Jungers (1976, 1978), which stresses the importance of long forelimbs to small, clawless animals engaging in vertical clinging or climbing. The ratios of relative hindlimb length clearly indicate that, while all leaping prosimians maximize the length of the hindlimb, each accomplishes this goal in a somewhat different manner. Tarsiidae consistently have the longest hindlimb elements among the leapers, followed by Indriidae, and then by Galagidae. The unique mode of hindlimb elongation in different families is further established by a consideration of the scaling of hindlimb length in the Indriidae and Galagidae. While both galagid and indriid forelimbs scale positively, the former show negative allometry in the hindlimb, while the latter scale isometrically in hindlimb length.

8.4. Functional Anatomy and Biomechanics

An important goal of my research was to discern the functional significance of morphological traits common to vertical clingers and leapers. The concept of the mechanical advantage of a bone-muscle system (Smith and Savage 1956) proved to be of great value in the biomechanical analyses. In this section I discuss three examples of changes in the mechanical advantage of the hindlimb of prosimian leapers: proximal placement of the femoral trochanters, increase in the dorso-ventral dimension of the femoral condyles, and elongation of the tarsus. Each of these examples demonstrates a different functional effect of the changed relations of the bone-muscle system involved.

The femoral trochanters are attachment sites for important muscles arising from the pelvis. The greater trochanter provides the insertion for *Mm. gluteus medius* and *minimus*, as well as the origin of *M. vastus lateralis*. The lesser trochanter bears the insertion of *M. iliopsoas*, while *Mm. gluteus superficialis pars anterior* and *tensor fasciae femoris* insert on the third trochanter. Each of the femoral trochanters is situated closer to the hip joint among leapers than among quadrupeds; this is clearly demonstrated in ratios F2, F3, F6, and F7 (Table 9 and Appendix C). The effect of insertion of these muscles close to the hip joint is to decrease the moment arm (lever arm)

of each muscle, and thus to decrease the mechanical advantage of the bone-muscle system. As demonstrated by Gregory (1912) and Smith and Savage (1956), a reduced mechanical advantage allows an increase in speed at the expense of power in muscular contractions. This is clearly advantageous to saltators (or cursors) who need to attain a relatively great acceleration in their hindlimbs during both the power stroke and the recovery stroke of locomotion. An additional benefit of the proximally restricted positions of the lesser and the third trochanters among leapers is that a greater proportion of the hindlimb muscle mass is retained close to the hip joint. The effect of this is to reduce the moment of inertia of the hindlimb. In rotational motion, moment of inertia is the analog of mass in linear motion. As such, it is a measure of the resistance of a body at rest to rotational motion. A decreased moment of inertia is clearly advantageous to animals utilizing rapid rotational motion of their limbs. Finally, the long ilium among leapers increases the average length of the muscle fibers of *M. gluteus medius*, which arise from its gluteal surface. Since all fibers of skeletal muscle contract approximately one third of their resting length, other factors being equal, long fibers provide greater velocity of contraction than do short muscular fibers.

A consideration of the dorso-ventral dimension of the femoral condyles (Ratio F4, Table 9 and Appendix C) demonstrates that leapers and, to a lesser extent, hindlimb-dominant lemurs, have increased the moment arm and mechanical advantage of a bone-muscle system for the resultant increase in power at the expense of speed. Leapers are unique in the possession of a patellar articular surface that is raised anterior to the femoral shaft, further increasing the dorso-ventral dimension of the condyles. As first pointed out by Walker (1967), the femoral condyles act as a pulley around which the M. quadriceps femoris acts to extend the lower leg. Increasing the height of this pulley increases the mechanical advantage of this bone-muscle system. The hypertrophied condition of M. vastus lateralis and the resultant increase in its cross-sectional area allows extremely powerful femoral extension in leaping. Its long and parallel muscular fibers ensure that speed is not totally sacrificed at the expense of power in the dynamic properties of M. vastus lateralis.

As described in detail in Chapter 5, galagids and tarsiids share extreme elongation of the calcaneus and navicular bones in the tarsus. Since the elongation occurs anterior to the tibiotalar joint, it has no effect on the moment arm of the plantarflexor musculature (M. triceps surae). Tarsal elongation does, however, affect the

mechanical advantage of plantarflexion since it greatly increases the load arm of this system. The net effect is a substantial decrease in mechanical advantage, resulting in a joint that is specialized for rapid plantarflexion. While the reduced mechanical advantage requires large muscular forces, it allows relatively great distal excursion at great speed; the hypertrophied condition and multipinnate arrangement of muscle fibers in *M. gastrocnemius* supply the necessary forces. An additional benefit of tarsal elongation in leaping prosimians is that it increases the overall length of the hindlimb.

8.5. Speculations on Phylogeny and Classification

As mentioned in the introduction to this chapter, the research discussed here is concerned mainly with the morphological component of the vertical clinging and leaping hypothesis. Consequently, I shall only briefly discuss the bearing of my work on the behavioral and evolutionary questions raised by a consideration of these fascinating animals. While some authors (e.g., Stern & Oxnard 1973) have questioned the validity of the behavioral category of vertical clinging and leaping, it is accepted here if for no other reason than its value as a heuristic device. Final resolution of questions concerning the positional behavior of Eocene adapid and omomyid primates must await further study of the fragmentary postcranial

remains of these extinct forms. If, however, my analysis of the morphological aspect of the VCL hypothesis is not entirely without merit, it should throw some light on both the behavioral and the evolutionary sides of this issue.

The presence among prosimian primates of two distinct morphological adaptations to an arboreal, saltatory way of life implies the existence of behavioral or ecological differences between galagos and tarsiers and the specialized leapers of Madagascar (indriids and Lepilemur). The literature review of the behavior and ecology of prosimians presented here illustrates the diversity among these animals and the need for additional data collection and analysis. Future behavioral studies of these animals should be directed towards gathering detailed information on the use of the limbs in both clinging and leaping, microhabitat preferences, feeding and resting behaviors, and other aspects of ecology and behavior. Comparison of more complete data on the type, frequency, and setting of positional behaviors in these two groups may lead to further insights concerning the significance of the morphological diversity noted here.

The results presented in this thesis clearly do not support the evolutionary aspect of the VCL hypothesis as stated by Napier and Walker (1967) and Walker (1967, 1974). The existence of more than one morphological adaptation to leaping among extant prosimians makes necessary a

reconsideration of the postcranial evidence for leaping among Eocene primates. The speculation that both the galagid-tarsiid and the hindlimb-dominant lemuriform types of morphology coexisted, respectively, among Eocene Omomyidae and Adapidae is, however, plausible (Stern & Oxnard 1973; Szalay & Delson 1979). Even if we accept this possibility, the difficulty of determining the degree to which individuals of these extinct taxa engaged in vertical clinging and leaping can be seen by a consideration of behavioral variability among the extant species of the genus Galago.

While each species of Galago possesses the elongated tarsal region which is so clearly a saltatorial adaptation, the extent to which individuals of the various species leap is quite variable. To be more specific, the recovery of fossil postcranial elements resembling those of G. crassicaudatus would lead any investigator to note the specialized nature of the tarsus, and to posit the possession of specialized saltatory habits. Yet as we have seen, extant individuals of G. crassicaudatus rarely leap, and in some ways they exhibit the locomotor behavior of lorisisds more than that of the more saltatory galagids (Bearder & Doyle 1974; Crompton 1980a, 1980b). Thus, in spite of the extremely distinctive nature of the galagid-tarsiid morphological adaptation to leaping, application of

this information to the fossil record remains problematic.

In addition to the complications created by the existence of behavioral variability within a morphological type, a further difficulty involved in reconstructing the behavior of extinct taxa lies in the fact that morphological change lags behind behavioral change. If the possession of certain morphological traits predisposes an animal toward a change in behavior, it is clear that during the early stages of that behavioral change, the attendant morphology will be, to some extent, decoupled from the behavior. As the new behavior becomes more important to the individuals, natural selection would lead to morphological change. During the early stages of this process, morphological change would clearly lag behind behavioral change, and thus complicate our ability to reconstruct behavior from morphology.

Unlike galagos and tarsiers, the indriids and Lepilemur lack a single, specialized morphological trait that might unequivocally indicate saltatory habits. In fact, much of the morphology of the specialized lemuriform leapers appears to be only a quantitative extension of the traits seen in the active quadrupedal lemurs. Determining the importance of leaping in fossil forms (e.g., Adapidae) that resemble modern Lemuriformes is consequently very difficult, and characterizing these taxa as 'hindlimb-dominant' is perhaps as much as we can safely say (Godfrey ms.).

The traditional inclusion of the Cheirogaleidae with all other Malagasy prosimians in Lemuriformes (Gregory 1915; Simpson 1945) has recently been questioned by several investigators (Charles-Dominique and Martin 1970; Szalay and Katz 1973; Tattersall and Schwartz 1974, 1975; Groves 1974). Tattersall (1982) has argued that the geographic isolation of the Malagasy fauna throughout much of the Tertiary has biased interpretations of the systematic relations of these taxa. Owing to the low probability of dispersal of primates across the Mozambique Channel, investigators have tended to view the modern Malagasy primate fauna (including subfossils) as a monophyletic adaptive radiation resulting from a single colonization event in the Paleocene or Eocene. A cladistic analysis of craniodental morphology led Tattersall and Schwartz (1974, 1975) to reevaluate the phylogenetic and systematic relationships of the strepsirhines, and especially, the position of Cheirogaleidae.

The existence of morphological similarities between Cheirogaleidae and Lorisiformes has been acknowledged for decades (Hill 1953). Charles-Dominique and Martin (1970) rekindled interest in the systematic and evolutionary implications of behavioral similarities between Microcebus murinus and Galago demidovii with their argument for the derivation of modern lemuriforms and lorisiforms from

ancestral stock resembling cheirogaleids and galagids, respectively. Szalay and Katz (1973) and Cartmill (1975b), in investigations of basicranial morphology among modern strepsirhines, argued for the shared, derived condition of aspects of bullar construction and carotid circulation among Cheirogaleidae and Lorisiformes. Building on this work, Tattersall and Schwartz (1974, 1975) and Groves (1974) removed Cheirogaleidae from Lemuriformes and allocated them to the superfamily Lorisioidea (Lorisiformes). An interesting historical implication of this classification is the probability of as many as three separate colonizations of Madagascar from mainland Africa involving the ancestors of the modern cheirogaleids, daubentoniids, and of the lemurid-lepilemurid-indriid group (Tattersall 1982; Groves 1974).

My analysis of hindlimb morphology provides little or no support for inclusion of Cheirogaleidae within Lorisiformes. In nearly all aspects of pelvic and femoral morphology, Cheirogaleidae are linked with all other Malagasy prosimians and are clearly distinct from galagos and lorises. It is intriguing, however, to consider the incipient elongation of the tarsus seen in Microcebus and its similarity to the condition in Galagidae. Whether tarsal elongation is a shared, derived character (synapomorphy), a primitive retention (symplesiomorphy), or simply a convergence is unclear; Charles-Dominique and

Martin (1970) conclude that many of the traits shared by galagids and cheirogaleids are, in fact, primitive among strepsirhines. On the basis of a purely phenetic comparison of the hindlimb, Cheirogaleidae would appear to be best left in Lemuriformes.

Some additional questions concerning the use and even the validity of classifications of positional behavior have been raised by some authors, and can be addressed at this point. In their consideration of the vertical clingers and leapers, Stern and Oxnard (1973) were struck by the degree of behavioral variability both within individual taxa and between different taxa whose members have been judged vertical clingers and leapers. Generalizing this phenomenon to other categories of positional behavior led these authors to discard the very notion of classifying primates on the basis of positional behavior. While it is certainly true that individuals of any VCL taxon do not exclusively rely on this mode of positional behavior, and that differences can be found in the positional behavior of galagos, tarsiers, and indriids, it does not necessarily follow that the category of vertical clinging and leaping is invalid. The classification of animals on the basis of their dominant pattern of positional behavior is of great value in morphological and functional studies like this one, inter- and intra-taxonal variation notwithstanding. If

the validity of classifying primate positional behavior is to be accepted, these classifications must be based on the observable behavior of extant animals. Napier's (1963) argument for 'pseudobehavioral' classifications based on anatomy rather than behavior must be rejected. It follows from this reasoning that morphological diversity among the animals classified as vertical clingers and leapers can not be used to argue against the validity of this behavioral class. There is certainly no a priori reason to expect that, given the vagaries of evolutionary history, all extant saltatory prosimians would have arrived at identical biomechanical solutions to the demands of an arboreal, saltatory way of life. Thus, while questioning the VCL hypothesis as developed in the works of Napier and Walker (1967) and Walker (1967, 1974), my work confirms the continuing relevance of this category of positional behavior to studies of the functional and evolutionary biology of the primates.

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Appendix A. Pelvic Ratios.

Ratio P1. Ischium Length 1 (Ischium L./Skeletal trunk L.).

<u>Family</u>	<u>LOR.</u>	<u>GAL.</u>	<u>TAR.</u>	<u>IND.</u>	<u>LEP.</u>	<u>LEM.</u>	<u>CHE.</u>	<u>TUP.</u>
mean	.077	.089	.102	.094	.099	.091	.099	.117
st.dev.	.007	.006	.005	.006	.005	.007	.006	.004
s.e.m.	.001	.001	.002	.001	.001	.001	.001	.001
N	51	64	8	22	36	39	25	20

<u>Genus</u>	<u>Lorisiidae</u>				<u>Indriidae</u>		
	<u>Arc.</u>	<u>Lor.</u>	<u>Nyc.</u>	<u>Per.</u>	<u>Avø.</u>	<u>Ind.</u>	<u>Pro.</u>
mean	.066	.068	.080	.081	.096	.096	.092
st.dev.	.004	.004	.004	.005	.006	.004	.006
s.e.m.	.002	.001	.001	.001	.002	.002	.002
N	4	9	20	18	9	3	10

<u>Genus</u>	<u>Lepilemuridae</u>		<u>Lemuridae</u>		<u>Cheirogaleidae</u>	
	<u>Lep.</u>	<u>Hap.</u>	<u>Lem.</u>	<u>Var.</u>	<u>Che.</u>	<u>Mic.</u>
mean	.100	.097	.094	.084	.097	.100
st.dev.	.005	.004	.005	.004	.005	.006
s.e.m.	.001	.001	.001	.001	.002	.001
N	20	16	27	12	6	19

<u>Species</u>	<u>Galago</u>				
	<u>G.all.</u>	<u>G.cra.</u>	<u>G.dem.</u>	<u>G.ele.</u>	<u>G.sen.</u>
mean	.090	.095	.083	.084	.087
st.dev.	.002	.003	.006	—	.005
s.e.m.	.001	.001	.002	—	.001
N	3	24	8	1	28

Ratio P2. Ischium Length 2 (Ischium L./Pelvic L.).

<u>Family</u>	<u>LOR.</u>	<u>GAL.</u>	<u>TAR.</u>	<u>IND.</u>	<u>LEP.</u>	<u>LEM.</u>	<u>CHE.</u>	<u>TUP.</u>
mean	.257	.276	.256	.281	.300	.294	.328	.402
st.dev.	.020	.015	.012	.013	.013	.013	.017	.011
s.e.m.	.003	.002	.004	.003	.002	.002	.003	.002
N	51	64	8	22	36	39	25	20

<u>Genus</u>	<u>Lorisidae</u>				<u>Indriidae</u>		
	<u>Arc.</u>	<u>Lor.</u>	<u>Nyc.</u>	<u>Per.</u>	<u>Ava.</u>	<u>Ind.</u>	<u>Pro.</u>
mean	.233	.241	.268	.257	.277	.287	.284
st.dev.	.015	.014	.018	.015	.013	.007	.014
s.e.m.	.008	.005	.004	.004	.004	.004	.005
N	4	9	20	18	9	3	10

<u>Genus</u>	<u>Lepilemuridae</u>		<u>Lemuridae</u>		<u>Cheirogaleidae</u>	
	<u>Lep.</u>	<u>Hap.</u>	<u>Lem.</u>	<u>Var.</u>	<u>Che.</u>	<u>Mic.</u>
mean	.299	.301	.296	.290	.340	.324
st.dev.	.012	.015	.013	.011	.011	.017
s.e.m.	.003	.004	.002	.003	.004	.004
N	20	16	27	12	6	19

<u>Species</u>	<u>Galago</u>				
	<u>G.all.</u>	<u>G.cra.</u>	<u>G.dem.</u>	<u>G.ele.</u>	<u>G.sen.</u>
mean	.272	.287	.278	.293	.265
st.dev.	.001	.009	.010	—	.013
s.e.m.	.000	.002	.004	—	.002
N	3	24	8	1	28

Ratio P3. Ischium Length 3 (Ischium L./Ilium L.).

<u>Family</u>	<u>LOR.</u>	<u>GAL.</u>	<u>TAR.</u>	<u>IND.</u>	<u>LEP.</u>	<u>LEM.</u>	<u>CHE.</u>	<u>TUP.</u>
mean	.349	.373	.330	.384	.414	.415	.469	.648
st.dev.	.034	.026	.018	.024	.021	.019	.033	.023
s.e.m.	.005	.003	.006	.005	.003	.003	.007	.005
N	51	64	8	22	36	39	25	20

<u>Genus</u>	<u>Lorisiidae</u>				<u>Indriidae</u>		
	<u>Arc.</u>	<u>Lor.</u>	<u>Nyc.</u>	<u>Per.</u>	<u>Ava.</u>	<u>Ind.</u>	<u>Pro.</u>
mean	.310	.309	.371	.353	.367	.398	.394
st.dev.	.021	.025	.023	.025	.019	.012	.023
s.e.m.	.010	.008	.005	.006	.006	.007	.007
N	4	9	20	18	9	3	10

<u>Genus</u>	<u>Lepilemuridae</u>		<u>Lemuridae</u>		<u>Cheirogaleidae</u>	
	<u>Lep.</u>	<u>Hap.</u>	<u>Lem.</u>	<u>Var.</u>	<u>Che.</u>	<u>Mic.</u>
mean	.414	.414	.418	.407	.505	.457
st.dev.	.017	.025	.019	.018	.009	.025
s.e.m.	.004	.006	.004	.005	.005	.006
N	20	16	27	12	6	19

<u>Species</u>	<u>Golego</u>				
	<u>G.all.</u>	<u>G.cra.</u>	<u>G.dem.</u>	<u>G.ele.</u>	<u>G.sen.</u>
mean	.366	.397	.369	.404	.352
st.dev.	.009	.017	.014	—	.017
s.e.m.	.005	.003	.005	—	.003
N	3	24	8	1	28

Ratio P4. Ischium Length 4 (Ischium L./Femur L.).

<u>Family</u>	<u>LOR.</u>	<u>GAL.</u>	<u>TAR.</u>	<u>IND.</u>	<u>LEP.</u>	<u>LEM.</u>	<u>CHE.</u>	<u>TUP.</u>
mean	.185	.161	.138	.133	.190	.190	.262	.335
st.dev.	.029	.021	.006	.007	.009	.009	.016	.016
s.e.m.	.004	.003	.002	.002	.001	.001	.003	.004
N	51	64	8	22	36	39	25	20

<u>Genus</u>	<u>Lorisiidae</u>				<u>Indriidae</u>		
	<u>Arc.</u>	<u>Lor.</u>	<u>Nyc.</u>	<u>Per.</u>	<u>Ava.</u>	<u>Ind.</u>	<u>Pro.</u>
mean	.161	.134	.196	.203	.134	.129	.132
st.dev.	.011	.013	.013	.014	.007	.005	.008
s.e.m.	.005	.004	.003	.003	.002	.003	.002
N	4	9	19	20	9	3	10

<u>Genus</u>	<u>Lepilemuridae</u>		<u>Lemuridae</u>		<u>Cheirogaleidae</u>	
	<u>Lep.</u>	<u>Hap.</u>	<u>Lem.</u>	<u>Var.</u>	<u>Che.</u>	<u>Mic.</u>
mean	.192	.187	.189	.191	.272	.259
st.dev.	.008	.009	.009	.007	.011	.016
s.e.m.	.002	.002	.002	.002	.005	.004
N	20	16	27	12	6	19

<u>Species</u>	<u>Golago</u>				
	<u>G.all.</u>	<u>G.cra.</u>	<u>G.dem.</u>	<u>G.ele.</u>	<u>G.sen.</u>
mean	.151	.183	.168	.155	.141
st.dev.	.002	.007	.007	—	.007
s.e.m.	.001	.001	.002	—	.001
N	3	24	8	1	28

Ratio P5. Pubic Length 1 (Pubis L. / Skeletal trunk L.).

<u>Family</u>	<u>LOR.</u>	<u>GAL.</u>	<u>TAR.</u>	<u>IND.</u>	<u>LEP.</u>	<u>LEM.</u>	<u>CHE.</u>	<u>TUP.</u>
mean	.133	.108	.151	.098	.093	.091	.107	.088
st.dev.	.009	.009	.011	.008	.009	.007	.013	.006
s.e.m.	.001	.001	.004	.002	.002	.001	.003	.001
N	51	64	8	22	36	39	25	20

	<u>Lorisiidae</u>				<u>Indriidae</u>		
<u>Genus</u>	<u>Arc.</u>	<u>Lor.</u>	<u>Nyc.</u>	<u>Per.</u>	<u>Ava.</u>	<u>Ind.</u>	<u>Pro.</u>
mean	.140	.124	.131	.138	.102	.096	.095
st.dev.	.007	.006	.006	.010	.006	.006	.008
s.e.m.	.003	.002	.001	.002	.002	.003	.003
N	4	9	20	18	9	3	10

	<u>Lepilemuridae</u>		<u>Lemuridae</u>		<u>Cheirogaleidae</u>	
<u>Genus</u>	<u>Lep.</u>	<u>Hap.</u>	<u>Lem.</u>	<u>Var.</u>	<u>Che.</u>	<u>Mic.</u>
mean	.086	.102	.095	.082	.092	.111
st.dev.	.003	.005	.004	.003	.008	.011
s.e.m.	.001	.001	.001	.001	.003	.002
N	20	16	27	12	6	19

	<u>Golago</u>				
<u>Species</u>	<u>G.all.</u>	<u>G.cro.</u>	<u>G.dem.</u>	<u>G.ele.</u>	<u>G.sen.</u>
mean	.109	.113	.102	.100	.105
st.dev.	.011	.008	.005	—	.008
s.e.m.	.006	.002	.002	—	.001
N	3	24	8	1	28

Ratio P6. Pubic Length 2 (Pubis L./Pelvic L.).

<u>Family</u>	<u>LOR.</u>	<u>GAL.</u>	<u>TAR.</u>	<u>IND.</u>	<u>LEP.</u>	<u>LEM.</u>	<u>CHE.</u>	<u>TUP.</u>
mean	.443	.332	.380	.292	.294	.283	.351	.304
st.dev.	.030	.024	.030	.020	.033	.013	.029	.021
s.e.m.	.004	.003	.011	.004	.006	.002	.006	.005
N	51	64	8	22	36	39	25	20

<u>Genus</u>	<u>Lorisiidae</u>				<u>Indriidae</u>		
	<u>Arc.</u>	<u>Lor.</u>	<u>Nyc.</u>	<u>Per.</u>	<u>Ava.</u>	<u>Ind.</u>	<u>Pro.</u>
mean	.496	.444	.439	.435	.293	.283	.294
st.dev.	.024	.024	.025	.028	.016	.011	.025
s.e.m.	.012	.008	.006	.007	.005	.007	.008
N	4	9	20	18	9	3	10

<u>Genus</u>	<u>Lepilemuridae</u>		<u>Lemuridae</u>		<u>Cheirogaleidae</u>	
	<u>Lep.</u>	<u>Hap.</u>	<u>Lem.</u>	<u>Var.</u>	<u>Che.</u>	<u>Mic.</u>
mean	.255	.317	.298	.284	.324	.360
st.dev.	.013	.013	.012	.011	.021	.025
s.e.m.	.003	.003	.002	.003	.009	.006
N	20	16	27	12	6	19

<u>Species</u>	<u>Galago</u>				
	<u>G.all.</u>	<u>G.cro.</u>	<u>G.dem.</u>	<u>G.ele.</u>	<u>G.sen.</u>
mean	.330	.343	.341	.351	.320
st.dev.	.029	.023	.016	—	.021
s.e.m.	.017	.005	.006	—	.004
N	3	24	8	1	28

Ratio P7. Pubic Length 3 (Pubic L./Ilium L.).

<u>Family</u>	<u>LOR.</u>	<u>GAL.</u>	<u>TAR.</u>	<u>IND.</u>	<u>LEP.</u>	<u>LEM.</u>	<u>CHE.</u>	<u>TUP.</u>
mean	.602	.449	.490	.399	.390	.414	.502	.489
st.dev.	.043	.037	.039	.027	.045	.020	.036	.031
s.e.m.	.006	.005	.014	.006	.007	.003	.007	.007
N	51	64	8	22	36	39	25	20

<u>Genus</u>	<u>Lorisiidae</u>				<u>Indriidae</u>		
	<u>Arc.</u>	<u>Lor.</u>	<u>Nyc.</u>	<u>Per.</u>	<u>Ava.</u>	<u>Ind.</u>	<u>Pro.</u>
mean	.659	.568	.608	.599	.389	.396	.408
st.dev.	.030	.039	.034	.043	.021	.017	.033
s.e.m.	.015	.013	.008	.010	.007	.010	.010
N	4	9	20	18	9	3	10

<u>Genus</u>	<u>Lepilemuridae</u>		<u>Lemuridae</u>		<u>Cheirogaleidae</u>	
	<u>Lep.</u>	<u>Hop.</u>	<u>Lem.</u>	<u>Var.</u>	<u>Che.</u>	<u>Mic.</u>
mean	.354	.435	.421	.399	.482	.509
st.dev.	.018	.021	.019	.012	.034	.035
s.e.m.	.004	.005	.004	.004	.014	.008
N	20	16	27	12	6	19

<u>Species</u>	<u>Galago</u>				
	<u>G.oll.</u>	<u>G.cro.</u>	<u>G.dem.</u>	<u>G.ele.</u>	<u>G.sen.</u>
mean	.443	.474	.453	.483	.425
st.dev.	.029	.036	.017	—	.027
s.e.m.	.017	.007	.006	—	.005
N	3	24	8	1	28

Ratio P8. Pubic Mechanical Advantage (Pubis L./Femur L.).

<u>Family</u>	<u>LOR.</u>	<u>GAL.</u>	<u>TAR.</u>	<u>IND.</u>	<u>LEP.</u>	<u>LEM.</u>	<u>CHE.</u>	<u>TUP.</u>
mean	.317	.194	.205	.138	.179	.190	.281	.253
st.dev.	.041	.026	.018	.010	.019	.011	.027	.023
s.e.m.	.006	.003	.006	.002	.003	.002	.005	.005
N	51	64	8	22	36	39	25	20

<u>Genus</u>	<u>Lorisiidae</u>				<u>Indriidae</u>		
	<u>Arc.</u>	<u>Lor.</u>	<u>Nyc.</u>	<u>Per.</u>	<u>Ava.</u>	<u>Ind.</u>	<u>Pro.</u>
mean	.343	.246	.321	.344	.142	.129	.137
st.dev.	.030	.018	.021	.022	.010	.010	.008
s.e.m.	.015	.006	.005	.005	.003	.006	.003
N	4	9	20	18	9	3	10

<u>Genus</u>	<u>Lepilemuridae</u>		<u>Lemuridae</u>		<u>Cheirogaleidae</u>	
	<u>Lep.</u>	<u>Hap.</u>	<u>Lem.</u>	<u>Var.</u>	<u>Che.</u>	<u>Mic.</u>
mean	.165	.197	.191	.187	.260	.288
st.dev.	.009	.010	.012	.009	.022	.025
s.e.m.	.002	.002	.002	.003	.009	.006
N	20	16	27	12	6	19

<u>Species</u>	<u>Golego</u>				
	<u>G.all.</u>	<u>G.cra.</u>	<u>G.dem.</u>	<u>G.ele.</u>	<u>G.sen.</u>
mean	.183	.219	.207	.186	.170
st.dev.	.014	.015	.010	—	.011
s.e.m.	.008	.003	.003	—	.002
N	3	24	8	1	28

Ratio P9. Ilium Length I (Ilium L./Skeletal trunk L.).

<u>Family</u>	<u>LOR.</u>	<u>GAL.</u>	<u>TAR.</u>	<u>IND.</u>	<u>LEP.</u>	<u>LEM.</u>	<u>CHE.</u>	<u>TUP.</u>
mean	.221	.240	.309	.246	.239	.219	.212	.180
st.dev.	.012	.013	.009	.018	.011	.012	.015	.005
s.e.m.	.002	.002	.003	.004	.002	.002	.003	.001
N	51	64	8	22	36	39	25	20

<u>Genus</u>	<u>Lorisiidae</u>				<u>Indriidae</u>		
	<u>Arc.</u>	<u>Lor.</u>	<u>Nyc.</u>	<u>Per.</u>	<u>Ava.</u>	<u>Ind.</u>	<u>Pro.</u>
mean	.213	.219	.216	.230	.262	.242	.233
st.dev.	.004	.012	.009	.012	.011	.004	.015
s.e.m.	.002	.004	.002	.003	.004	.002	.005
N	4	9	20	18	9	3	10

<u>Genus</u>	<u>Lepilemuridae</u>		<u>Lemuridae</u>		<u>Cheirogaleidae</u>	
	<u>Lep.</u>	<u>Hop.</u>	<u>Lem.</u>	<u>Var.</u>	<u>Che.</u>	<u>Mic.</u>
mean	.243	.235	.225	.206	.192	.218
st.dev.	.009	.012	.008	.006	.007	.010
s.e.m.	.002	.003	.002	.002	.003	.002
N	20	16	27	12	6	19

<u>Species</u>	<u>Galago</u>				
	<u>G.all.</u>	<u>G.cra.</u>	<u>G.dem.</u>	<u>G.ele.</u>	<u>G.sen.</u>
mean	.246	.238	.224	.207	.247
st.dev.	.009	.010	.011	—	.009
s.e.m.	.005	.002	.004	—	.002
N	3	24	8	1	28

Ratio P10. Ilium Length 2 (Ilium L./Pelvic L.).

<u>Family</u>	<u>LOR.</u>	<u>GAL.</u>	<u>TAR.</u>	<u>IND.</u>	<u>LEP.</u>	<u>LEM.</u>	<u>CHE.</u>	<u>TUP.</u>
mean	.737	.740	.775	.733	.724	.710	.700	.621
st.dev.	.026	.019	.013	.021	.017	.010	.021	.010
s.e.m.	.004	.002	.004	.005	.003	.002	.004	.002
N	51	64	8	22	36	39	25	20

<u>Genus</u>	<u>Lorisiidae</u>				<u>Indriidae</u>		
	<u>Arc.</u>	<u>Lor.</u>	<u>Nyc.</u>	<u>Per.</u>	<u>Ava.</u>	<u>Ind.</u>	<u>Pro.</u>
mean	.752	.782	.723	.727	.754	.713	.720
st.dev.	.009	.025	.011	.011	.013	.005	.012
s.e.m.	.004	.008	.002	.003	.004	.003	.004
N	4	9	20	18	9	3	10

<u>Genus</u>	<u>Lepilemuridae</u>		<u>Lemuridae</u>		<u>Cheirogaleidae</u>	
	<u>Lep.</u>	<u>Hop.</u>	<u>Lem.</u>	<u>Var.</u>	<u>Che.</u>	<u>Mic.</u>
mean	.721	.728	.709	.712	.674	.708
st.dev.	.020	.011	.010	.010	.020	.014
s.e.m.	.004	.003	.002	.003	.008	.003
N	20	16	27	12	6	19

<u>Species</u>	<u>Galago</u>				
	<u>G.all.</u>	<u>G.cro.</u>	<u>G.dem.</u>	<u>G.ele.</u>	<u>G.sen.</u>
mean	.744	.723	.753	.726	.752
st.dev.	.017	.013	.009	—	.012
s.e.m.	.010	.003	.003	—	.002
N	3	24	8	1	28

Ratio P11. Pubic Symphysis Length 1 (Pubic Symphysis L./Skeletal trunk L.)

<u>Family</u>	<u>LOR.</u>	<u>GAL.</u>	<u>TAR.</u>	<u>IND.</u>	<u>LEP.</u>	<u>LEM.</u>	<u>CHE.</u>	<u>TUP.</u>
mean	.029	.058	.067	.076	.051	.057	.036	.081
st.dev.	.007	.008	.006	.009	.005	.005	.006	.006
s.e.m.	.001	.001	.002	.002	.001	.001	.001	.001
N	51	64	8	22	36	39	25	20

<u>Genus</u>	<u>Lorisidae</u>				<u>Indriidae</u>		
	<u>Arc.</u>	<u>Lor.</u>	<u>Nyc.</u>	<u>Per.</u>	<u>Ava.</u>	<u>Ind.</u>	<u>Pro.</u>
mean	.024	.032	.033	.025	.076	.090	.072
st.dev.	.005	.002	.008	.004	.004	.007	.009
s.e.m.	.002	.001	.002	.001	.001	.004	.003
N	4	9	20	18	9	3	10

<u>Genus</u>	<u>Lepilemuridae</u>		<u>Lemuridae</u>		<u>Cheirogaleidae</u>	
	<u>Lep.</u>	<u>Hap.</u>	<u>Lem.</u>	<u>Var.</u>	<u>Che.</u>	<u>Mic.</u>
mean	.051	.050	.058	.055	.042	.034
st.dev.	.003	.007	.005	.004	.003	.006
s.e.m.	.001	.002	.001	.001	.001	.001
N	20	16	27	12	6	19

<u>Species</u>	<u>Galago</u>				
	<u>G.all.</u>	<u>G.cra.</u>	<u>G.dem.</u>	<u>G.ele.</u>	<u>G.sen.</u>
mean	.044	.061	.050	.047	.060
st.dev.	.002	.007	.006	—	.006
s.e.m.	.001	.001	.002	—	.001
N	3	24	8	1	28

Ratio P 12. Pubic Symphysis Length 2 (Pubic Symphysis L./Pelvis L.).

<u>Family</u>	<u>LOR.</u>	<u>GAL.</u>	<u>TAR.</u>	<u>IND.</u>	<u>LEP.</u>	<u>LEM.</u>	<u>CHE.</u>	<u>TUP.</u>
mean	.098	.179	.168	.228	.155	.187	.120	.281
st.dev.	.025	.021	.019	.023	.015	.017	.023	.018
s.e.m.	.003	.003	.007	.005	.003	.003	.005	.004
N	51	64	8	22	36	39	25	20

<u>Genus</u>	<u>Lorisidae</u>				<u>Indriidae</u>		
	<u>Arc.</u>	<u>Lor.</u>	<u>Nyc.</u>	<u>Per.</u>	<u>Ava.</u>	<u>Ind.</u>	<u>Pro.</u>
mean	.083	.114	.110	.080	.220	.265	.224
st.dev.	.017	.007	.028	.012	.011	.021	.022
s.e.m.	.009	.002	.006	.003	.004	.012	.007
N	4	9	20	18	9	3	10

<u>Genus</u>	<u>Lepilemuridae</u>		<u>Lemuridae</u>		<u>Cheirogaleidae</u>	
	<u>Lep.</u>	<u>Hop.</u>	<u>Lem.</u>	<u>Var.</u>	<u>Che.</u>	<u>Mic.</u>
mean	.153	.157	.184	.192	.148	.111
st.dev.	.010	.020	.016	.017	.006	.019
s.e.m.	.002	.005	.003	.005	.002	.004
N	20	16	27	12	6	19

<u>Species</u>	<u>Galego</u>				
	<u>G.all.</u>	<u>G.cro.</u>	<u>G.dem.</u>	<u>G.ele.</u>	<u>G.sen.</u>
mean	.133	.186	.168	.164	.183
st.dev.	.009	.020	.017	—	.016
s.e.m.	.005	.004	.006	—	.003
N	3	24	8	1	28

Ratio P13. Dorsoventral Length 1 (Dorsoventral Pelvic L./Skeletal trunk L.).

<u>Family</u>	<u>LOR.</u>	<u>GAL.</u>	<u>TAR.</u>	<u>IND.</u>	<u>LEP.</u>	<u>LEM.</u>	<u>CHE.</u>	<u>TUP.</u>
mean	.161	.154	.206	.138	.137	.135	.135	.137
st.dev.	.009	.011	.012	.010	.007	.008	.007	.006
s.e.m.	.001	.001	.004	.002	.001	.001	.001	.001
N	51	64	8	22	36	39	25	20

<u>Genus</u>	<u>Lorisidae</u>				<u>Indriidae</u>		
	<u>Arc.</u>	<u>Lor.</u>	<u>Nuc.</u>	<u>Per.</u>	<u>Ava.</u>	<u>Ind.</u>	<u>Pro.</u>
mean	.158	.154	.162	.164	.141	.138	.135
st.dev.	.008	.006	.008	.011	.011	.004	.010
s.e.m.	.004	.002	.002	.003	.004	.002	.003
N	4	9	20	18	9	3	10

<u>Genus</u>	<u>Lepilemuridae</u>		<u>Lemuridae</u>		<u>Cheirogaleidae</u>	
	<u>Lep.</u>	<u>Hap.</u>	<u>Lem.</u>	<u>Var.</u>	<u>Che.</u>	<u>Mic.</u>
mean	.133	.140	.139	.125	.133	.135
st.dev.	.006	.006	.005	.004	.008	.007
s.e.m.	.001	.001	.001	.001	.003	.002
N	20	16	27	12	6	19

<u>Species</u>	<u>Galago</u>				
	<u>G.all.</u>	<u>G.cro.</u>	<u>G.dem.</u>	<u>G.ele.</u>	<u>G.sen.</u>
mean	.155	.162	.138	.143	.151
st.dev.	.005	.007	.008	—	.007
s.e.m.	.003	.001	.003	—	.001
N	3	24	8	1	28

Ratio P14. Dorsoventral Length 2 (Dorsoventral Pelvic L./Pelvic L.).

<u>Family</u>	<u>LOR.</u>	<u>GAL.</u>	<u>TAR.</u>	<u>IND.</u>	<u>LEP.</u>	<u>LEM.</u>	<u>CHE.</u>	<u>TUP.</u>
mean	.538	.473	.516	.412	.414	.437	.446	.471
st.dev.	.033	.021	.029	.027	.027	.015	.018	.017
s.e.m.	.005	.003	.010	.006	.005	.002	.004	.004
N	51	64	8	22	36	39	25	20

	<u>Lorisiidae</u>				<u>Indriidae</u>		
<u>Genus</u>	<u>Arc.</u>	<u>Lor.</u>	<u>Nyc.</u>	<u>Per.</u>	<u>Ava.</u>	<u>Ind.</u>	<u>Pro.</u>
mean	.560	.552	.545	.519	.407	.408	.418
st.dev.	.021	.033	.026	.035	.026	.007	.032
s.e.m.	.010	.011	.006	.008	.009	.004	.010
N	4	9	20	18	9	3	10

	<u>Lepilemuridae</u>		<u>Lemuridae</u>		<u>Cheirogaleidae</u>	
<u>Genus</u>	<u>Lep.</u>	<u>Hop.</u>	<u>Lem.</u>	<u>Var.</u>	<u>Che.</u>	<u>Mic.</u>
mean	.397	.436	.439	.432	.467	.439
st.dev.	.015	.023	.016	.010	.013	.014
s.e.m.	.003	.006	.003	.003	.005	.003
N	20	16	27	12	6	19

	<u>Galago</u>				
<u>Species</u>	<u>G.all.</u>	<u>G.cro.</u>	<u>G.dem.</u>	<u>G.ele.</u>	<u>G.sen.</u>
mean	.469	.490	.463	.501	.461
st.dev.	.005	.018	.013	—	.017
s.e.m.	.003	.004	.004	—	.003
N	3	24	8	1	28

Ratio P15. Ischiopubic Ramus Length 1 (Ischiopubic L./Skeletal trunk L.).

<u>Family</u>	<u>LOR.</u>	<u>GAL.</u>	<u>TAR.</u>	<u>IND.</u>	<u>LEP.</u>	<u>LEM.</u>	<u>CHE.</u>	<u>TUP.</u>
mean	.148	.118	.150	.087	.103	.100	.107	.091
st.dev.	.010	.009	.011	.007	.011	.008	.007	.005
s.e.m.	.001	.001	.004	.002	.002	.001	.001	.001
N	51	64	8	22	36	39	25	20

<u>Genus</u>	<u>Lorisidae</u>				<u>Indriidae</u>		
	<u>Arc.</u>	<u>Lor.</u>	<u>Nyc.</u>	<u>Per.</u>	<u>Ava.</u>	<u>Ind.</u>	<u>Pro.</u>
mean	.149	.143	.147	.150	.086	.081	.089
st.dev.	.012	.005	.009	.011	.005	.004	.009
s.e.m.	.006	.002	.002	.003	.002	.002	.003
N	4	9	20	18	9	3	10

<u>Genus</u>	<u>Lepilemuridae</u>		<u>Lemuridae</u>		<u>Cheirogaleidae</u>	
	<u>Lep.</u>	<u>Hap.</u>	<u>Lem.</u>	<u>Var.</u>	<u>Che.</u>	<u>Mic.</u>
mean	.096	.111	.102	.095	.109	.107
st.dev.	.009	.007	.007	.006	.009	.007
s.e.m.	.002	.002	.001	.002	.004	.002
N	20	16	27	12	6	19

<u>Species</u>	<u>Galago</u>				
	<u>G.all.</u>	<u>G.cra.</u>	<u>G.dem.</u>	<u>G.ele.</u>	<u>G.sen.</u>
mean	.130	.122	.109	.115	.116
st.dev.	.006	.008	.008	—	.008
s.e.m.	.004	.002	.003	—	.002
N	3	24	8	1	28
N	4	1	18	2	

Ratio P16. Ischiopubic Ramus Length 2 (Ischiopubic Ramus L./Pelvic L.).

<u>Family</u>	<u>LOR.</u>	<u>GAL.</u>	<u>TAR.</u>	<u>IND.</u>	<u>LEP.</u>	<u>LEM.</u>	<u>CHE.</u>	<u>TUP.</u>
mean	.492	.363	.377	.259	.311	.324	.355	.312
st.dev.	.034	.023	.027	.029	.037	.021	.026	.017
s.e.m.	.005	.003	.010	.006	.006	.003	.005	.004
N	51	64	8	22	36	39	25	20

<u>Genus</u>	<u>Lorisiidae</u>				<u>Indriidae</u>		
	<u>Arc.</u>	<u>Lor.</u>	<u>Nyc.</u>	<u>Per.</u>	<u>Ava.</u>	<u>Ind.</u>	<u>Pro.</u>
mean	.527	.513	.492	.475	.248	.238	.276
st.dev.	.036	.022	.029	.034	.014	.008	.035
s.e.m.	.018	.007	.006	.008	.005	.005	.011
N	4	9	20	18	9	3	10

<u>Genus</u>	<u>Lepilemuridae</u>		<u>Lemuridae</u>		<u>Cheirogaleidae</u>	
	<u>Lep.</u>	<u>Hop.</u>	<u>Lem.</u>	<u>Var.</u>	<u>Che.</u>	<u>Mic.</u>
mean	.286	.343	.322	.328	.384	.345
st.dev.	.026	.019	.024	.015	.026	.019
s.e.m.	.006	.005	.005	.004	.011	.004
N	20	16	27	12	6	19

<u>Species</u>	<u>Galago</u>				
	<u>G.all.</u>	<u>G.cro.</u>	<u>G.dem.</u>	<u>G.ele.</u>	<u>G.sen.</u>
mean	.391	.369	.367	.403	.353
st.dev.	.014	.023	.016	—	.019
s.e.m.	.008	.005	.006	—	.004
N	3	24	8	1	28

Ratio P17. Iliac Crest Length 1 (Iliac Crest L./Skeletal trunk L.).

<u>Family</u>	<u>LOR.</u>	<u>GAL.</u>	<u>TAR.</u>	<u>IND.</u>	<u>LEP.</u>	<u>LEM.</u>	<u>CHE.</u>	<u>TUP.</u>
mean	.052	.069	.073	.107	.075	.069	.044	.068
st.dev.	.005	.008	.007	.013	.013	.008	.002	.007
s.e.m.	.001	.001	.002	.003	.002	.001	.001	.002
N	51	64	8	22	36	39	25	20

<u>Genus</u>	<u>Lorisidae</u>				<u>Indriidae</u>		
	<u>Arc.</u>	<u>Lor.</u>	<u>Nyc.</u>	<u>Per.</u>	<u>Ava.</u>	<u>Ind.</u>	<u>Pro.</u>
mean	.049	.052	.055	.049	.105	.107	.108
st.dev.	.006	.003	.004	.005	.012	.005	.016
s.e.m.	.003	.001	.001	.001	.004	.003	.005
N	4	9	20	18	9	3	10

<u>Genus</u>	<u>Lepilemuridae</u>		<u>Lemuridae</u>		<u>Cheirogaleidae</u>	
	<u>Lep.</u>	<u>Hap.</u>	<u>Lem.</u>	<u>Var.</u>	<u>Che.</u>	<u>Mic.</u>
mean	.066	.086	.073	.059	.044	.044
st.dev.	.006	.010	.006	.005	.003	.002
s.e.m.	.001	.003	.001	.001	.001	.001
N	20	16	27	12	6	19

<u>Species</u>	<u>Galago</u>				
	<u>G.all.</u>	<u>G.cra.</u>	<u>G.dem.</u>	<u>G.ele.</u>	<u>G.sen.</u>
mean	.062	.071	.060	.066	.070
st.dev.	.009	.008	.007	—	.008
s.e.m.	.005	.002	.002	—	.001
N	3	24	8	1	28

Ratio P18. Iliac Crest Length 2 (Iliac Crest L./Pelvic L.).

<u>Family</u>	<u>LOR.</u>	<u>GAL.</u>	<u>TAR.</u>	<u>IND.</u>	<u>LEP.</u>	<u>LEM.</u>	<u>CHE.</u>	<u>TUP.</u>
mean	.175	.212	.183	.319	.227	.222	.145	.234
st.dev.	.020	.024	.016	.034	.044	.021	.010	.024
s.e.m.	.003	.003	.006	.007	.007	.003	.002	.005
N	51	64	8	22	36	39	25	20

<u>Genus</u>	<u>Lorisidae</u>				<u>Indriidae</u>		
	<u>Arc.</u>	<u>Lor.</u>	<u>Nyc.</u>	<u>Per.</u>	<u>Ava.</u>	<u>Ind.</u>	<u>Pro.</u>
mean	.172	.188	.186	.156	.303	.315	.335
st.dev.	.020	.011	.015	.015	.033	.021	.034
s.e.m.	.010	.004	.003	.003	.011	.012	.011
N	4	9	20	18	9	3	10

<u>Genus</u>	<u>Lepilemuridae</u>		<u>Lemuridae</u>		<u>Cheirogaleidae</u>	
	<u>Lep.</u>	<u>Hop.</u>	<u>Lem.</u>	<u>Var.</u>	<u>Che.</u>	<u>Mic.</u>
mean	.196	.266	.229	.206	.154	.143
st.dev.	.021	.034	.020	.014	.012	.008
s.e.m.	.005	.009	.004	.004	.005	.002
N	20	16	27	12	6	19

<u>Species</u>	<u>Galago</u>				
	<u>G.all.</u>	<u>G.cro.</u>	<u>G.dem.</u>	<u>G.ele.</u>	<u>G.sen.</u>
mean	.186	.215	.203	.233	.213
st.dev.	.025	.026	.025	—	.020
s.e.m.	.014	.005	.009	—	.004
N	3	24	8	1	28

Ratio P19. Iliac Crest Length 3 (Iliac Crest L./Ilium L.).

<u>Family</u>	<u>LOR.</u>	<u>GAL.</u>	<u>TAR.</u>	<u>IND.</u>	<u>LEP.</u>	<u>LEM.</u>	<u>CHE.</u>	<u>TUP.</u>
mean	.237	.286	.236	.436	.314	.313	.208	.377
st.dev.	.028	.035	.021	.052	.062	.030	.019	.040
s.e.m.	.004	.004	.008	.011	.010	.005	.004	.009
N	51	64	8	22	36	39	25	20

<u>Genus</u>	<u>Lorisiidae</u>				<u>Indriidae</u>		
	<u>Arc.</u>	<u>Lor.</u>	<u>Nyc.</u>	<u>Per.</u>	<u>Ava.</u>	<u>Ind.</u>	<u>Pro.</u>
mean	.229	.240	.257	.215	.402	.441	.465
st.dev.	.026	.019	.022	.020	.043	.027	.049
s.e.m.	.013	.006	.005	.005	.014	.015	.016
N	4	9	20	18	9	3	10

<u>Genus</u>	<u>Lepilemuridae</u>		<u>Lemuridae</u>		<u>Cheirogaleidae</u>	
	<u>Lep.</u>	<u>Hap.</u>	<u>Lem.</u>	<u>Var.</u>	<u>Che.</u>	<u>Mic.</u>
mean	.273	.366	.324	.288	.228	.202
st.dev.	.032	.050	.028	.019	.020	.013
s.e.m.	.007	.013	.005	.005	.008	.003
N	20	16	27	12	6	19

<u>Species</u>	<u>Galago</u>				
	<u>G.all.</u>	<u>G.cra.</u>	<u>G.dem.</u>	<u>G.ele.</u>	<u>G.sen.</u>
mean	.250	.298	.270	.321	.283
st.dev.	.029	.039	.034	—	.027
s.e.m.	.017	.008	.012	—	.005
N	3	24	8	1	28

Ratio 20. Relative Pelvic Length (Pelvic L./Skeletal trunk L.).

<u>Family</u>	<u>LOR.</u>	<u>GAL.</u>	<u>TAR.</u>	<u>IND.</u>	<u>LEP.</u>	<u>LEM.</u>	<u>CHE.</u>	<u>TUP.</u>
mean	.300	.324	.399	.335	.330	.308	.303	.290
st.dev.	.018	.016	.011	.020	.015	.016	.015	.008
s.e.m.	.003	.002	.004	.004	.003	.003	.003	.002
N	51	64	8	22	36	39	25	20

<u>Genus</u>	<u>Lorisiidae</u>				<u>Indriidae</u>		
	<u>Arc.</u>	<u>Lor.</u>	<u>Nyc.</u>	<u>Per.</u>	<u>Ava.</u>	<u>Ind.</u>	<u>Pro.</u>
mean	.283	.280	.298	.316	.348	.339	.323
st.dev.	.004	.009	.012	.015	.013	.008	.022
s.e.m.	.002	.003	.003	.004	.004	.004	.007
N	4	9	20	18	9	3	10

<u>Genus</u>	<u>Lepilemuridae</u>		<u>Lemuridae</u>		<u>Cheirogaleidae</u>	
	<u>Lep.</u>	<u>Hap.</u>	<u>Lem.</u>	<u>Var.</u>	<u>Che.</u>	<u>Mic.</u>
mean	.337	.323	.317	.289	.285	.309
st.dev.	.014	.013	.010	.008	.012	.012
s.e.m.	.003	.003	.002	.002	.005	.003
N	20	16	27	12	6	19

<u>Species</u>	<u>Galago</u>				
	<u>G.all.</u>	<u>G.cra.</u>	<u>G.dem.</u>	<u>G.ele.</u>	<u>G.sen.</u>
mean	.331	.330	.298	.285	.328
st.dev.	.008	.011	.016	—	.010
s.e.m.	.005	.002	.006	—	.002
N	3	24	8	1	28

Appendix B. Tarsal Ratios.

Ratio T1. Calcaneal Index (Posterior calcaneus l./Anterior calcaneus l.)

<u>Family</u>	<u>GAL.</u>	<u>TAR.</u>	<u>IND.</u>	<u>LEP.</u>	<u>LEM.</u>	<u>CHE.</u>	<u>TUP.</u>
mean	.433	.315	1.42	1.13	1.21	.730	1.55
st.dev.	.092	.012	.097	.071	.090	.168	.123
s.e.m.	.012	.016	.021	.018	.020	.031	.031
N	54	5	21	35	39	29	16

<u>Genus</u>	<u>Indriidae</u>			<u>Cheirogaleidae</u>	
	<u>Ava.</u>	<u>Ind.</u>	<u>Pro.</u>	<u>Che.</u>	<u>Mic.</u>
mean	1.41	1.34	1.46	.998	.644
st.dev.	.133	.051	.051	.102	.055
s.e.m.	.047	.029	.016	.039	.012
N	8	3	10	7	22

<u>Genus</u>	<u>Lepilemuridae</u>		<u>Lemuridae</u>	
	<u>Lep.</u>	<u>Hop.</u>	<u>Lem.</u>	<u>Var.</u>
mean	1.13	1.14	1.22	1.46
st.dev.	.065	.074	.089	.075
s.e.m.	.015	.019	.017	.024
N	20	15	29	10

<u>Species</u>	<u>Galago</u>				
	<u>G.all</u>	<u>G.cra.</u>	<u>G.dem.</u>	<u>G.ele.</u>	<u>G.sen.</u>
mean	.412	.534	.308	.545	.378
st.dev.	.009	.027	.012	—	.020
s.e.m.	.006	.006	.004	—	.004
N	2	21	8	1	22

Ratio T2. Mechanical Advantage (Posterior calcaneus 1./Load arm 1.)

<u>Family</u>	<u>GAL.</u>	<u>TAR.</u>	<u>IND.</u>	<u>LEP.</u>	<u>LEM.</u>	<u>CHE.</u>	<u>TUP.</u>
mean	.326	.276	.745	.636	.679	.452	.764
st. dev.	.050	.003	.035	.034	.051	.086	.066
s.e.m.	.007	.001	.008	.008	.012	.016	.017
N	54	4	20	35	39	28	16

<u>Genus</u>	<u>Indriidae</u>			<u>Cheirogaleidae</u>	
	<u>Ava.</u>	<u>Ind.</u>	<u>Pro.</u>	<u>Che.</u>	<u>Mic.</u>
mean	.762	.734	.734	.585	.407
st.dev.	.034	.060	.028	.052	.031
s.e.m.	.013	.034	.009	.020	.007
N	7	3	10	7	21

<u>Genus</u>	<u>Lepilemuridae</u>		<u>Lemuridae</u>	
	<u>Lep.</u>	<u>Hop.</u>	<u>Lem.</u>	<u>Var.</u>
mean	.647	.620	.657	.746
st.dev.	.034	.036	.056	.045
s.e.m.	.008	.009	.010	.014
N	15	20	29	10

<u>Species</u>	<u>Galago</u>				
	<u>G.all.</u>	<u>G.cra.</u>	<u>G.dem.</u>	<u>G.ele.</u>	<u>G.sen.</u>
mean	.305	.378	.248	.389	.302
st.dev.	.006	.019	.010	—	.014
s.e.m.	.004	.004	.004	—	.003
N	2	21	8	1	22

Ratio T3. Relative Calcaneal Length (Calcaneus l./Skeletal trunk l.)

<u>Family</u>	<u>GAL.</u>	<u>TAR.</u>	<u>IND.</u>	<u>LEP.</u>	<u>LEM.</u>	<u>CHE.</u>	<u>TUP.</u>
mean	.234	.331	.110	.112	.092	.120	.084
st. dev.	.043	.018	.009	.006	.006	.019	.008
s.e.m.	.006	.008	.002	.002	.001	.003	.002
N	54	5	21	35	39	29	16

	<u>Indriidae</u>			<u>Cheirogaleidae</u>	
<u>Genus</u>	<u>Ava.</u>	<u>Ind.</u>	<u>Pro.</u>	<u>Che.</u>	<u>Mic.</u>
mean	.117	.111	.105	.091	.129
st.dev.	.012	.003	.004	.007	.008
s.e.m.	.004	.002	.001	.003	.002
N	8	3	10	7	22

	<u>Lepilemuridae</u>		<u>Lemuridae</u>	
<u>Genus</u>	<u>Lep.</u>	<u>Hop.</u>	<u>Lem.</u>	<u>Var.</u>
mean	.120	.100	.097	.086
st.dev.	.005	.008	.006	.004
s.e.m.	.001	.002	.001	.001
N	20	15	29	10

	<u>Galago</u>				
<u>Species</u>	<u>G.all.</u>	<u>G.cra.</u>	<u>G.dem.</u>	<u>G.ele.</u>	<u>G.sen.</u>
mean	.250	.186	.259	.174	.272
st.dev.	.030	.008	.027	—	.012
s.e.m.	.021	.002	.009	—	.003
N	2	21	8	1	22

Ratio T4. Relative Cuboid Length (Cuboid 1./Skeletal trunk 1.)

<u>Family</u>	<u>GAL.</u>	<u>TAR.</u>	<u>IND.</u>	<u>LEP.</u>	<u>LEM.</u>	<u>CHE.</u>	<u>TUP.</u>
mean	.060	.045	.047	.047	.044	.049	.038
st.dev.	.004	.001	.005	.003	.003	.007	.003
s.e.m.	.001	.001	.001	.001	.001	.001	.001
N	54	4	18	35	38	28	16

	<u>Indriidae</u>			<u>Cheirogaleidae</u>	
<u>Genus</u>	<u>Ava.</u>	<u>Ind.</u>	<u>Pro.</u>	<u>Che.</u>	<u>Mic.</u>
mean	.052	.046	.045	.040	.052
st.dev.	.005	.002	.004	.002	.005
s.e.m.	.002	.001	.001	.001	.001
N	5	3	10	7	21

	<u>Lepilemuridae</u>		<u>Lemuridae</u>	
<u>Genus</u>	<u>Lep.</u>	<u>Hap.</u>	<u>Lem.</u>	<u>Var.</u>
mean	.049	.045	.045	.041
st.dev.	.002	.003	.003	.002
s.e.m.	.001	.001	.001	.001
N	20	15	29	9

	<u>Galago</u>				
<u>Species</u>	<u>G.all.</u>	<u>G.cra.</u>	<u>G.dem.</u>	<u>G.ele.</u>	<u>G.sen.</u>
mean	.069	.060	.059	.059	.061
st.dev.	.006	.003	.007	—	.002
s.e.m.	.004	.001	.002	—	.001
N	2	21	8	1	22

Ratio T5. Relative Navicular Length (Navicular 1./Skeletal trunk 1.)

<u>Family</u>	<u>GAL.</u>	<u>TAR.</u>	<u>IND.</u>	<u>LEP.</u>	<u>LEM.</u>	<u>CHE.</u>	<u>TUP.</u>
mean	.177	.261	.039	.059	.042	.078	.018
st.dev.	.040	.011	.005	.004	.003	.020	.002
s.e.m.	.005	.005	.001	.001	.001	.004	.001
N	54	5	21	35	38	29	16

<u>Genus</u>	<u>Indriidae</u>			<u>Cheirogaleidae</u>	
	<u>Ava.</u>	<u>Ind.</u>	<u>Pro.</u>	<u>Che.</u>	<u>Mic.</u>
mean	.044	.033	.036	.046	.089
st.dev.	.003	.002	.003	.004	.007
s.e.m.	.001	.001	.001	.001	.001
N	8	3	10	7	22

<u>Genus</u>	<u>Lepilemuridae</u>		<u>Lemuridae</u>	
	<u>Lep.</u>	<u>Hap.</u>	<u>Lem.</u>	<u>Var.</u>
mean	.063	.049	.045	.033
st.dev.	.004	.004	.003	.002
s.e.m.	.001	.001	.001	.001
N	20	15	29	9

<u>Species</u>	<u>Galago</u>				
	<u>G.all.</u>	<u>G.cra.</u>	<u>G.dem.</u>	<u>G.ele.</u>	<u>G.sen.</u>
mean	.197	.135	.180	.127	.216
st.dev.	.025	.012	.028	—	.011
s.e.m.	.018	.003	.010	—	.002
N	2	21	8	1	22

Appendix C. Femoral Ratios.

Ratio F1. Relative Femoral Length (Femur 1./Skeletal trunk 1.)

<u>Family</u>	<u>LOR.</u>	<u>GAL.</u>	<u>TAR.</u>	<u>IND.</u>	<u>LEP.</u>	<u>LEM.</u>	<u>CHE.</u>	<u>TUP.</u>
mean	.426	.562	.738	.711	.519	.478	.377	.349
st.dev.	.045	.057	.027	.034	.018	.018	.023	.013
s.e.m.	.006	.007	.010	.007	.005	.004	.004	.003
N	54	63	7	24	38	40	27	20

	<u>Lorisidae</u>				<u>Indriidae</u>		
<u>Genus</u>	<u>Arc.</u>	<u>Lor.</u>	<u>Nyc.</u>	<u>Per.</u>	<u>Ava.</u>	<u>Ind.</u>	<u>Pro.</u>
mean	.415	.506	.409	.400	.718	.743	.693
st.dev.	.024	.031	.017	.012	.034	.022	.028
s.e.m.	.014	.009	.004	.003	.011	.011	.008
N	3	11	20	20	9	4	11

	<u>Lepilemuridae</u>		<u>Lemuridae</u>		<u>Cheirogaleidae</u>	
<u>Genus</u>	<u>Lep.</u>	<u>Hop.</u>	<u>Lem.</u>	<u>Var.</u>	<u>Che.</u>	<u>Mic.</u>
mean	.522	.515	.499	.436	.349	.387
st.dev.	.016	.023	.028	.011	.025	.011
s.e.m.	.004	.006	.005	.003	.010	.003
N	21	17	29	11	7	20

	<u>Galago</u>				
<u>Species</u>	<u>G.all.</u>	<u>G.cra.</u>	<u>G.dem.</u>	<u>G.ele.</u>	<u>G.sen.</u>
mean	.596	.517	.492	.539	.618
st.dev.	.014	.019	.025	—	.015
s.e.m.	.005	.008	.008	—	.003
N	3	22	9	1	28

Ratio F2. Hip Flexor Index (Lesser trochanter 1./Femur 1.)

<u>Family</u>	<u>LOR.</u>	<u>GAL.</u>	<u>TAR.</u>	<u>IND.</u>	<u>LEP.</u>	<u>LEM.</u>	<u>CHE.</u>	<u>TUP.</u>
mean	.181	.161	.136	.129	.148	.167	.180	.188
st.dev.	.033	.018	.006	.013	.009	.012	.012	.014
s.e.m.	.005	.002	.002	.003	.002	.003	.004	.003
N	54	63	7	24	38	40	27	20

	<u>Lorisidae</u>				<u>Indriidae</u>		
<u>Genus</u>	<u>Arc.</u>	<u>Lor.</u>	<u>Nyc.</u>	<u>Per.</u>	<u>Ava.</u>	<u>Ind.</u>	<u>Pro.</u>
mean	.156	.124	.189	.207	.125	.123	.135
st.dev.	.014	.012	.009	.011	.016	.010	.009
s.e.m.	.008	.004	.002	.003	.005	.005	.003
N	3	11	20	20	9	4	11

	<u>Lepilemuridae</u>		<u>Lemuridae</u>		<u>Cheirogaleidae</u>	
<u>Genus</u>	<u>Lep.</u>	<u>Hap.</u>	<u>Lem.</u>	<u>Var.</u>	<u>Che.</u>	<u>Mic.</u>
mean	.146	.149	.158	.189	.203	.171
st.dev.	.007	.009	.013	.010	.015	.010
s.e.m.	.001	.002	.002	.003	.006	.002
N	21	17	29	11	7	20

	<u>Galago</u>				
<u>Species</u>	<u>G.all.</u>	<u>G.cra.</u>	<u>G.dem.</u>	<u>G.ele.</u>	<u>G.sen.</u>
mean	.165	.182	.161	.159	.145
st.dev.	.009	.009	.010	—	.145
s.e.m.	.003	.002	.003	—	.001
N	3	22	9	1	28

Ratio F3. Gluteal Index (Third trochanter 1./Femur 1.)

<u>Family</u>	<u>LOR.</u>	<u>GAL.</u>	<u>TAR.</u>	<u>IND.</u>	<u>LEP.</u>	<u>LEM.</u>	<u>CHE.</u>	<u>TUP.</u>
mean	.150	.125	.109	.129	.140	.166	.136	.342
st.dev.	.021	.020	.006	.017	.012	.012	.008	.028
s.e.m.	.004	.003	.002	.003	.002	.004	.002	.002
N	30	63	7	24	38	40	27	20

<u>Genus</u>	<u>Lorisiidae</u>				<u>Indriidae</u>		
	<u>Arc.</u>	<u>Lor.</u>	<u>Nyc.</u>	<u>Per.</u>	<u>Ava.</u>	<u>Ind.</u>	<u>Pro.</u>
mean	.124	.125	—	.163	.115	.132	.139
st.dev.	.019	.014	—	.009	.016	.013	.010
s.e.m.	.011	.005	—	.002	.005	.007	.003
N	3	7	*	20	9	4	11

<u>Genus</u>	<u>Lepilemuridae</u>		<u>Lemuridae</u>		<u>Cheirogaleidae</u>	
	<u>Lep.</u>	<u>Hap.</u>	<u>Lem.</u>	<u>Var.</u>	<u>Che.</u>	<u>Mic.</u>
mean	.127	.154	.163	.173	.156	.129
st.dev.	.010	.015	.012	.013	.005	.010
s.e.m.	.002	.004	.002	.004	.002	.002
N	21	17	29	11	7	20

<u>Species</u>	<u>Golago</u>				
	<u>G.all.</u>	<u>G.cra.</u>	<u>G.dem.</u>	<u>G.ele.</u>	<u>G.sen.</u>
mean	.131	.145	.121	.155	.108
st.dev.	.013	.013	.010	—	.008
s.e.m.	.004	.003	.003	—	.002
N	3	22	9	1	28

* Nycticebus lacks a third trochanter.

Ratio F4. Condylar Index (Dorso-ventral/Medio-lateral condylar l.)

<u>Family</u>	<u>LOR.</u>	<u>GAL.</u>	<u>TAR.</u>	<u>IND.</u>	<u>LEP.</u>	<u>LEM.</u>	<u>CHE.</u>	<u>TUP.</u>
mean	.840	1.08	1.17	1.12	1.10	1.01	1.03	.914
st.dev.	.051	.057	.060	.104	.030	.035	.036	.040
s.e.m.	.007	.007	.023	.021	.007	.009	.010	.009
N	54	63	7	24	38	40	27	20

<u>Genus</u>	<u>Lorisidae</u>				<u>Indriidae</u>		
	<u>Arc.</u>	<u>Lor.</u>	<u>Nyc.</u>	<u>Per.</u>	<u>Ava.</u>	<u>Ind.</u>	<u>Pro.</u>
mean	.915	.866	.850	.806	1.21	1.02	1.08
st.dev.	.032	.041	.044	.041	.034	.032	.101
s.e.m.	.018	.012	.010	.009	.011	.016	.031
N	3	7	20	20	9	4	11

<u>Genus</u>	<u>Lepilemuridae</u>		<u>Lemuridae</u>		<u>Cheirogaleidae</u>	
	<u>Lep.</u>	<u>Hap.</u>	<u>Lem.</u>	<u>Var.</u>	<u>Che.</u>	<u>Mic.</u>
mean	1.15	1.04	1.02	.985	1.04	1.02
st.dev.	.026	.037	.041	.032	.032	.042
s.e.m.	.006	.009	.008	.010	.012	.009
N	21	17	29	11	7	20

<u>Species</u>	<u>Galago</u>				
	<u>G.all.</u>	<u>G.cra.</u>	<u>G.dem.</u>	<u>G.ele.</u>	<u>G.sen.</u>
mean	1.11	1.02	1.04	1.12	1.13
st.dev.	.011	.020	.034	—	.032
s.e.m.	.005	.004	.011	—	.006
N	3	22	9	1	28

Ratio F5. Femoral Head Index (Height/Breadth Femoral Head)

<u>Family</u>	<u>LOR.</u>	<u>GAL.</u>	<u>TAR.</u>	<u>IND.</u>	<u>LEP.</u>	<u>LEM.</u>	<u>CHE.</u>	<u>TUP.</u>
mean	.933	.897	.921	.976	.977	.967	.980	.979
st.dev.	.025	.049	.031	.019	.025	.024	.028	.023
s.e.m.	.003	.006	.012	.004	.005	.007	.010	.005
N	54	63	7	24	38	40	27	20

<u>Genus</u>	<u>Lorisiidae</u>				<u>Indriidae</u>		
	<u>Arc.</u>	<u>Lor.</u>	<u>Nyc.</u>	<u>Per.</u>	<u>Ava.</u>	<u>Ind.</u>	<u>Pro.</u>
mean	.933	.952	.916	.939	.975	.967	.980
st.dev.	.010	.015	.022	.026	.019	.032	.013
s.e.m.	.006	.005	.005	.006	.006	.016	.004
N	3	11	20	20	9	4	11

<u>Genus</u>	<u>Lepilemuridae</u>		<u>Lemuridae</u>		<u>Cheirogaleidae</u>	
	<u>Lep.</u>	<u>Hap.</u>	<u>Lem.</u>	<u>Var.</u>	<u>Che.</u>	<u>Mic.</u>
mean	.978	.974	.972	.959	.951	.994
st.dev.	.028	.020	.019	.030	.029	.028
s.e.m.	.006	.005	.004	.009	.011	.006
N	21	17	29	11	7	20

<u>Species</u>	<u>Galago</u>				
	<u>G.all.</u>	<u>G.cro.</u>	<u>G.dem.</u>	<u>G.ele.</u>	<u>G.sen.</u>
mean	.910	.928	.922	.906	.863
st.dev.	.041	.031	.042	—	.045
s.e.m.	.010	.007	.014	—	.008
N	3	22	9	1	28

Ratio F6. Greater Trochanter Index 1 (Head-Greater troch. 1./Femur 1.)

<u>Family</u>	<u>LOR.</u>	<u>GAL.</u>	<u>TAR.</u>	<u>IND.</u>	<u>LEP.</u>	<u>LEM.</u>	<u>CHE.</u>	<u>TUP.</u>
mean	.155	.150	.141	.154	.161	.182	.177	.189
st.dev.	.022	.012	.006	.008	.008	.008	.008	.010
s.e.m.	.003	.001	.002	.002	.002	.002	.002	.002
N	54	63	7	24	38	40	27	20

	<u>Lorisidae</u>				<u>Indriidae</u>		
<u>Genus</u>	<u>Arc.</u>	<u>Lor.</u>	<u>Nyc.</u>	<u>Per.</u>	<u>Ava.</u>	<u>Ind.</u>	<u>Pro.</u>
mean	.136	.120	.159	.173	.152	.151	.156
st.dev.	.010	.010	.007	.010	.009	.009	.007
s.e.m.	.006	.003	.001	.002	.003	.004	.002
N	3	11	20	20	9	4	11

	<u>Lepilemuridae</u>		<u>Lemuridae</u>		<u>Cheirogaleidae</u>	
<u>Genus</u>	<u>Lep.</u>	<u>Hop.</u>	<u>Lem.</u>	<u>Var.</u>	<u>Che.</u>	<u>Mic.</u>
mean	.157	.168	.178	.189	.190	.171
st.dev.	.008	.006	.008	.006	.008	.007
s.e.m.	.002	.001	.002	.002	.003	.002
N	21	17	29	11	7	20

	<u>Galago</u>				
<u>Species</u>	<u>G.all.</u>	<u>G.cra.</u>	<u>G.dem.</u>	<u>G.ele.</u>	<u>G.sen.</u>
mean	.154	.161	.154	.145	.140
st.dev.	.013	.006	.008	—	.006
s.e.m.	.005	.001	.003	—	.001
N	3	22	9	1	28

Ratio F7. Greater Trochanter Index 2 (Head-Greater troch. 1./Femur 1.)

<u>Family</u>	<u>LOR.</u>	<u>GAL.</u>	<u>TAR.</u>	<u>IND.</u>	<u>LEP.</u>	<u>LEM.</u>	<u>CHE.</u>	<u>TUP.</u>
mean	.132	.115	.124	.112	.127	.139	.136	.166
st.dev.	.020	.018	.006	.006	.005	.007	.008	.011
s.e.m.	.003	.002	.001	.001	.001	.002	.002	.002
N	54	63	7	24	38	40	27	20

<u>Genus</u>	<u>Lorisiidae</u>				<u>Indriidae</u>		
	<u>Arc.</u>	<u>Lor.</u>	<u>Nyc.</u>	<u>Per.</u>	<u>Ava.</u>	<u>Ind.</u>	<u>Pro.</u>
mean	.126	.098	.138	.145	.108	.113	.114
st.dev.	.005	.008	.010	.010	.006	.007	.005
s.e.m.	.003	.003	.002	.002	.002	.003	.001
N	3	11	20	20	9	4	11

<u>Genus</u>	<u>Lepilemuridae</u>		<u>Lemuridae</u>		<u>Cheirogaleidae</u>	
	<u>Lep.</u>	<u>Hap.</u>	<u>Lem.</u>	<u>Var.</u>	<u>Che.</u>	<u>Mic.</u>
mean	.123	.131	.137	.143	.143	.132
st.dev.	.005	.007	.006	.007	.010	.006
s.e.m.	.001	.001	.001	.002	.004	.001
N	21	17	29	11	7	20

<u>Species</u>	<u>Galago</u>				
	<u>G.all.</u>	<u>G.cra.</u>	<u>G.dem.</u>	<u>G.ele.</u>	<u>G.sen.</u>
mean	.113	.116	.120	.120	.112
st.dev.	.003	.019	.009	—	.021
s.e.m.	.002	.004	.003	—	.004
N	3	22	9	1	28

Appendix D. Limb Proportion Ratios.

Ratio LP1. Intermembral Index (Humerus 1. + Radius 1./Femur 1. + Tibio 1.)

<u>Family</u>	<u>LOR.</u>	<u>GAL.</u>	<u>TAR.</u>	<u>IND.</u>	<u>LEP.</u>	<u>LEM.</u>	<u>CHE.</u>	<u>TUP.</u>
mean	.881	.606	.577	.592	.607	.702	.706	.725
st.dev.	.022	.077	.015	.033	.020	.010	.014	.013
s.e.m.	.003	.011	.006	.007	.004	.003	.003	.003
N	51	51	7	24	35	35	27	15

	<u>Lorisidae</u>				<u>Indriidae</u>		
<u>Genus</u>	<u>Arc.</u>	<u>Lor.</u>	<u>Nyc.</u>	<u>Per.</u>	<u>Ava.</u>	<u>Ind.</u>	<u>Pro.</u>
mean	.895	.893	.879	.873	.566	.645	.594
st.dev.	.021	.024	.017	.023	.011	.010	.026
s.e.m.	.012	.008	.004	.005	.004	.005	.008
N	3	10	20	18	9	4	11

	<u>Lepilemuridae</u>		<u>Lemuridae</u>		<u>Cheirogaleidae</u>	
<u>Genus</u>	<u>Lep.</u>	<u>Hap.</u>	<u>Lem.</u>	<u>Var.</u>	<u>Che.</u>	<u>Mic.</u>
mean	.591	.630	.697	.719	.707	.706
st.dev.	.015	.029	.016	.006	.017	.013
s.e.m.	.003	.008	.003	.002	.006	.003
N	21	14	26	9	7	20

	<u>Galago</u>				
<u>Species</u>	<u>G.all.</u>	<u>G.cra.</u>	<u>G.dem.</u>	<u>G.ele.</u>	<u>G.sen.</u>
mean	.634	.683	.670	.647	.525
st.dev.	.009	.014	.015	—	.019
s.e.m.	.002	.003	.005	—	.004
N	3	16	8	1	23

Ratio LP2. Crural Index (Tibia I./Femur I.)

<u>Family</u>	<u>LOR.</u>	<u>GAL.</u>	<u>TAR.</u>	<u>IND.</u>	<u>LEP.</u>	<u>LEM.</u>	<u>CHE.</u>	<u>TUP.</u>
mean	.950	.956	1.008	.863	.954	.942	1.082	1.079
st.dev.	.025	.066	.018	.017	.027	.014	.061	.028
s.e.m.	.004	.009	.007	.003	.006	.004	.012	.007
N	51	60	7	24	36	39	27	15

	<u>Lorisidae</u>				<u>Indriidae</u>		
<u>Genus</u>	<u>Arc.</u>	<u>Lor.</u>	<u>Nyc.</u>	<u>Per.</u>	<u>Ava.</u>	<u>Ind.</u>	<u>Pro.</u>
mean	.906	.964	.952	.947	.866	.864	.859
st.dev.	.037	.018	.022	.022	.021	.016	.013
s.e.m.	.021	.006	.005	.005	.007	.008	.004
N	3	10	20	18	9	4	11

	<u>Lepilemuridae</u>		<u>Lemuridae</u>		<u>Cheirogaleidae</u>	
<u>Genus</u>	<u>Lep.</u>	<u>Hap.</u>	<u>Lem.</u>	<u>Var.</u>	<u>Che.</u>	<u>Mic.</u>
mean	.947	.964	.952	.915	1.008	1.109
st.dev.	.023	.032	.016	.012	.026	.047
s.e.m.	.005	.008	.003	.004	.010	.010
N	21	15	28	11	7	20

	<u>Galego</u>				
<u>Species</u>	<u>G.all.</u>	<u>G.cro.</u>	<u>G.dem.</u>	<u>G.ele.</u>	<u>G.sen.</u>
mean	.948	.940	1.085	.928	.926
st.dev.	.050	.018	.042	—	.045
s.e.m.	.016	.004	.014	—	.009
N	3	22	9	1	25

Ratio LP3. Relative Tibial Length (Tibia 1./Skeletal trunk 1.)

<u>Family</u>	<u>LOR.</u>	<u>GAL.</u>	<u>TAR.</u>	<u>IND.</u>	<u>LEP.</u>	<u>LEM.</u>	<u>CHE.</u>	<u>TUP.</u>
mean	.405	.533	.744	.613	.495	.451	.408	.378
st.dev.	.046	.047	.033	.031	.023	.018	.040	.018
s.e.m.	.006	.006	.013	.006	.005	.005	.008	.005
N	51	66	7	24	36	39	27	15

	<u>Lorisidae</u>				<u>Indriidae</u>		
<u>Genus</u>	<u>Arc.</u>	<u>Lor.</u>	<u>Nyc.</u>	<u>Per.</u>	<u>Ava.</u>	<u>Ind.</u>	<u>Pro.</u>
mean	.376	.490	.389	.379	.621	.642	.596
st.dev.	.034	.026	.015	.012	.031	.021	.024
s.e.m.	.020	.008	.003	.003	.010	.011	.007
N	3	10	20	18	9	4	11

	<u>Lepilemuridae</u>		<u>Lemuridae</u>		<u>Cheirogaleidae</u>	
<u>Genus</u>	<u>Lep.</u>	<u>Hap.</u>	<u>Lem.</u>	<u>Var.</u>	<u>Che.</u>	<u>Mic.</u>
mean	.494	.497	.474	.399	.351	.428
st.dev.	.020	.030	.027	.010	.020	.021
s.e.m.	.004	.008	.005	.003	.008	.005
N	21	15	28	11	7	20

	<u>Galego</u>				
<u>Species</u>	<u>G.all.</u>	<u>G.cra.</u>	<u>G.dem.</u>	<u>G.ele.</u>	<u>G.sen.</u>
mean	.564	.486	.534	.500	.571
st.dev.	.020	.020	.037	—	.031
s.e.m.	.006	.004	.012	—	.006
N	3	24	8	1	28

Ratio LP4. Relative Hindlimb Length (Femur l. + Tibia l./Skeletal trunk l.)

<u>Family</u>	<u>LOR.</u>	<u>GAL.</u>	<u>TAR.</u>	<u>IND.</u>	<u>LEP.</u>	<u>LEM.</u>	<u>CHE.</u>	<u>TUP.</u>
mean	.831	1.092	1.482	1.324	1.013	.930	.785	.728
st.dev.	.091	.097	.059	.064	.038	.040	.061	.029
s.e.m.	.013	.013	.022	.013	.010	.010	.012	.008
N	51	60	7	24	36	39	27	15

	<u>Lorisidae</u>				<u>Indriidae</u>		
<u>Genus</u>	<u>Arc.</u>	<u>Lor.</u>	<u>Nyc.</u>	<u>Per.</u>	<u>Ava.</u>	<u>Ind.</u>	<u>Pro.</u>
mean	.791	.999	.799	.779	1.339	1.385	1.289
st.dev.	.058	.057	.031	.022	.063	.042	.051
s.e.m.	.033	.018	.007	.005	.021	.021	.015
N	3	10	20	18	9	4	11

	<u>Lepilemuridae</u>		<u>Lemuridae</u>		<u>Cheirogaleidae</u>	
<u>Genus</u>	<u>Lep.</u>	<u>Hap.</u>	<u>Lem.</u>	<u>Var.</u>	<u>Che.</u>	<u>Mic.</u>
mean	1.015	1.012	.973	.835	.700	.815
st.dev.	.034	.053	.054	.021	.045	.029
s.e.m.	.007	.014	.010	.006	.017	.006
N	21	15	28	11	7	20

	<u>Galago</u>				
<u>Species</u>	<u>G.all.</u>	<u>G.cra.</u>	<u>G.dem.</u>	<u>G.ele.</u>	<u>G.sen.</u>
mean	1.161	1.004	1.026	1.039	1.188
st.dev.	.025	.038	.059	—	.040
s.e.m.	.010	.008	.020	—	.008
N	3	24	8	1	28

Ratio LP5. Brachial Index (Radius 1./Humerus 1.)

<u>Family</u>	<u>LOR.</u>	<u>GAL.</u>	<u>TAR.</u>	<u>IND.</u>	<u>LEP.</u>	<u>LEM.</u>	<u>CHE.</u>	<u>TUP.</u>
mean	1.02	1.07	1.25	1.15	1.10	1.03	1.07	.928
st.dev.	.060	.047	.039	.070	.037	.020	.067	.036
s.e.m.	.008	.007	.015	.014	.010	.007	.013	.009
N	51	52	7	24	35	35	27	17

<u>Genus</u>	<u>Lorisidae</u>				<u>Indriidae</u>		
	<u>Arc.</u>	<u>Lor.</u>	<u>Nyc.</u>	<u>Per.</u>	<u>Ava.</u>	<u>Ind.</u>	<u>Pro.</u>
mean	1.03	1.12	.980	1.02	1.21	1.20	1.08
st.dev.	.041	.042	.023	.030	.029	.013	.035
s.e.m.	.023	.013	.005	.007	.010	.007	.011
N	3	10	20	18	9	4	11

<u>Genus</u>	<u>Lepilemuridae</u>		<u>Lemuridae</u>		<u>Cheirogaleidae</u>	
	<u>Lep.</u>	<u>Hap.</u>	<u>Lem.</u>	<u>Var.</u>	<u>Che.</u>	<u>Mic.</u>
mean	1.08	1.12	1.06	.964	.998	1.10
st.dev.	.034	.040	.031	.015	.053	.050
s.e.m.	.007	.011	.006	.005	.020	.011
N	21	14	26	9	7	20

<u>Species</u>	<u>Galago</u>				
	<u>G.all.</u>	<u>G.cra.</u>	<u>G.dem.</u>	<u>G.ele.</u>	<u>G.sen.</u>
mean	1.06	1.04	1.15	1.05	1.07
st.dev.	.035	.023	.054	—	.031
s.e.m.	.020	.006	.019	—	.006
N	3	16	8	1	24

Ratio LP6. Relative Forelimb Length (Humerus l. + Radius l./STL)

<u>Family</u>	<u>LOR.</u>	<u>GAL.</u>	<u>TAR.</u>	<u>IND.</u>	<u>LEP.</u>	<u>LEM.</u>	<u>CHE.</u>	<u>TUP.</u>
mean	.732	.657	.855	.784	.616	.655	.554	.531
st.dev.	.088	.040	.028	.065	.025	.020	.043	.020
s.e.m.	.012	.006	.010	.013	.006	.005	.008	.005
N	51	52	7	24	35	35	27	17

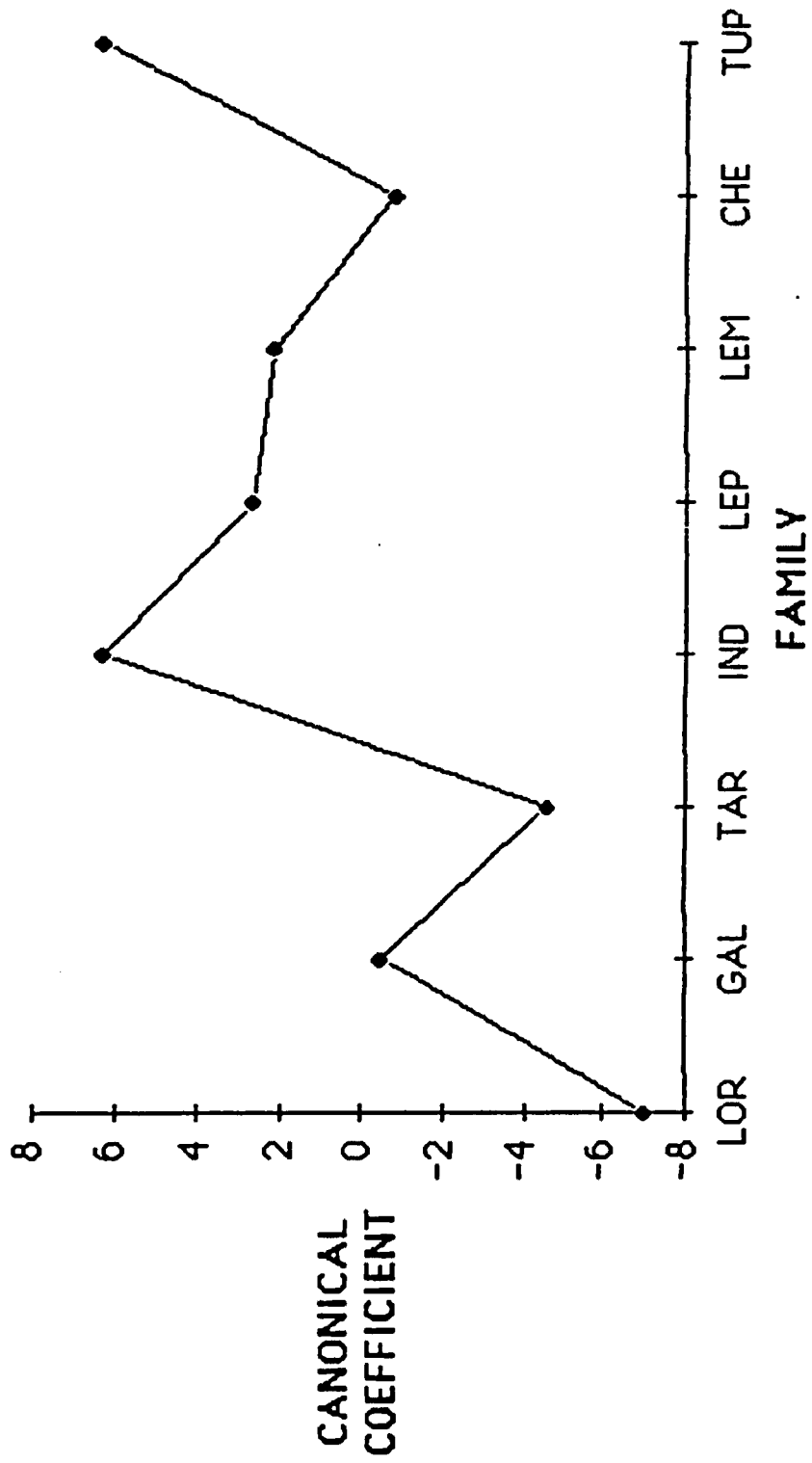
	<u>Lorisidae</u>				<u>Indriidae</u>		
<u>Genus</u>	<u>Arc.</u>	<u>Lor.</u>	<u>Nyc.</u>	<u>Per.</u>	<u>Ava.</u>	<u>Ind.</u>	<u>Pro.</u>
mean	.708	.893	.702	.680	.758	.893	.766
st.dev.	.046	.059	.029	.018	.041	.017	.050
s.e.m.	.027	.019	.007	.004	.014	.008	.015
N	3	10	20	18	9	4	11

	<u>Lepilemuridae</u>		<u>Lemuridae</u>		<u>Cheirogaleidae</u>	
<u>Genus</u>	<u>Lep.</u>	<u>Hop.</u>	<u>Lem.</u>	<u>Var.</u>	<u>Che.</u>	<u>Mic.</u>
mean	.600	.636	.679	.598	.495	.575
st.dev.	.021	.037	.035	.015	.030	.021
s.e.m.	.005	.010	.007	.005	.011	.005
N	21	14	26	9	7	20

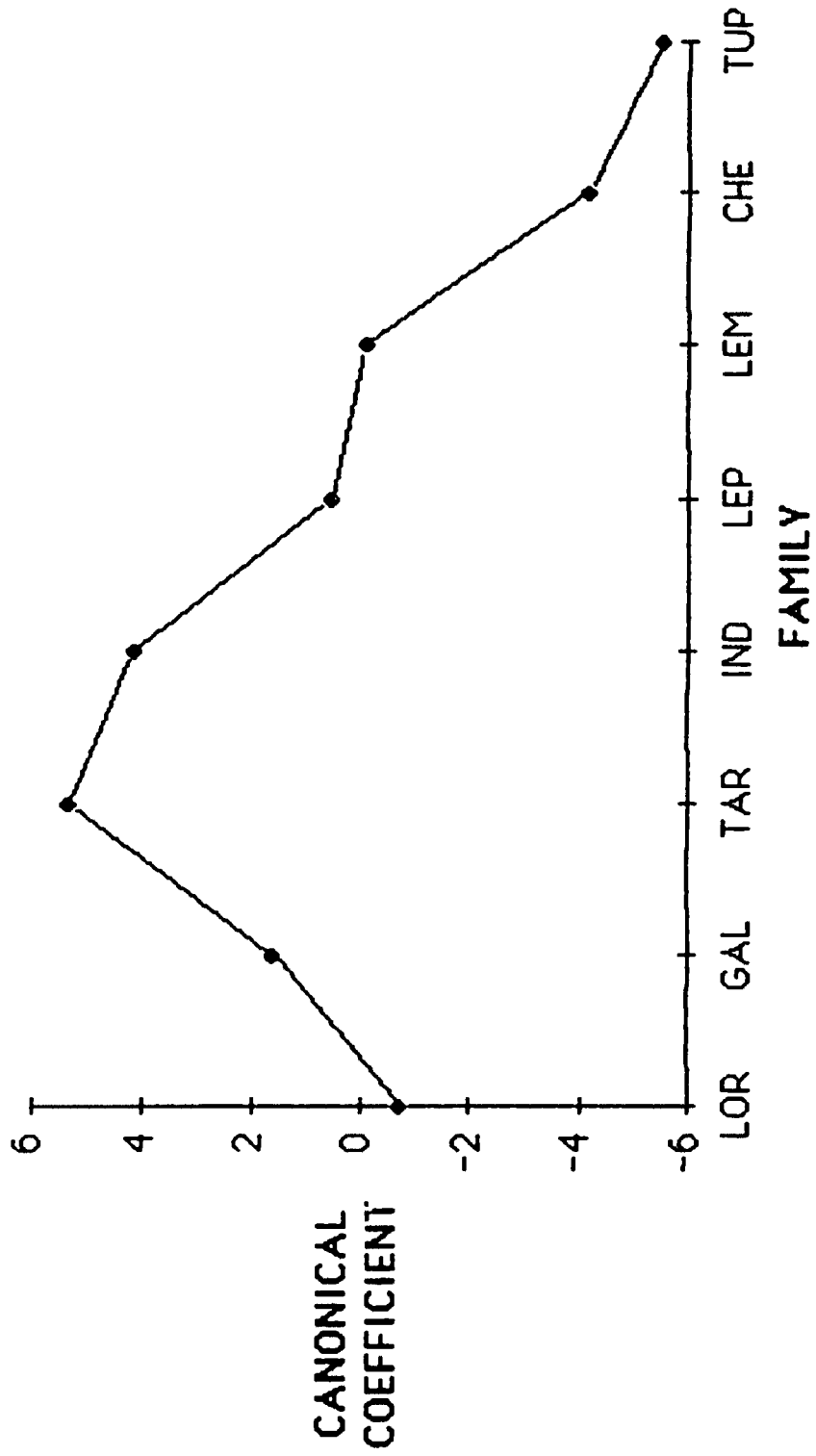
	<u>Galago</u>				
<u>Species</u>	<u>G.all.</u>	<u>G.cra.</u>	<u>G.dem.</u>	<u>G.ele.</u>	<u>G.sen.</u>
mean	.735	.679	.694	.672	.622
st.dev.	.009	.014	.033	—	.022
s.e.m.	.005	.003	.012	—	.005
N	3	16	8	1	24

Appendix E. Pelvic Discriminant Plots

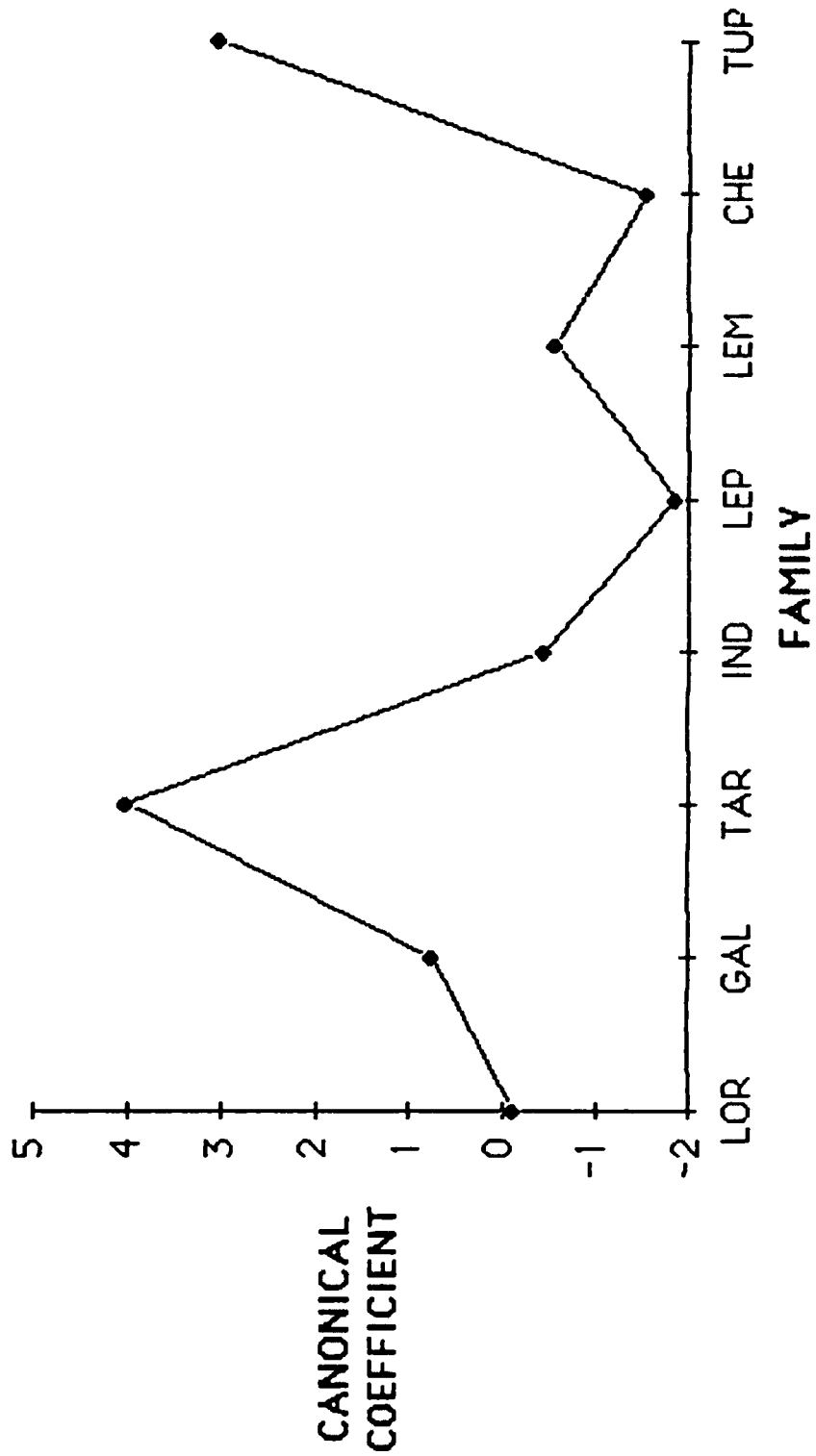
Plot 1. Discriminant Axis 1. Pelvic Ratios.



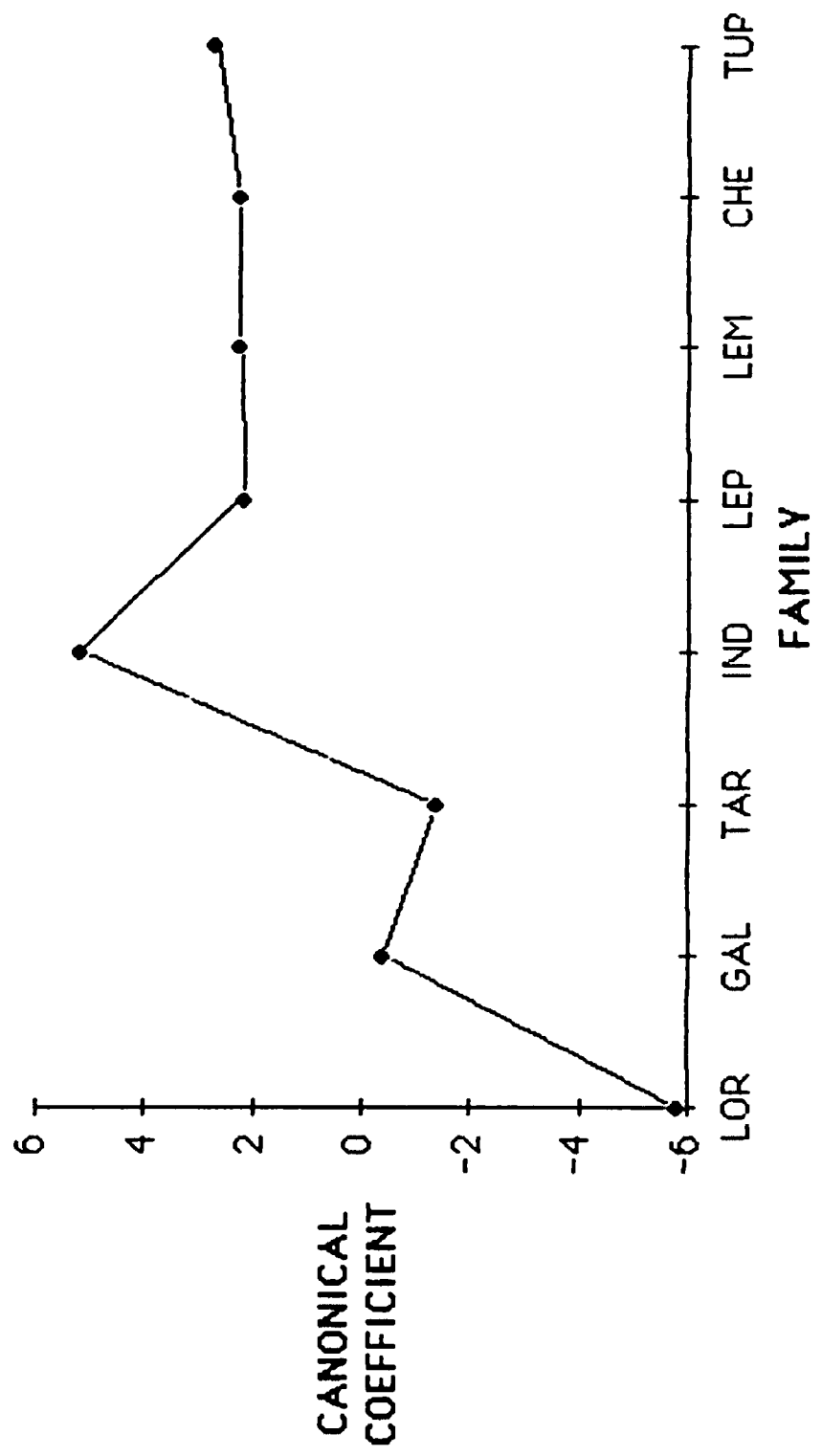
Plot 2. Discriminant Axis 2. Pelvic Ratios.



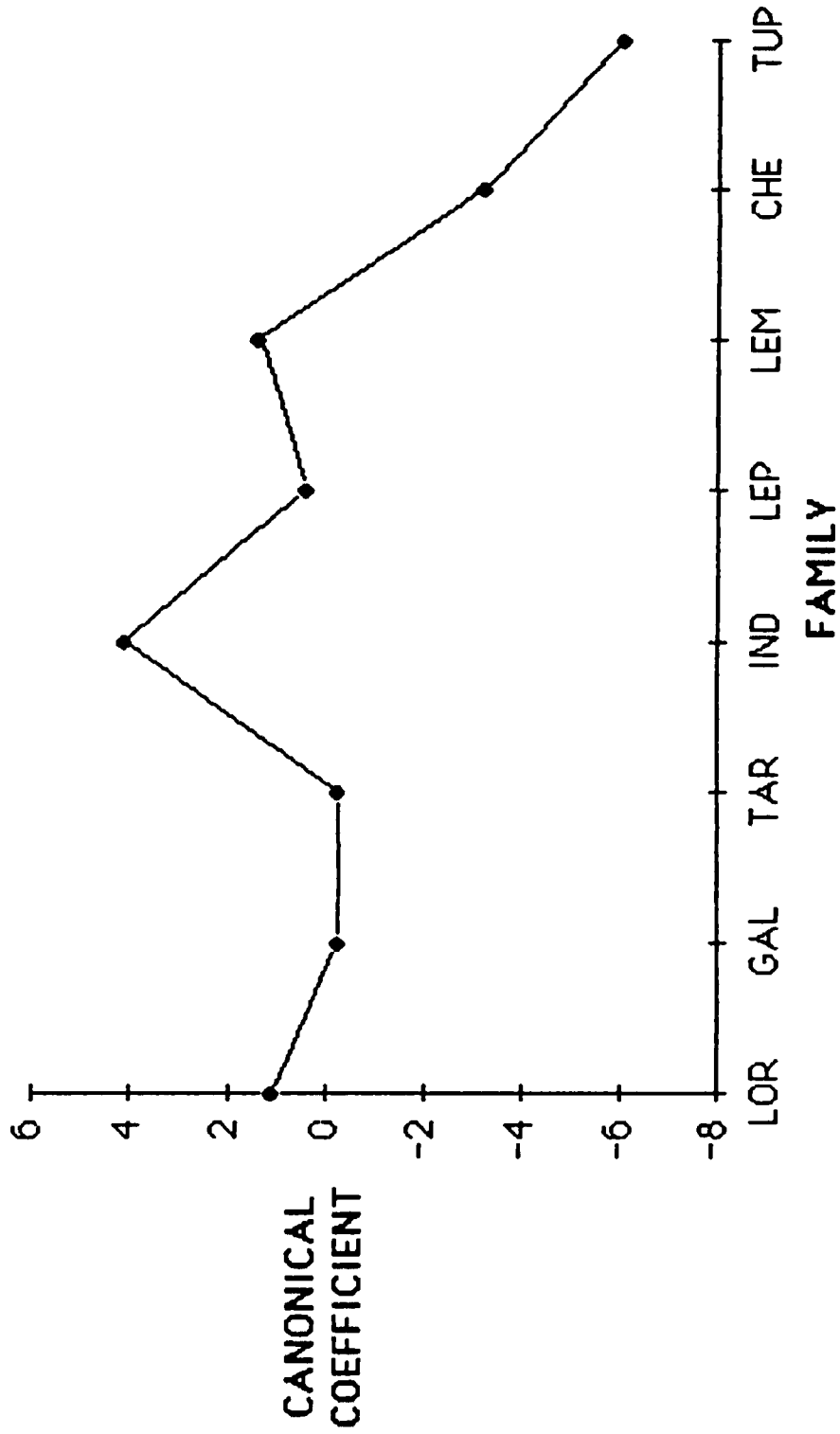
Plot 3. Discriminant Axis 3. Pelvic Ratios.



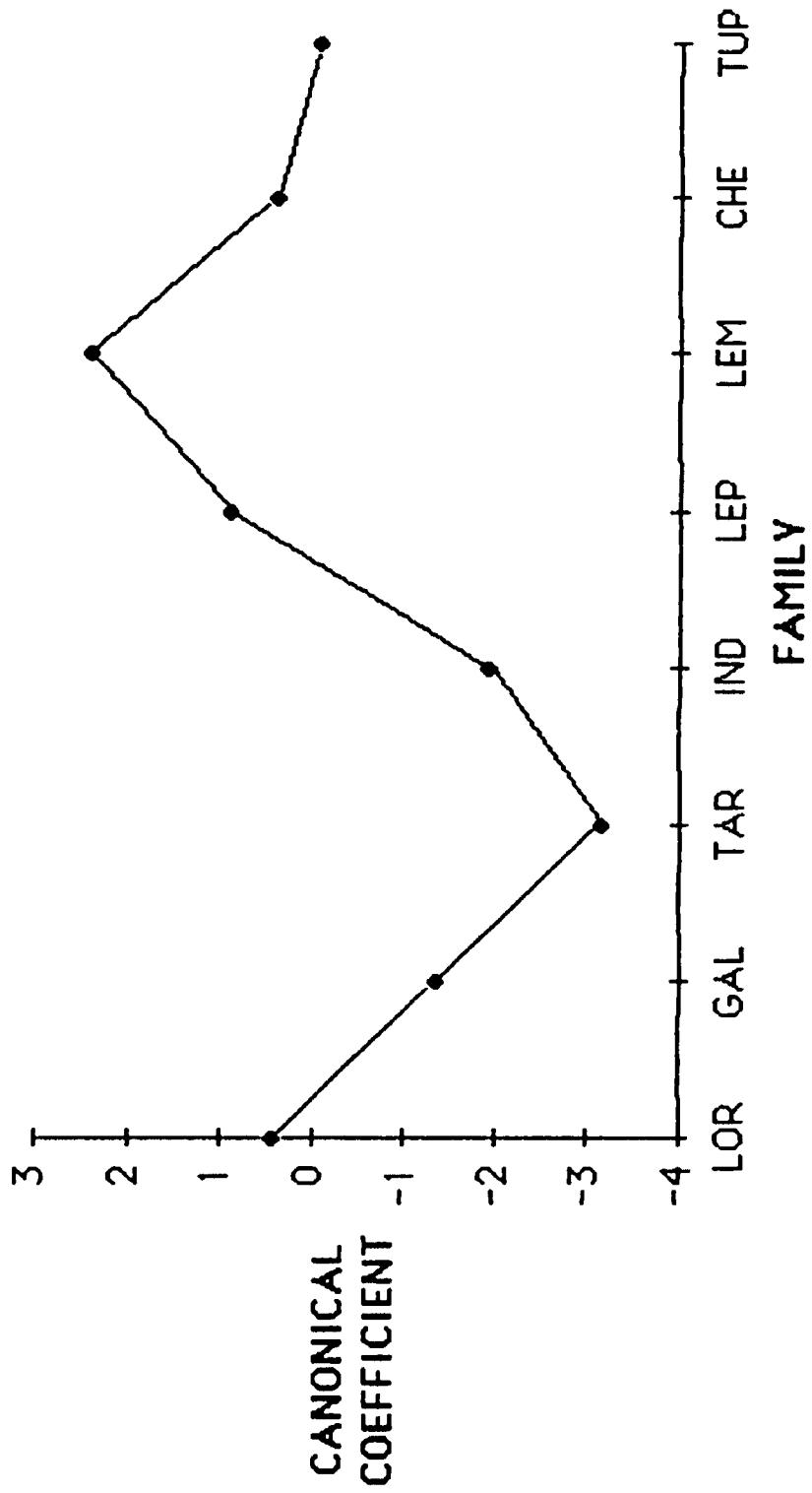
Plot 4. Discriminant Axis 1. Pelvic Raw Data.



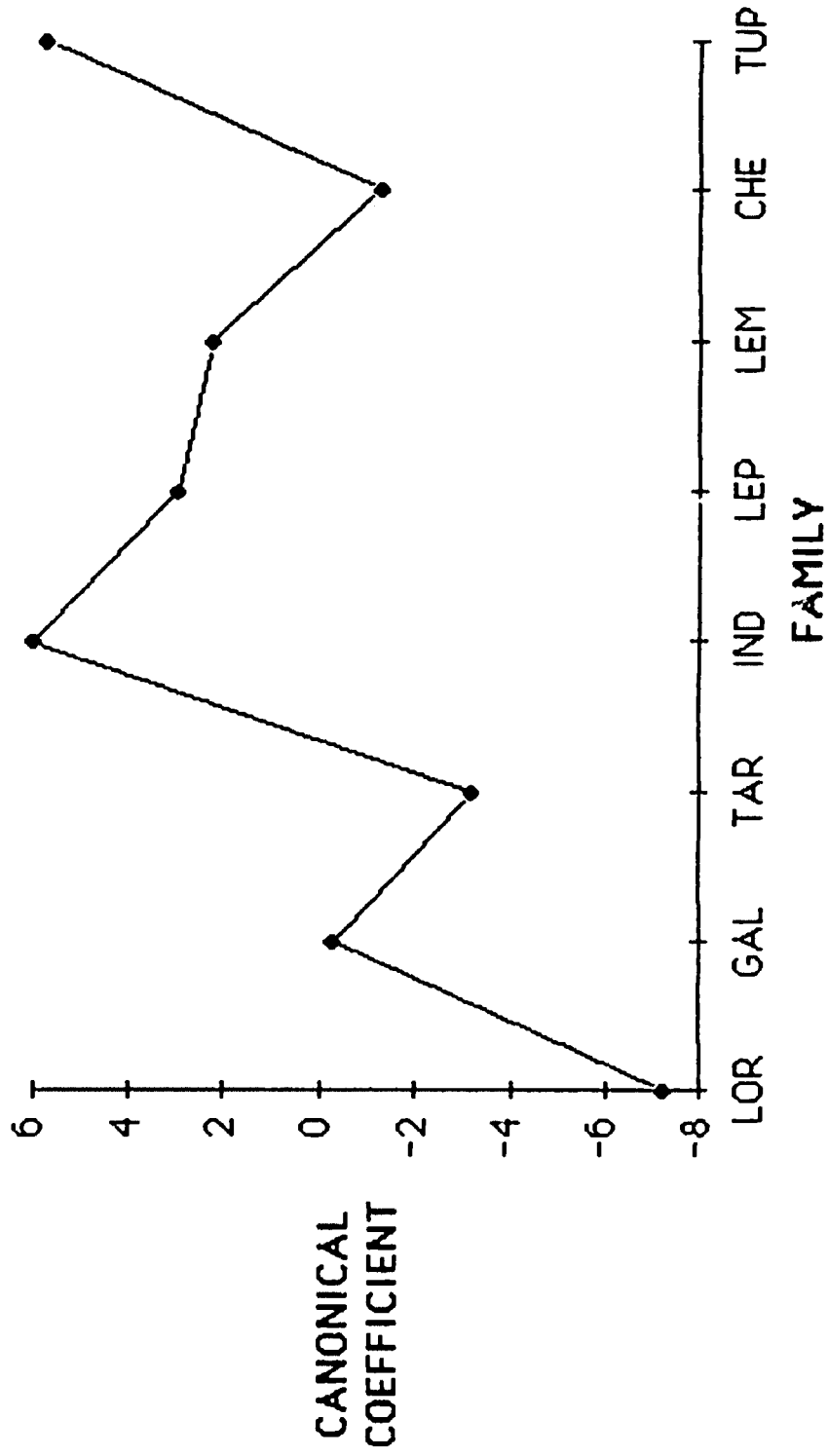
Plot 5. Discriminant Axis 2. Pelvic Raw Data.



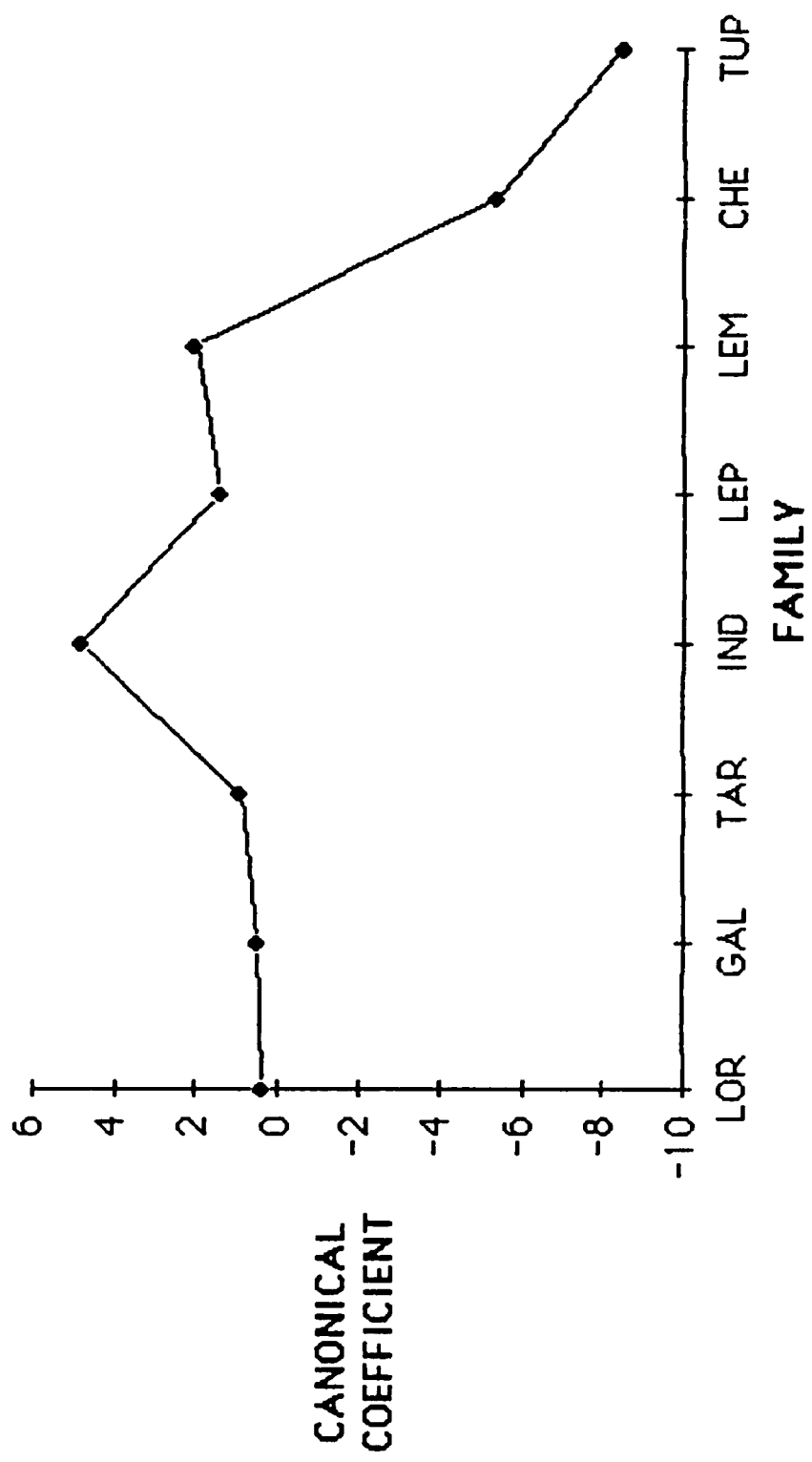
Plot 6. Discriminant Axis 3. Pelvic Raw Data.



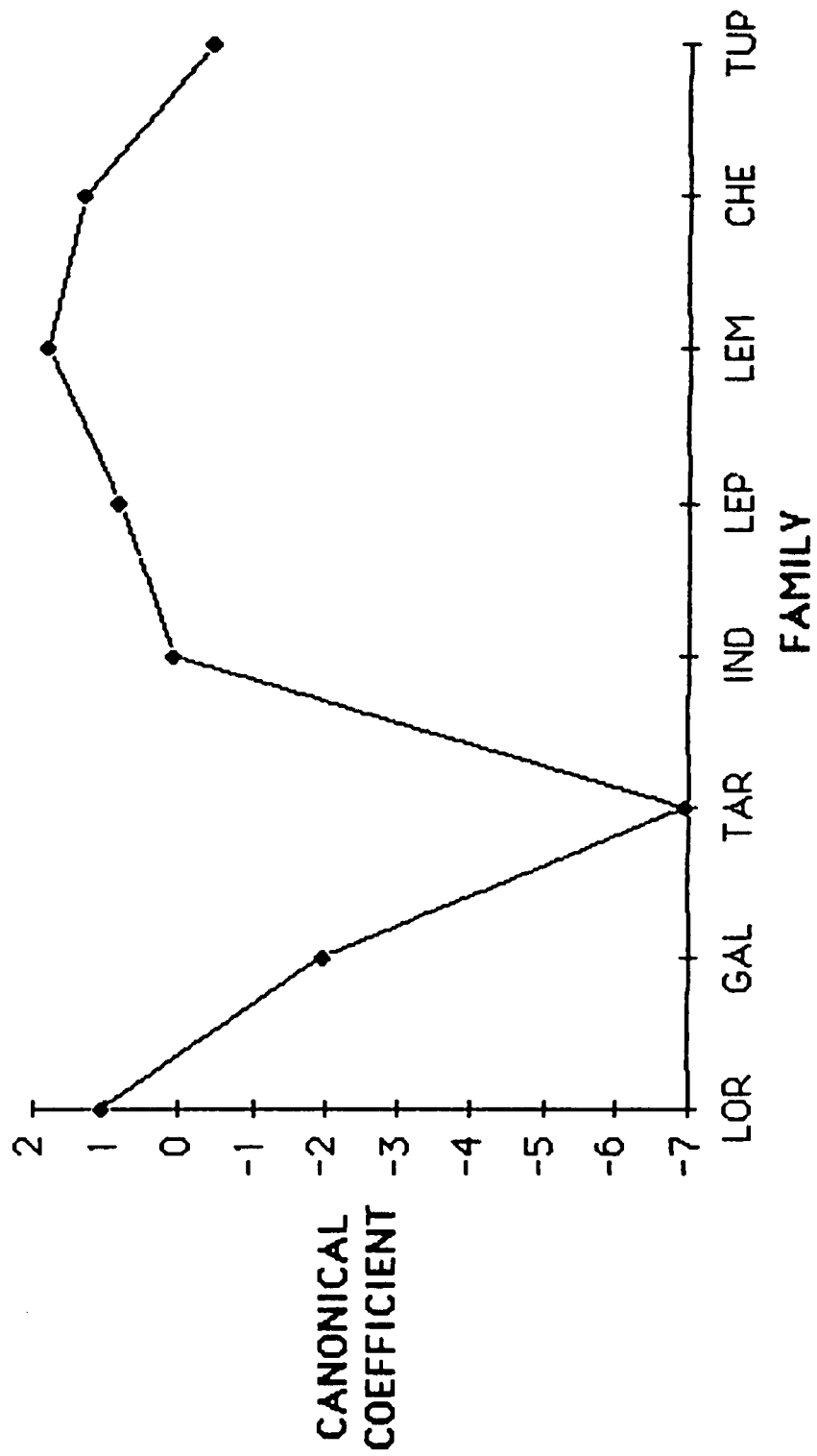
Plot 7. Discriminant Axis 1. Pelvic Log Data.



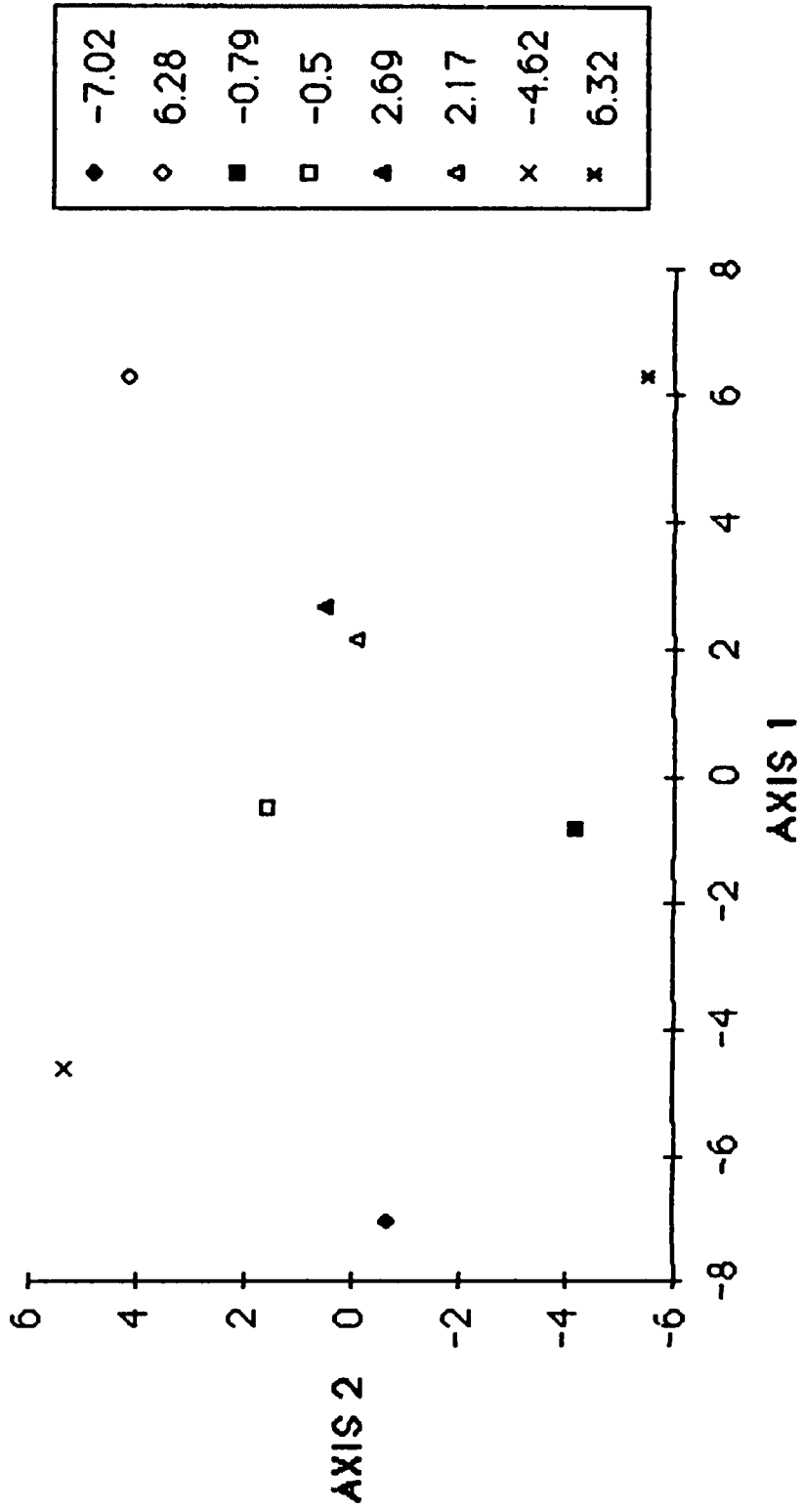
Plot 8. Discriminant Axis 2. Pelvic Log Data.



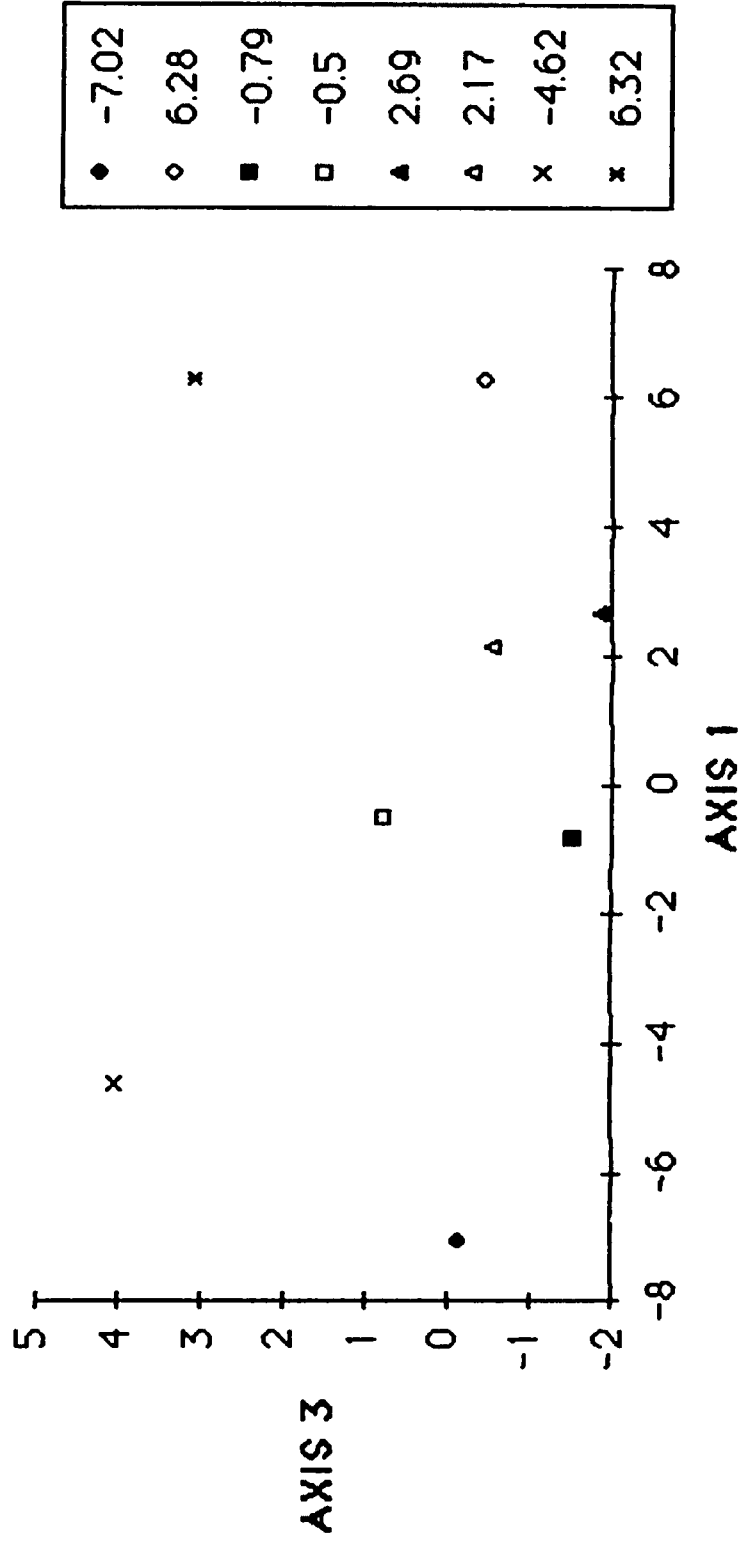
Plot 9. Discriminant Axis 3. Pelvic Log Data.



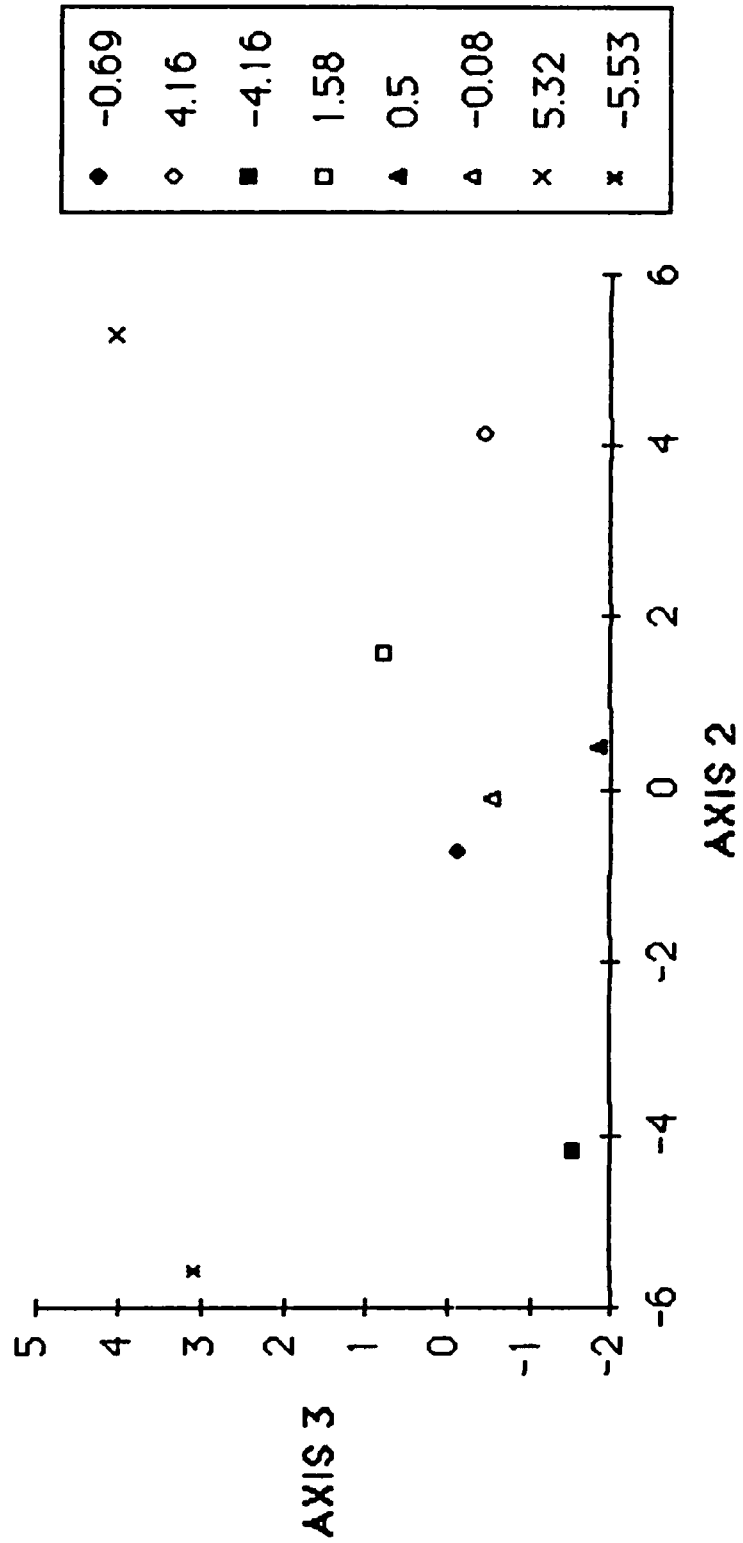
Plot 10. Discriminant Axes 1 and 2. Pelvic Ratios.



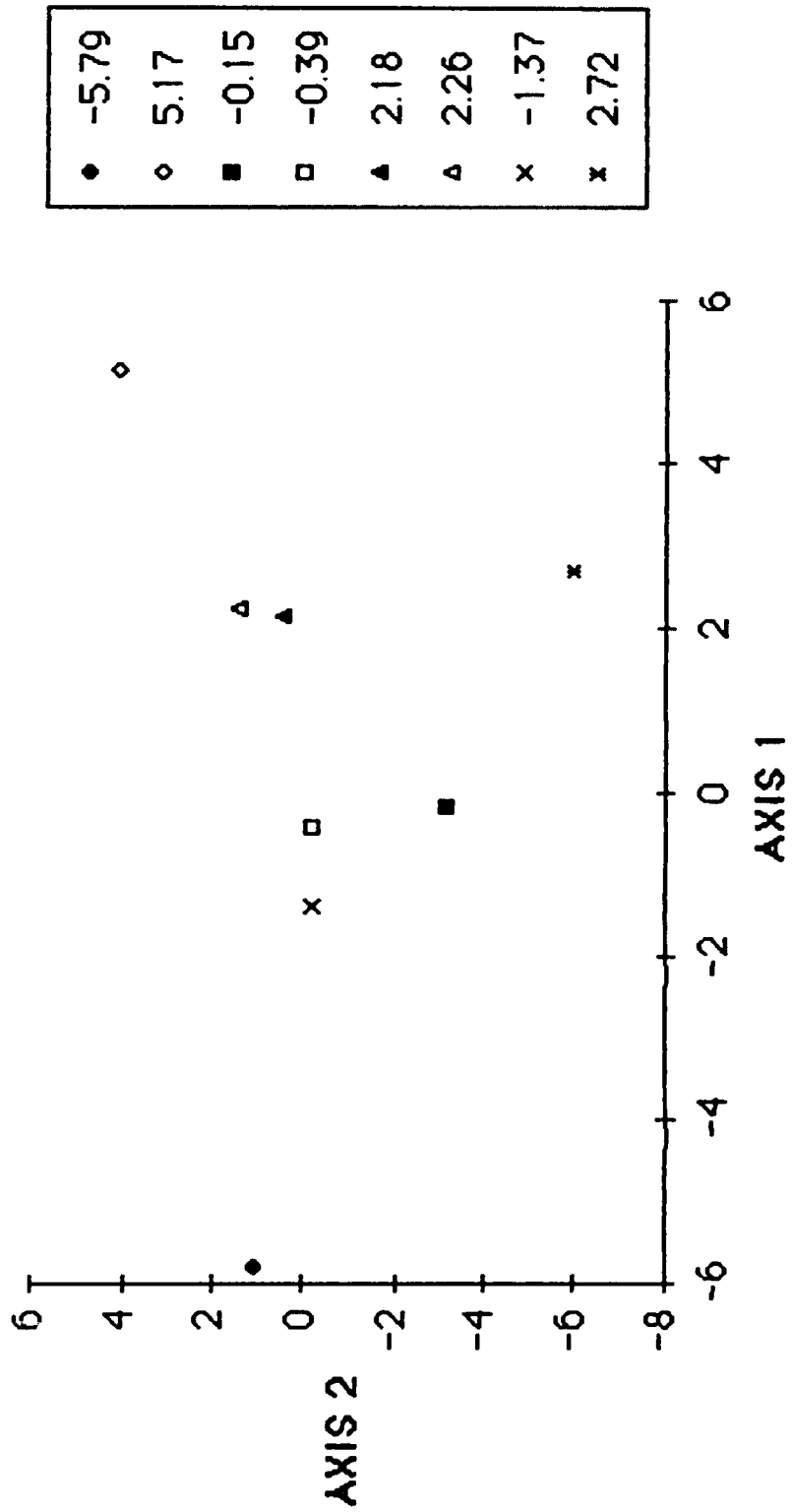
Plot 11. Discriminant Axes 1 and 3. Pelvic Ratios.



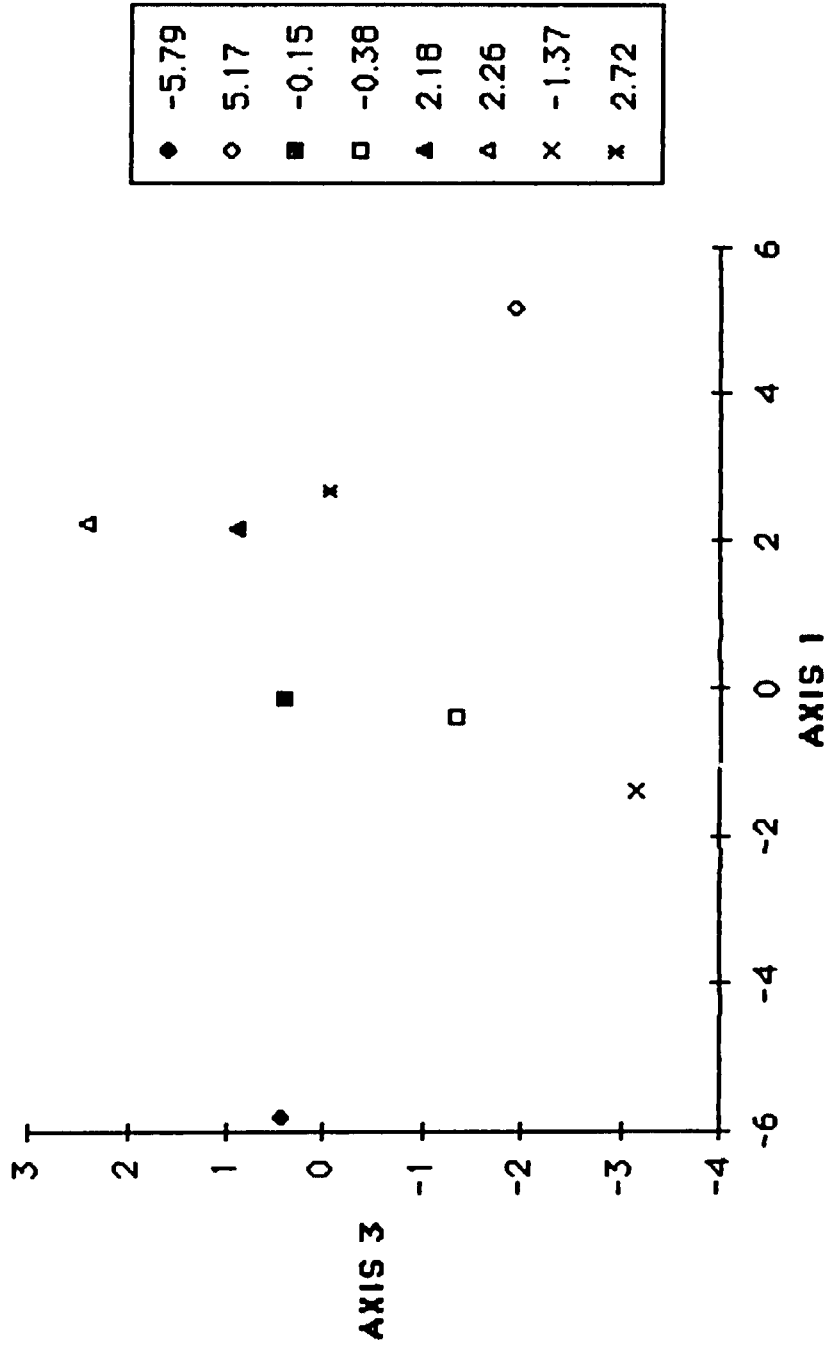
Plot 12. Discriminant Axes 2 and 3. Pelvic Ratios.



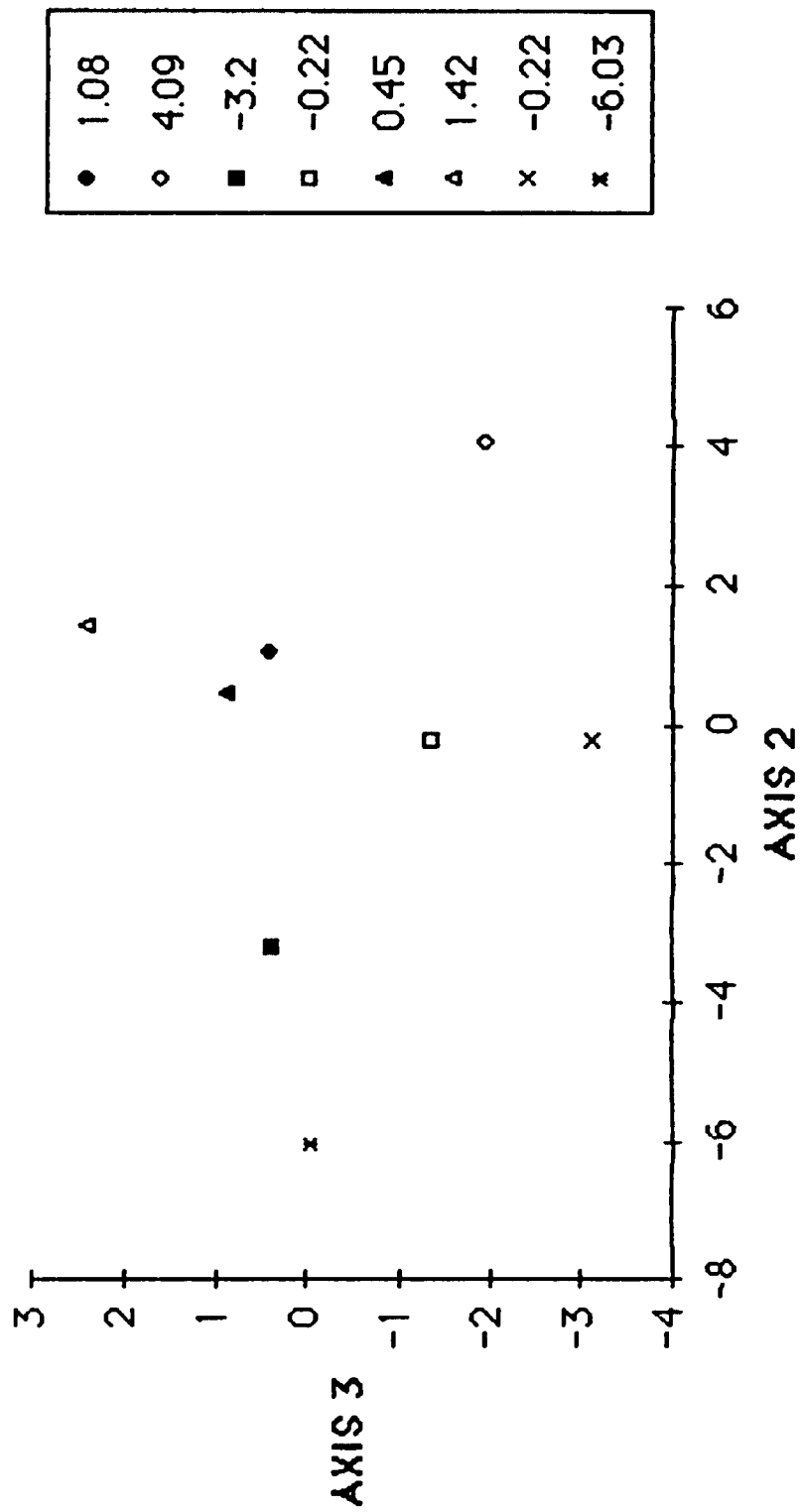
Plot 13. Discriminant Axes 1 and 2. Pelvic Raw Data.



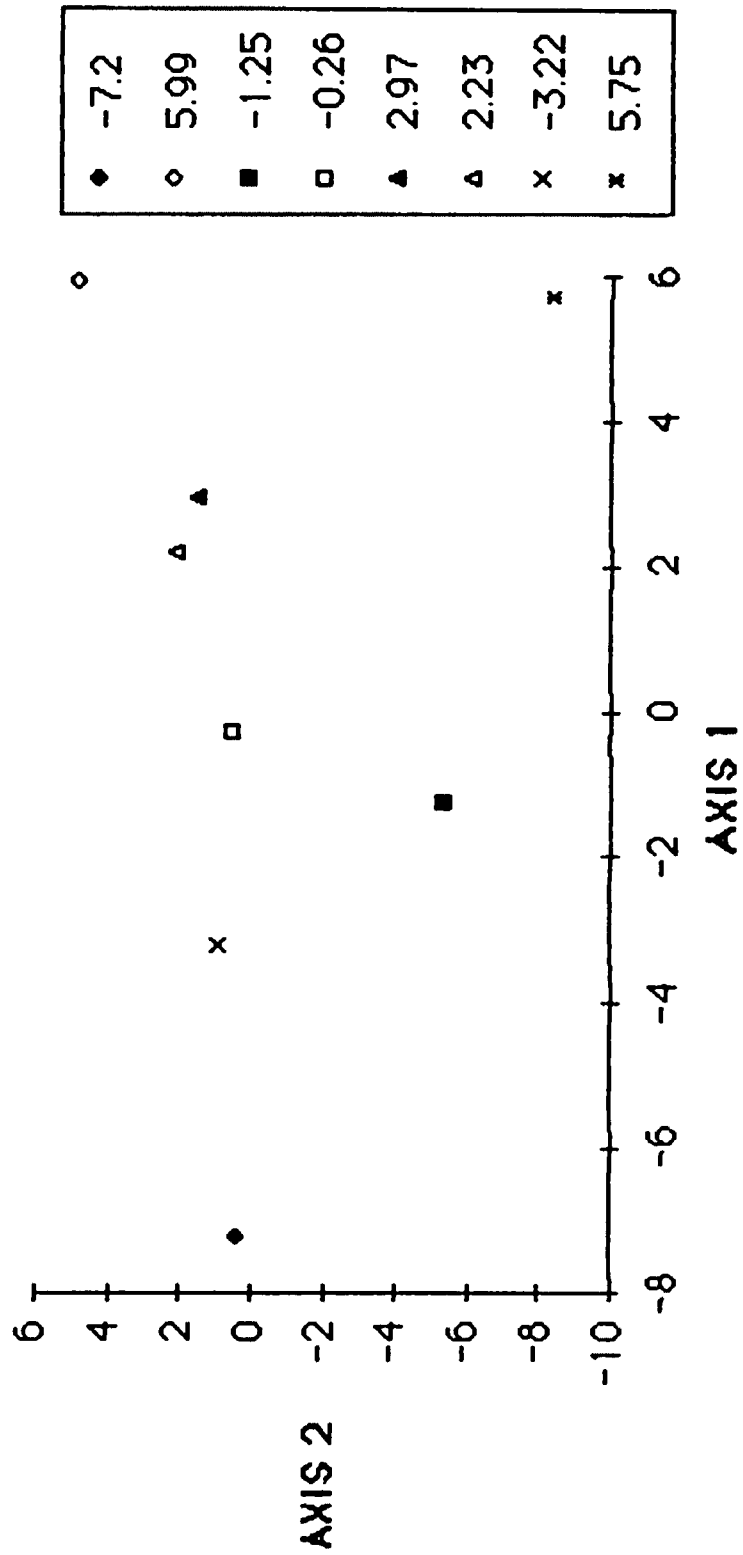
Plot 14. Discriminant Axes 1 and 3. Pelvic Raw Data.



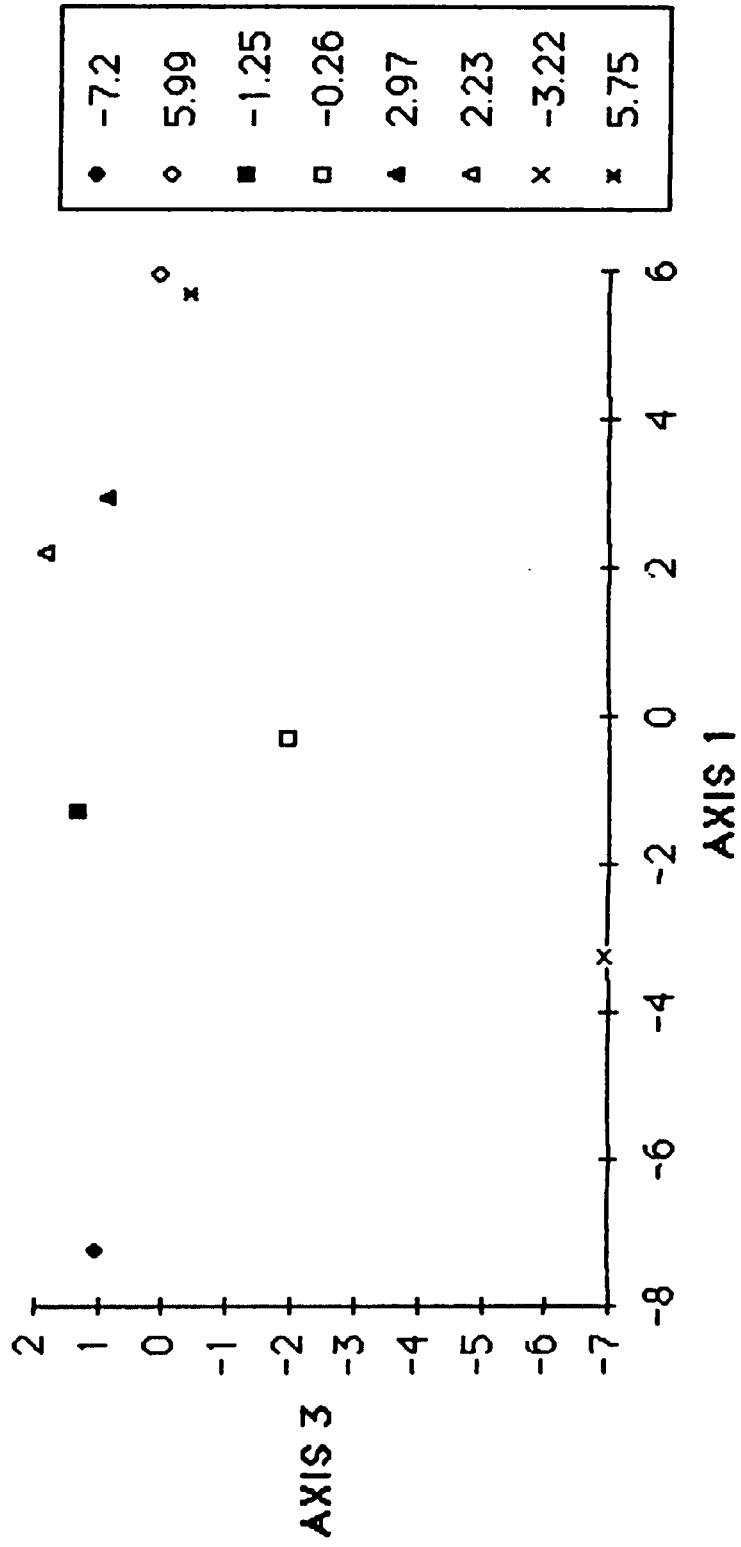
Plot 15. Discriminant Axes 2 and 3. Pelvic Raw Data.



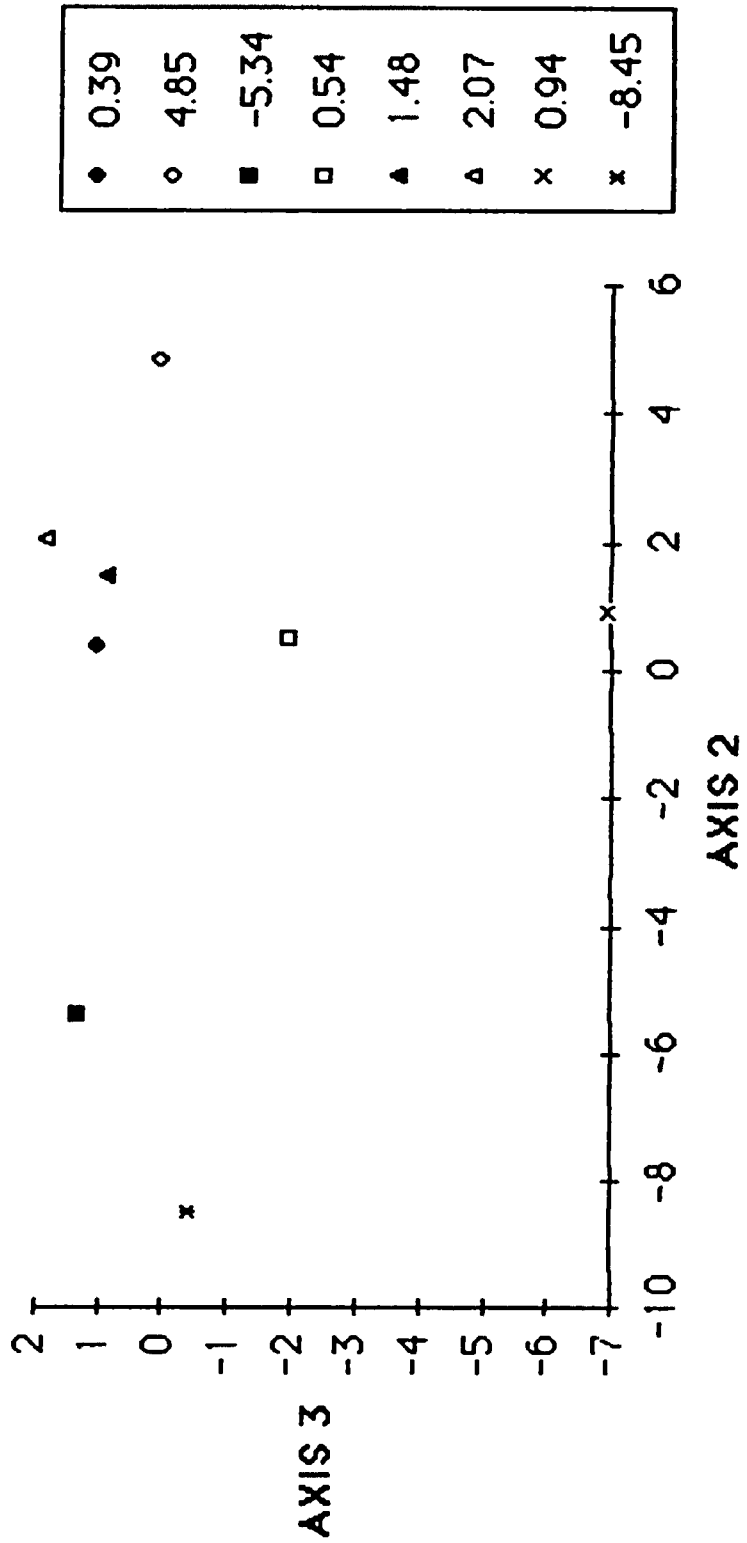
Plot 16. Discriminant Axes 1 and 2. Pelvic Log Data.



Plot 17. Discriminant Axes 1 and 3. Pelvic Log Data.

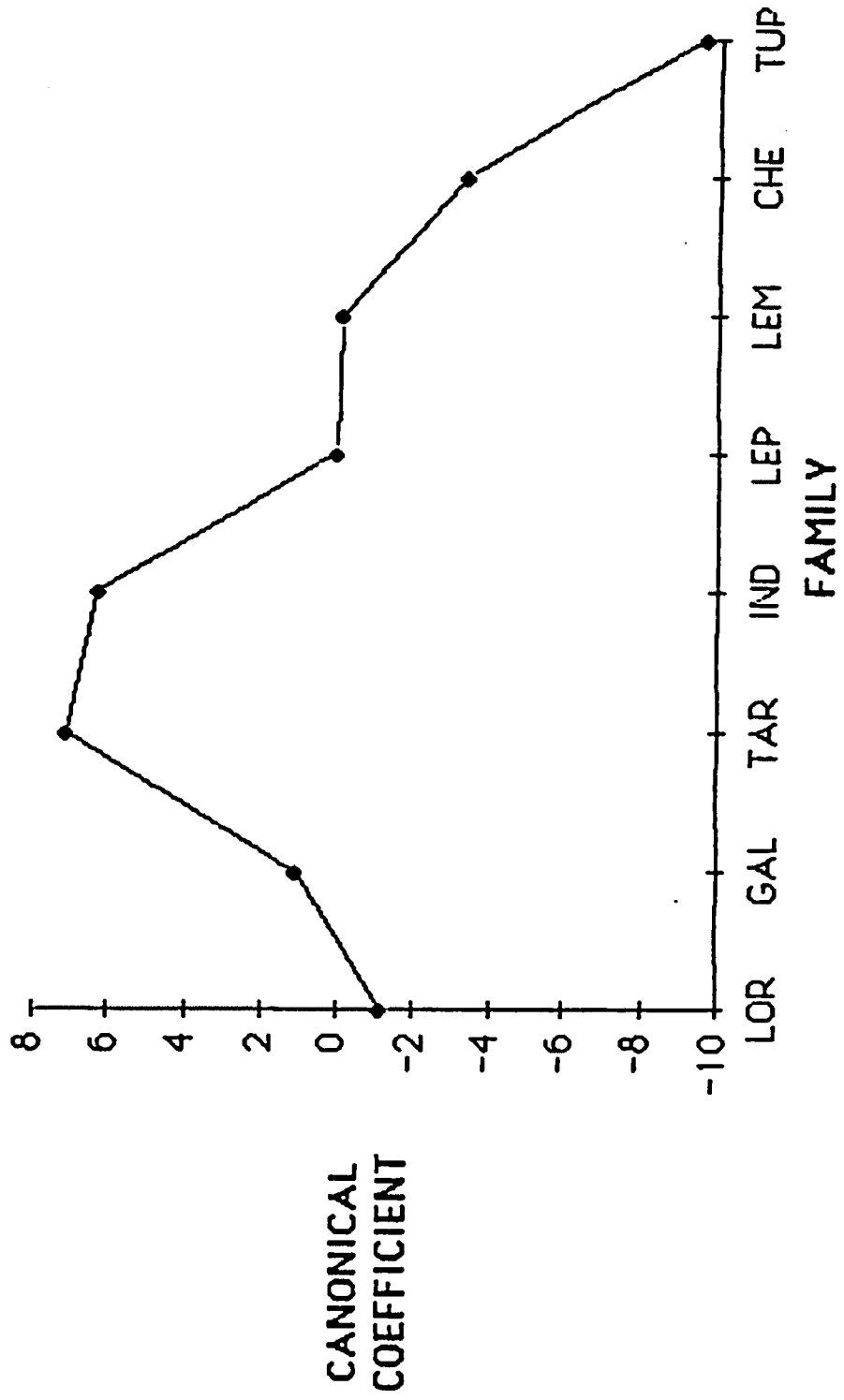


Plot 18. Discriminant Axes 2 and 3. Pelvic Log Data.

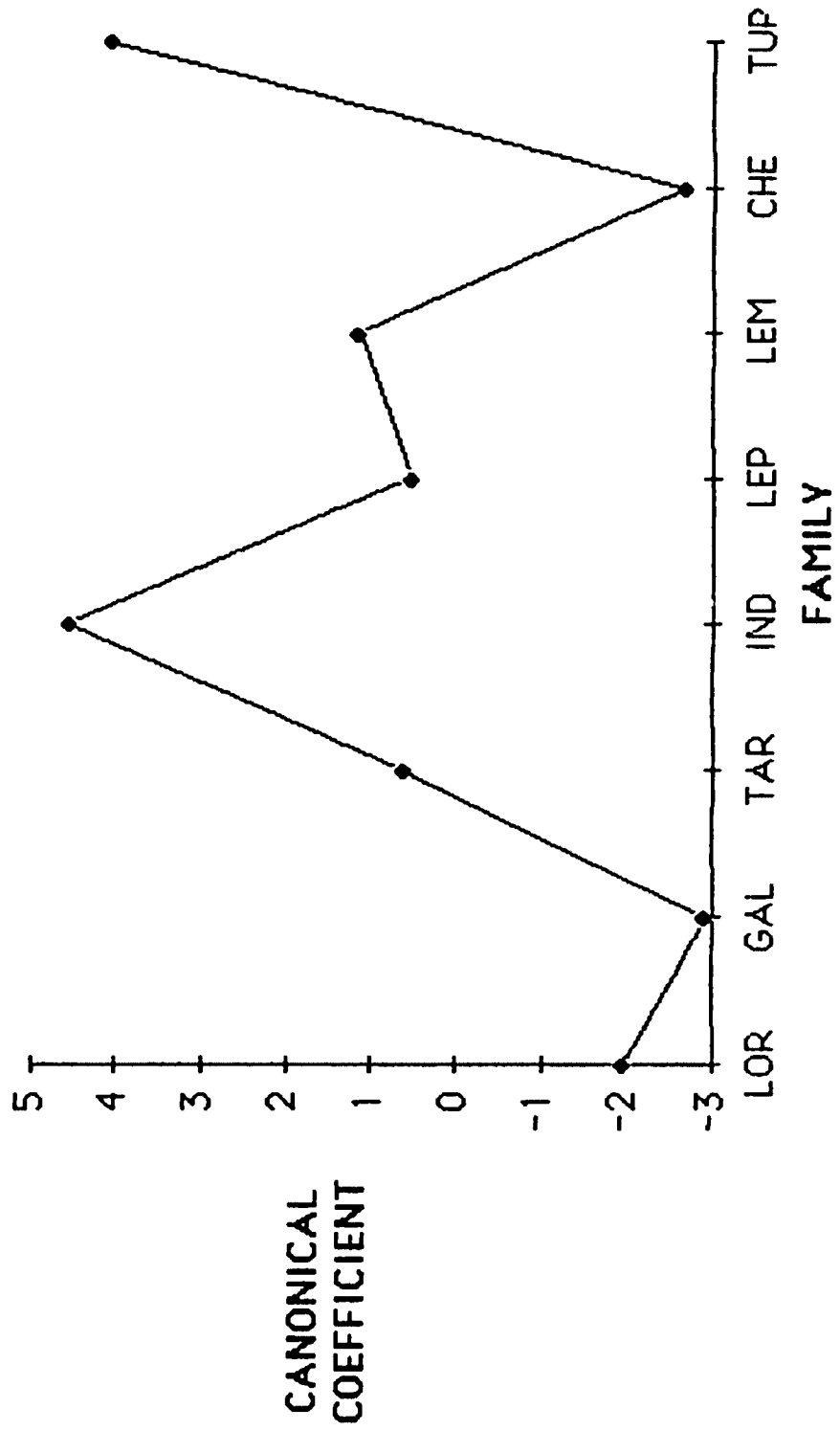


Appendix F. Femoral Discriminant Plots.

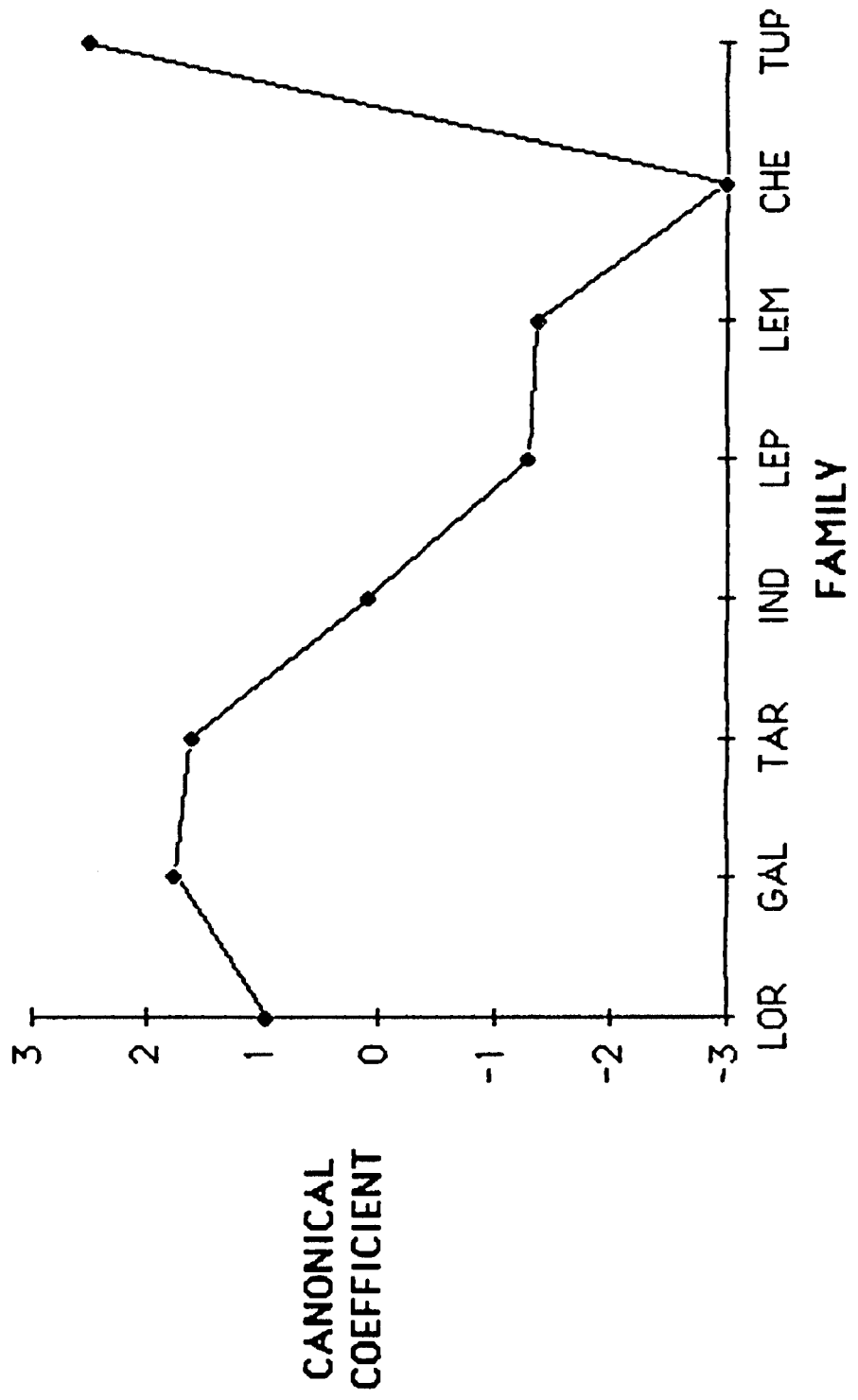
Plot 19. Discriminant Axis 1. Femoral Ratios.



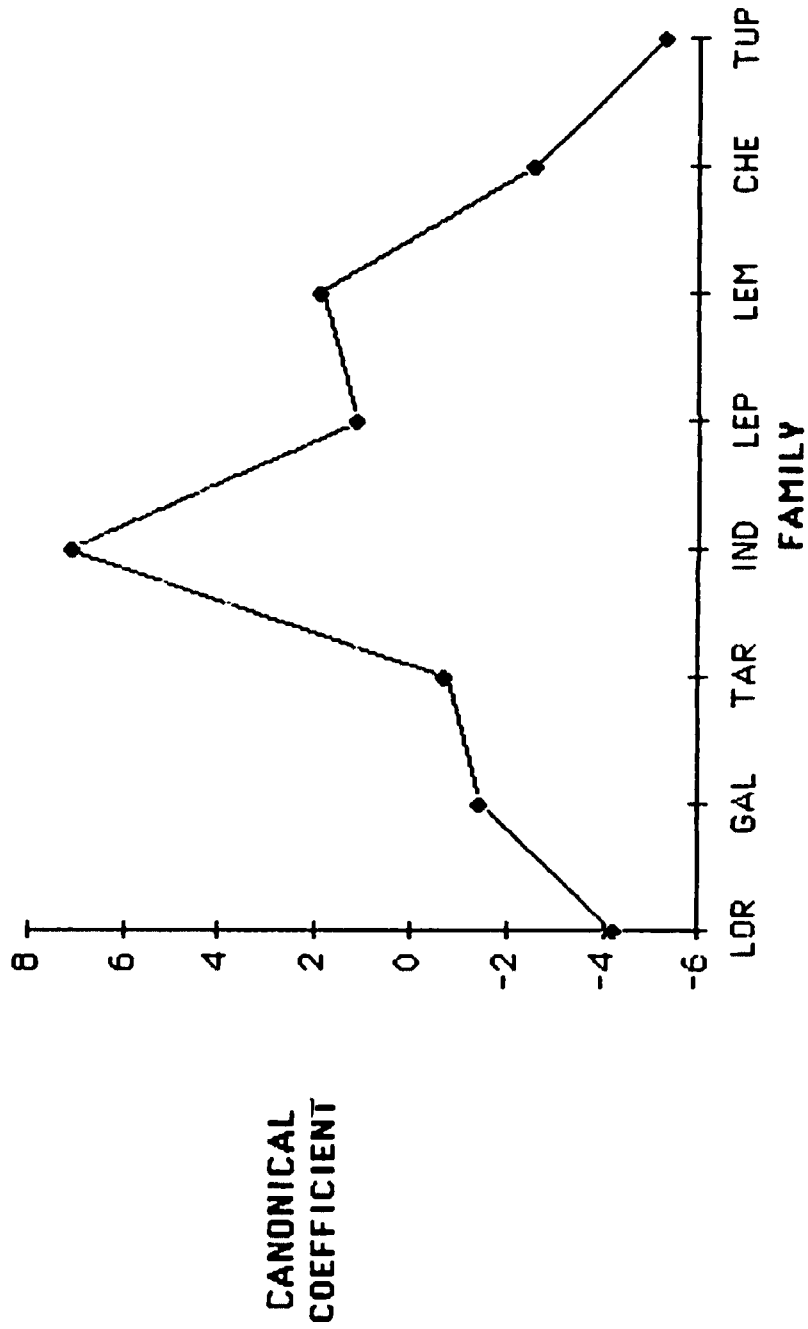
Plot 20. Discriminant Axis 2. Femoral Ratios.



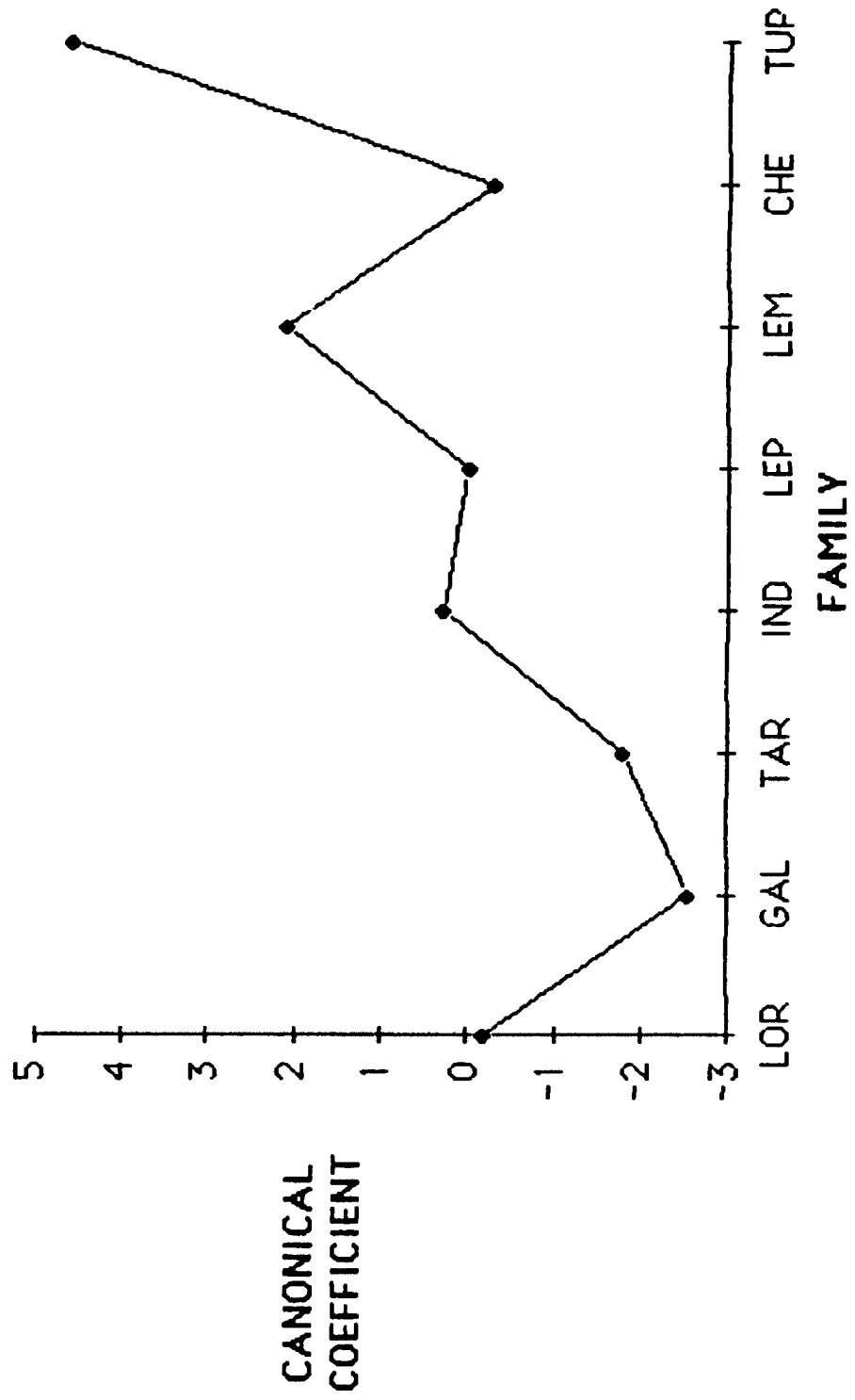
Plot 21. Discriminant Axis 3. Femoral Ratios.



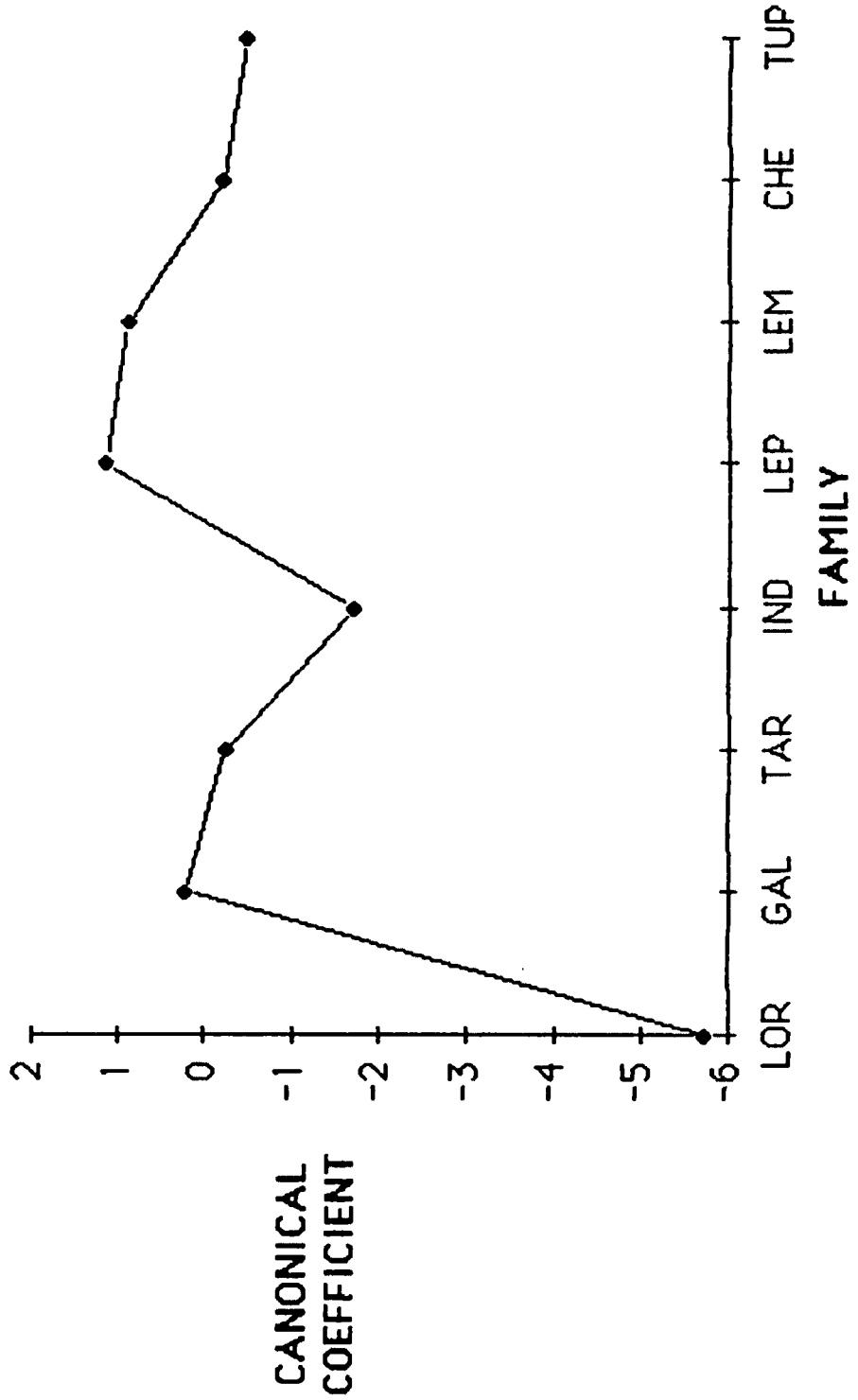
Plot 22. Discriminant Axis 1. Femoral Row Data.



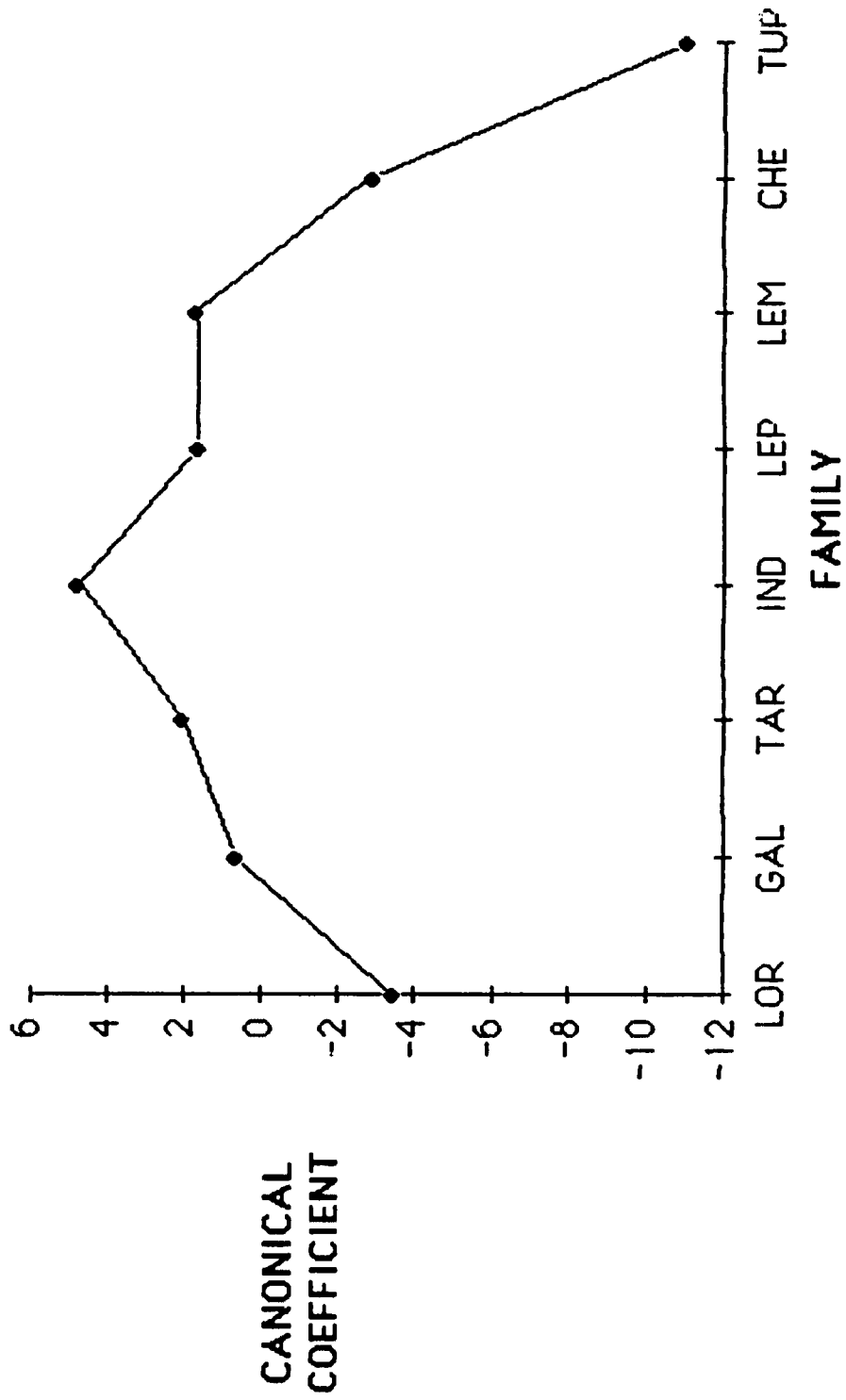
Plot 23. Discriminant Axis 2. Femoral Raw Data.



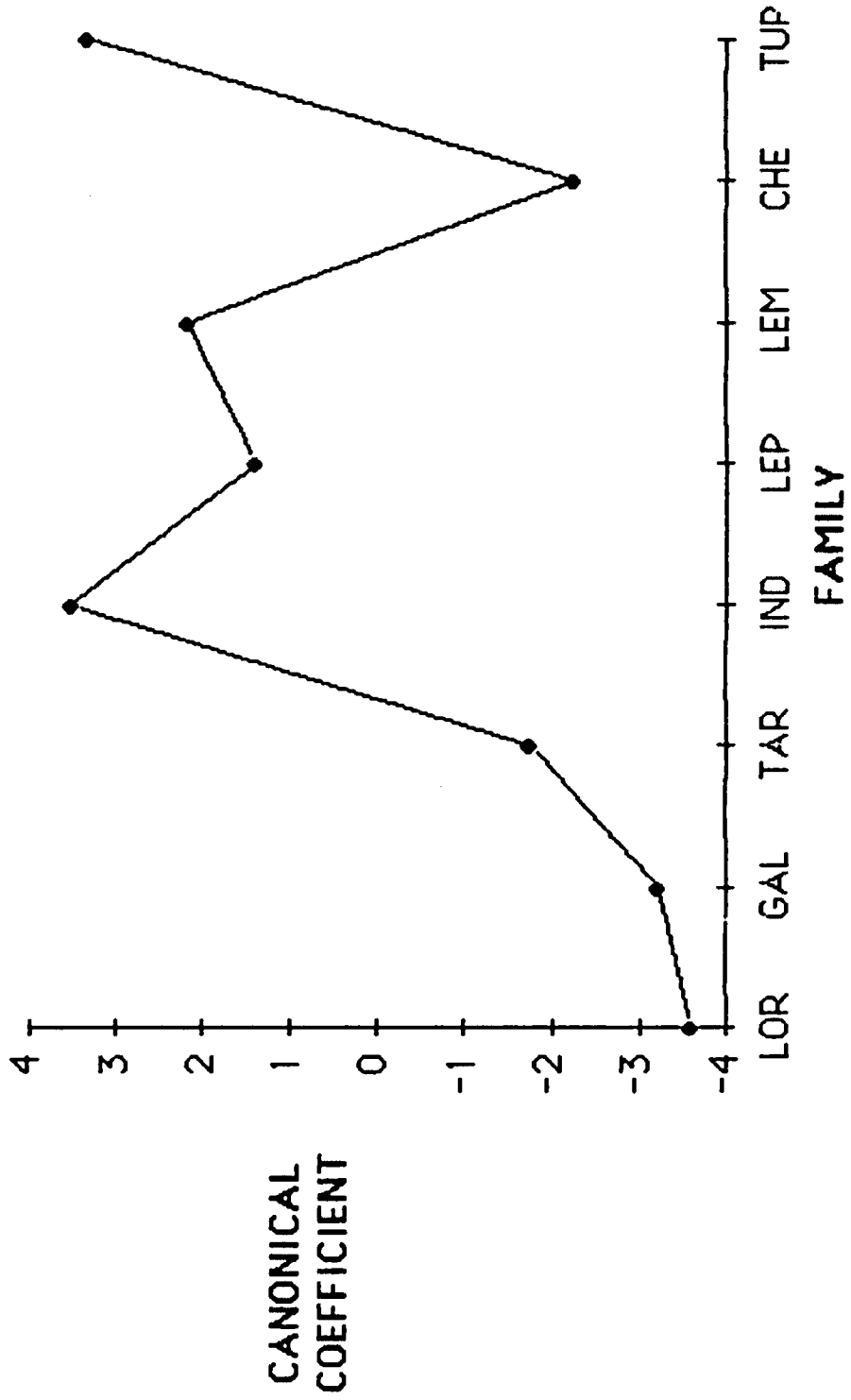
Plot 24. Discriminant Axis 3. Femoral Raw Data.



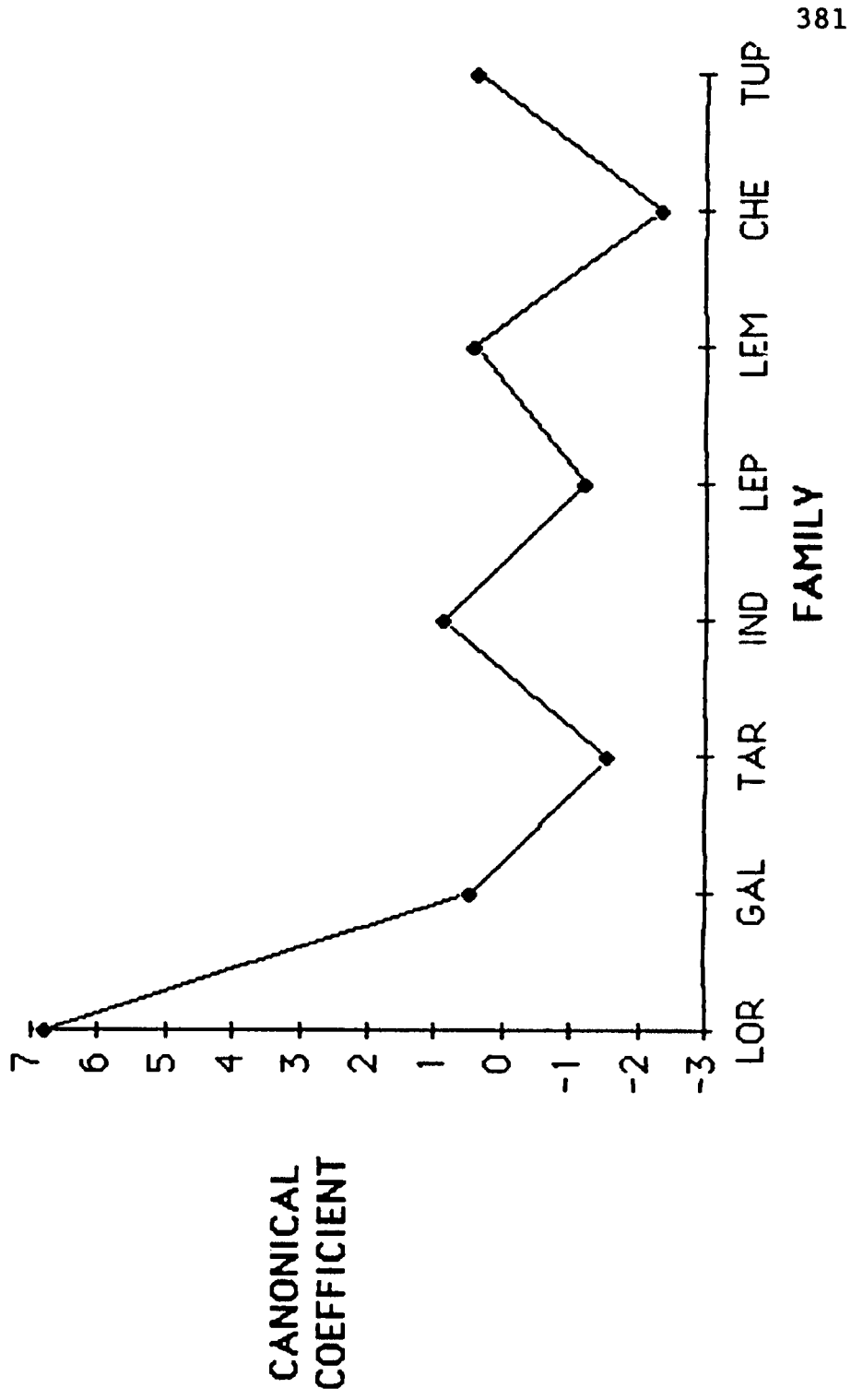
Plot 25. Discriminant Axis 1. Femoral Log Data.



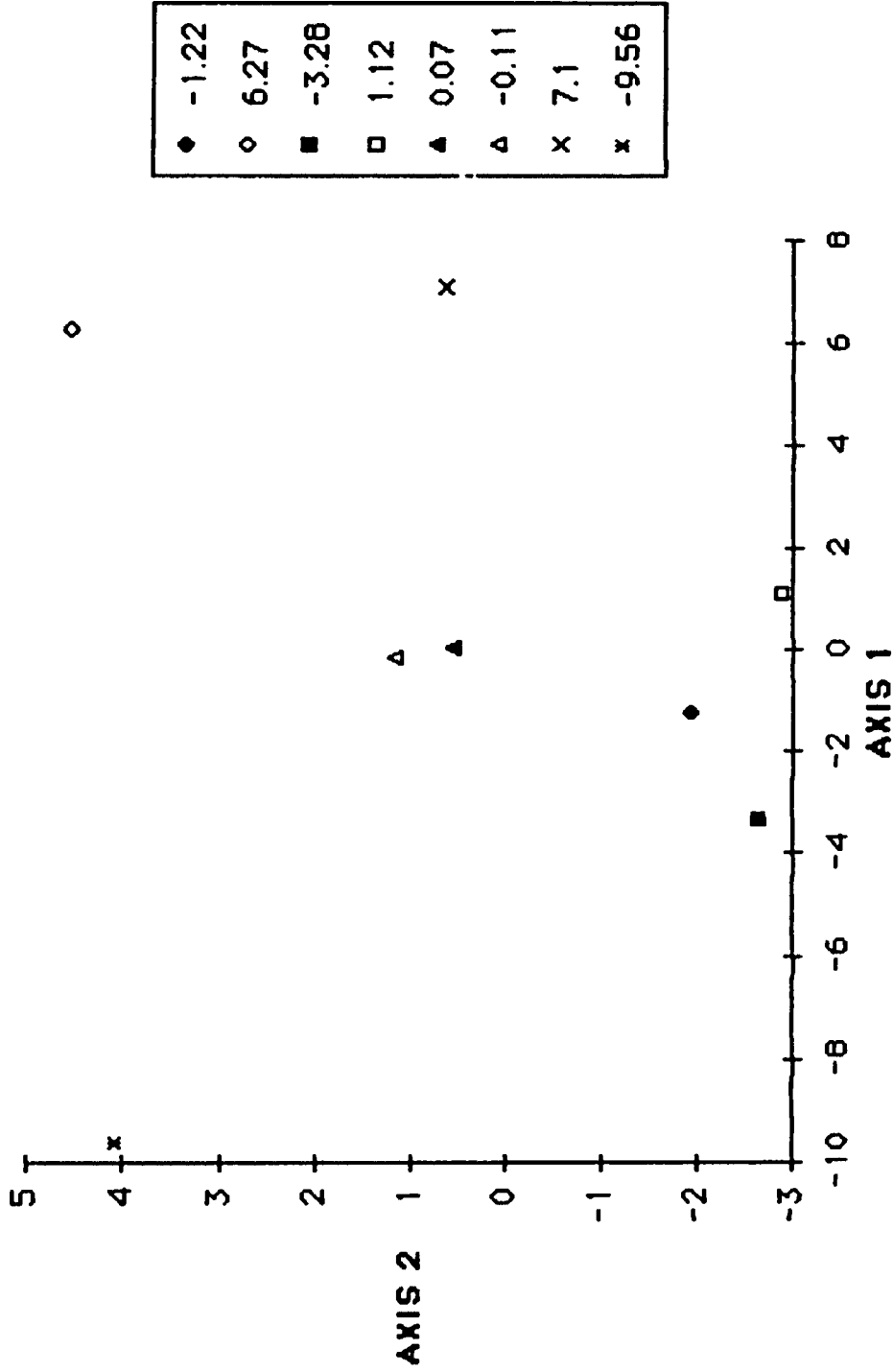
Plot 26. Discriminant Axis 2. Femoral Log Data.



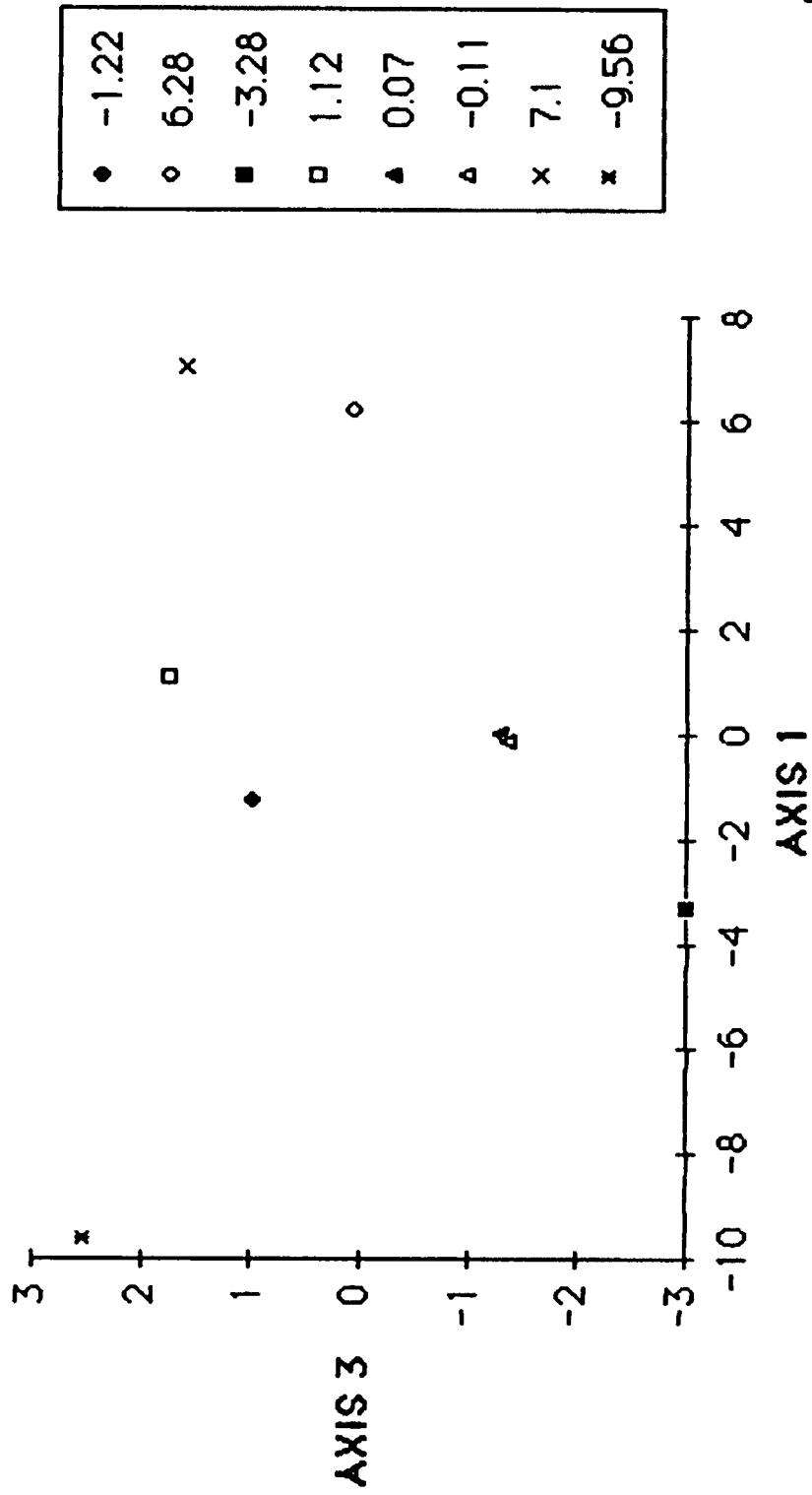
Plot 27. Discriminant Axis 3. Femoral Log Data.



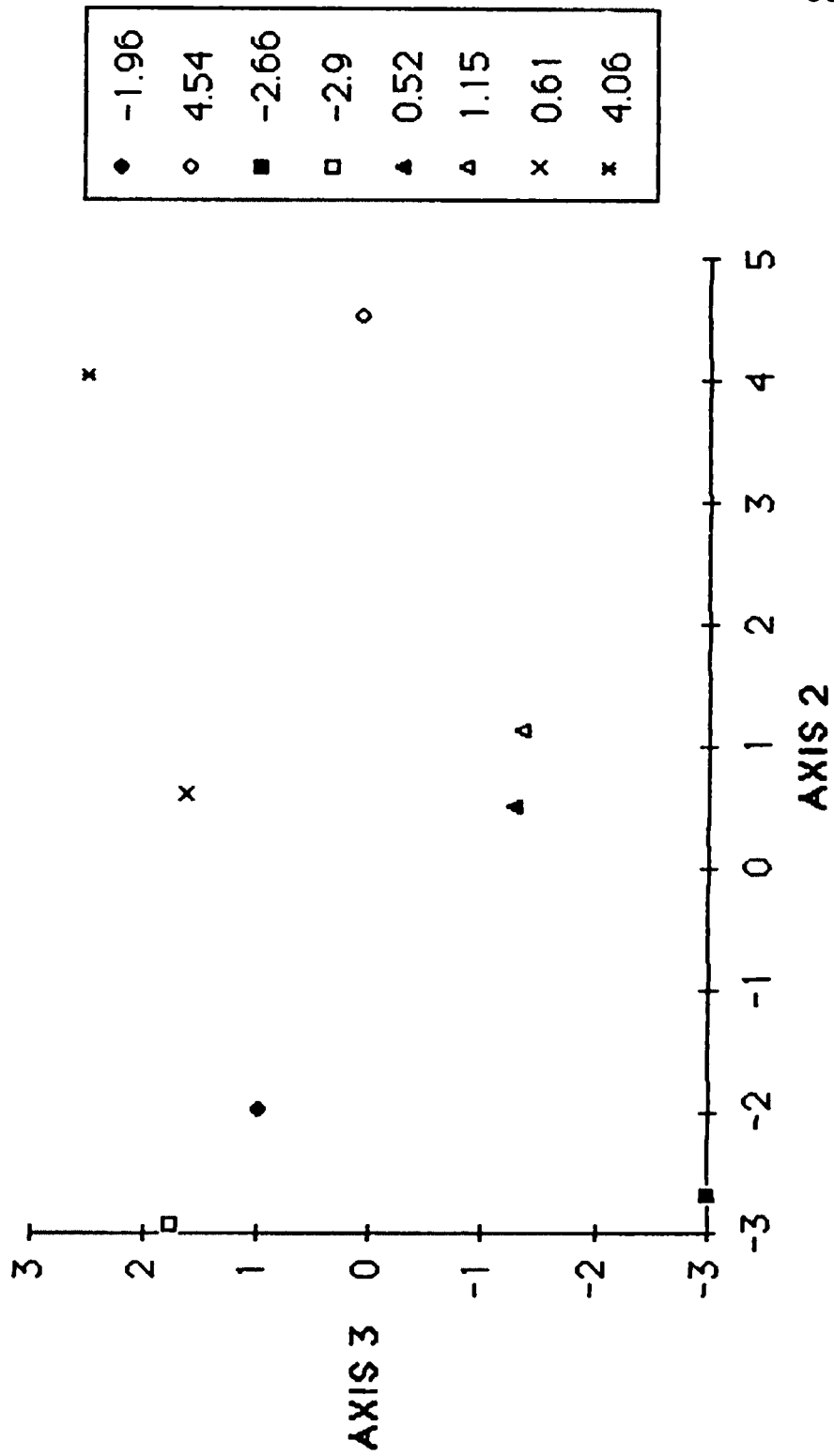
Plot 28. Discriminant Axes 1 and 2. Femoral Ratios.



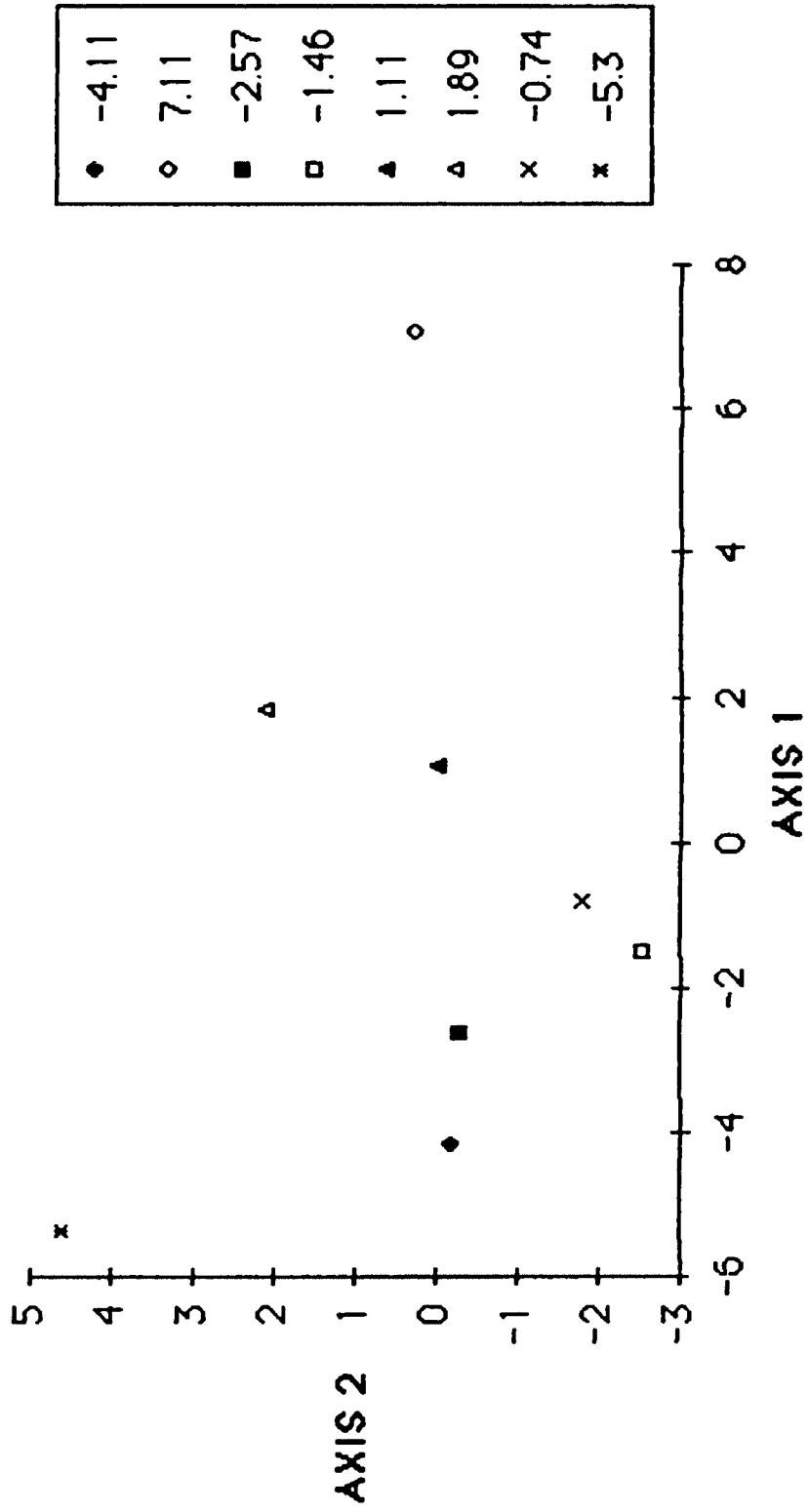
Plot 29. Discriminant Axes 1 and 3. Femoral Ratios.



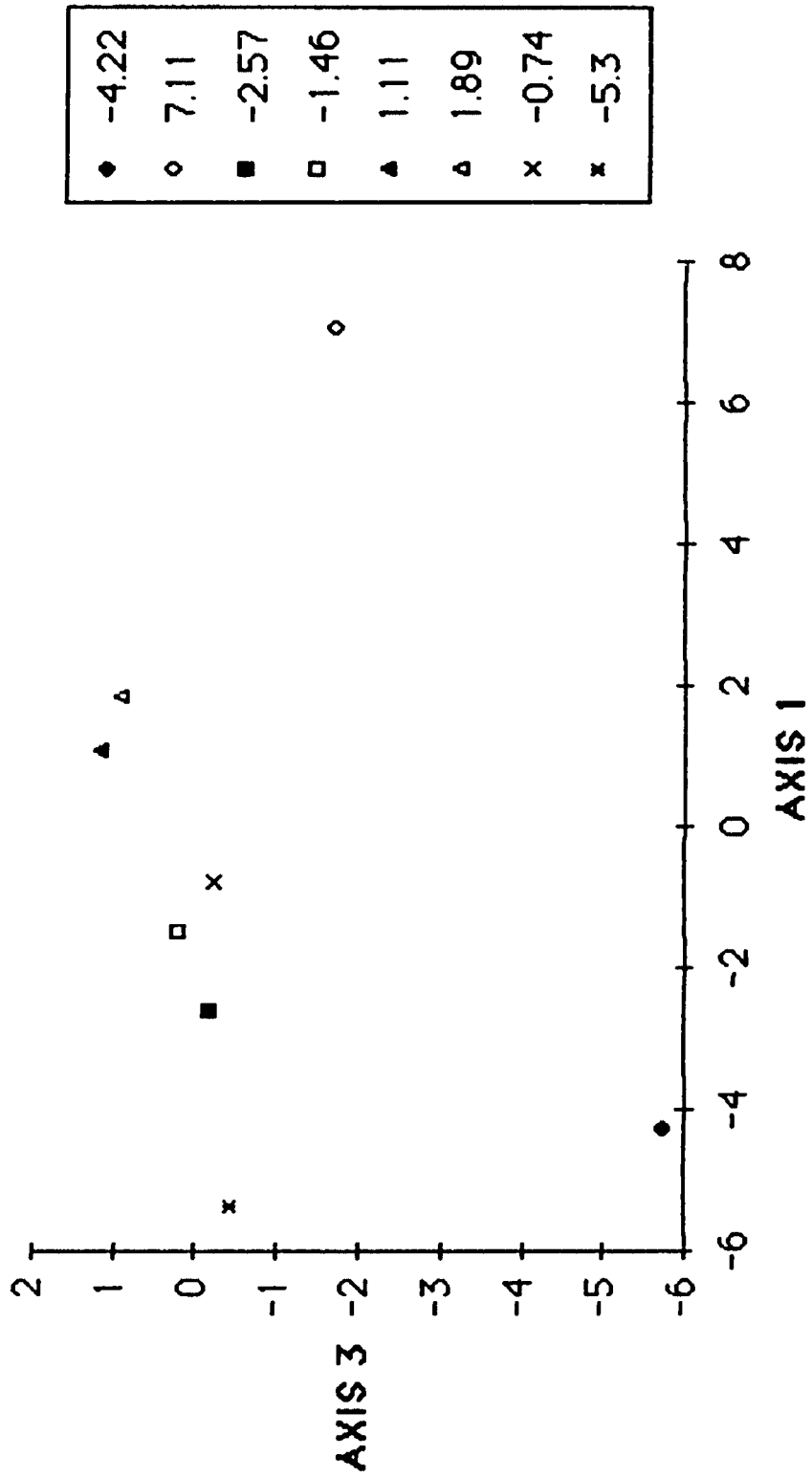
Plot 30. Discriminant Axes 2 and 3. Femoral Ratios.



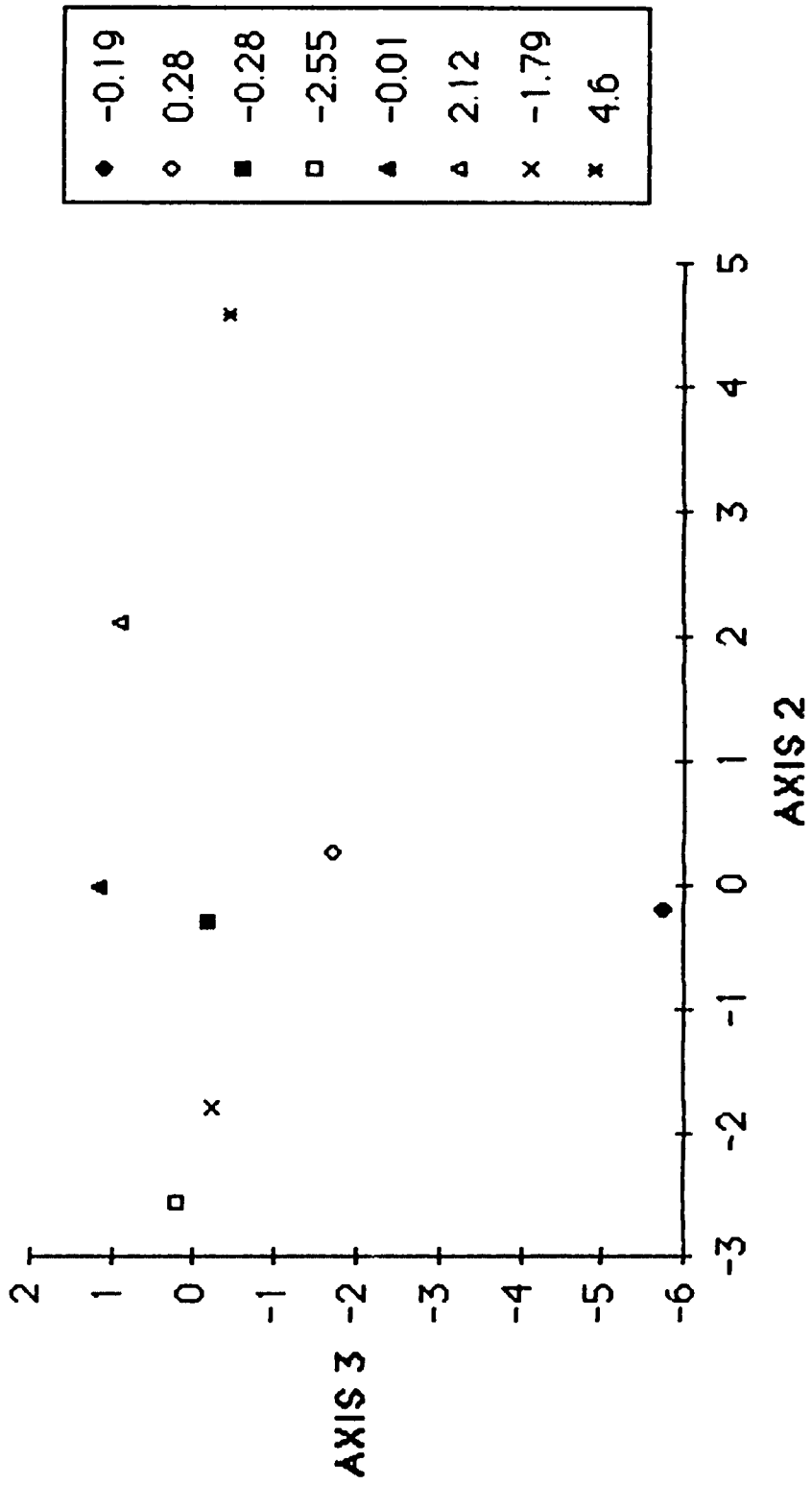
Plot 31. Discriminant Axes 1 and 2. Femoral Raw Data.



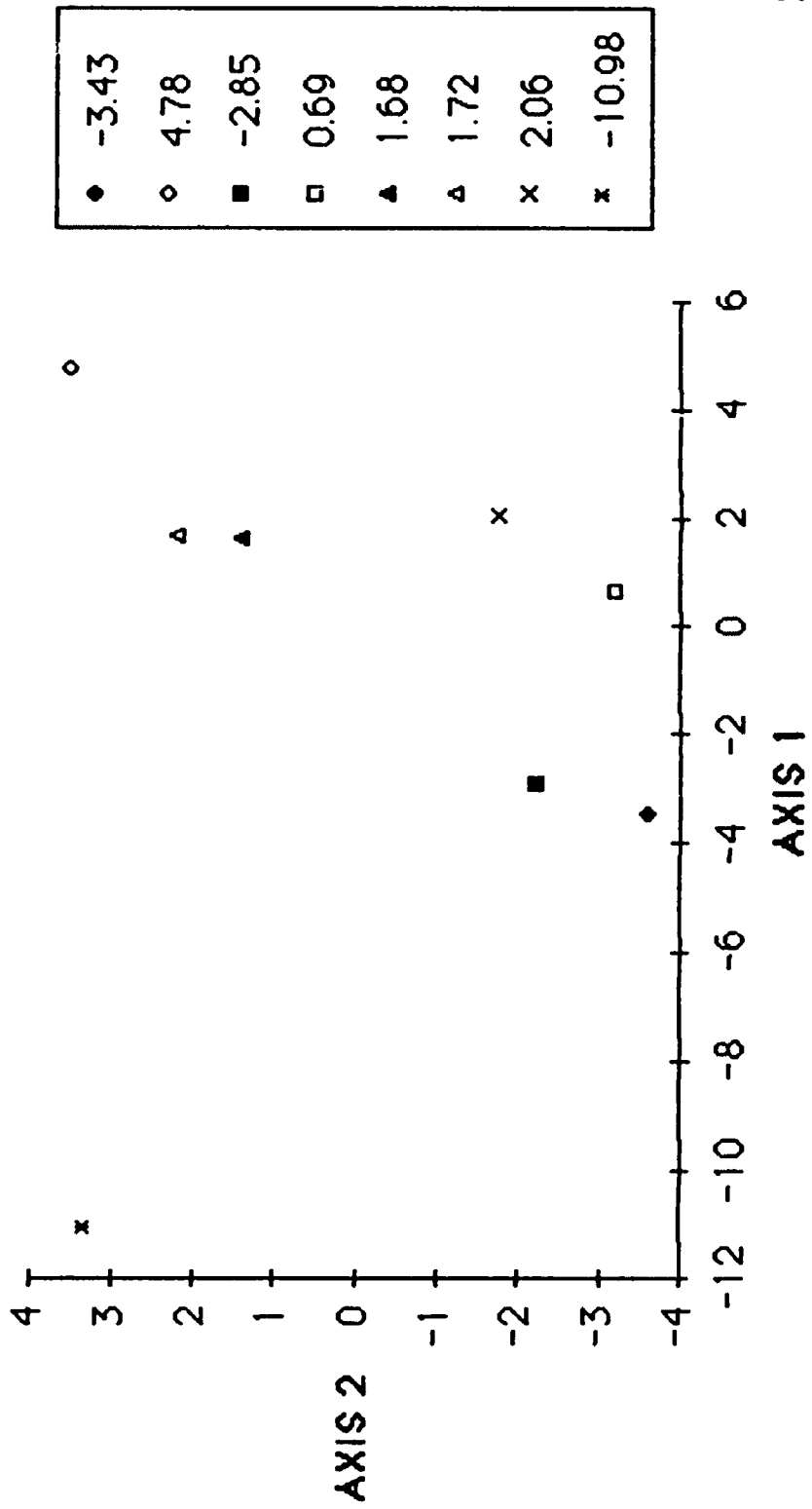
Plot 32. Discriminant Axes 1 and 3. Femoral Raw Data.



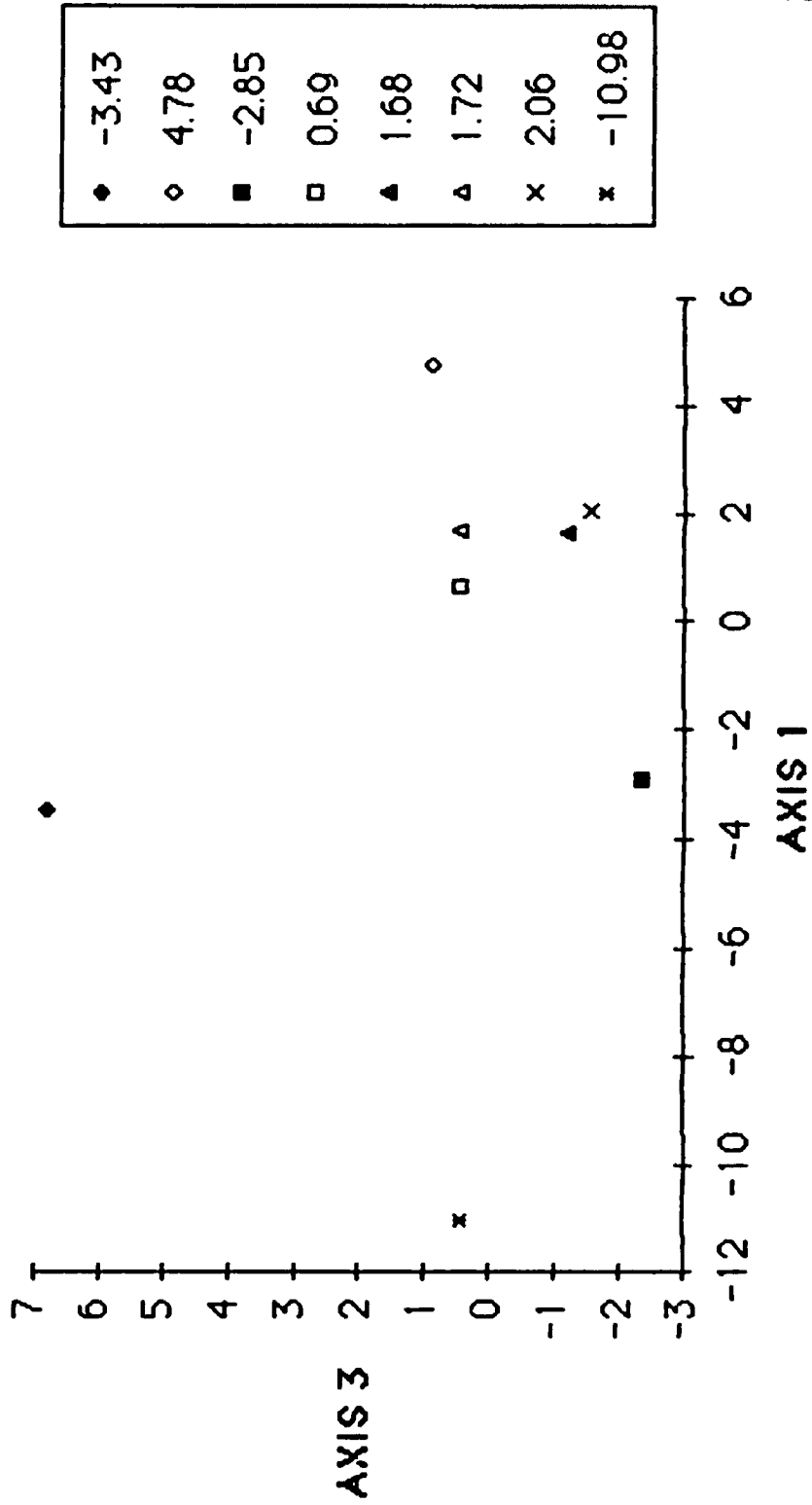
Plot 33. Discriminant Axes 2 and 3. Femoral Raw Data.



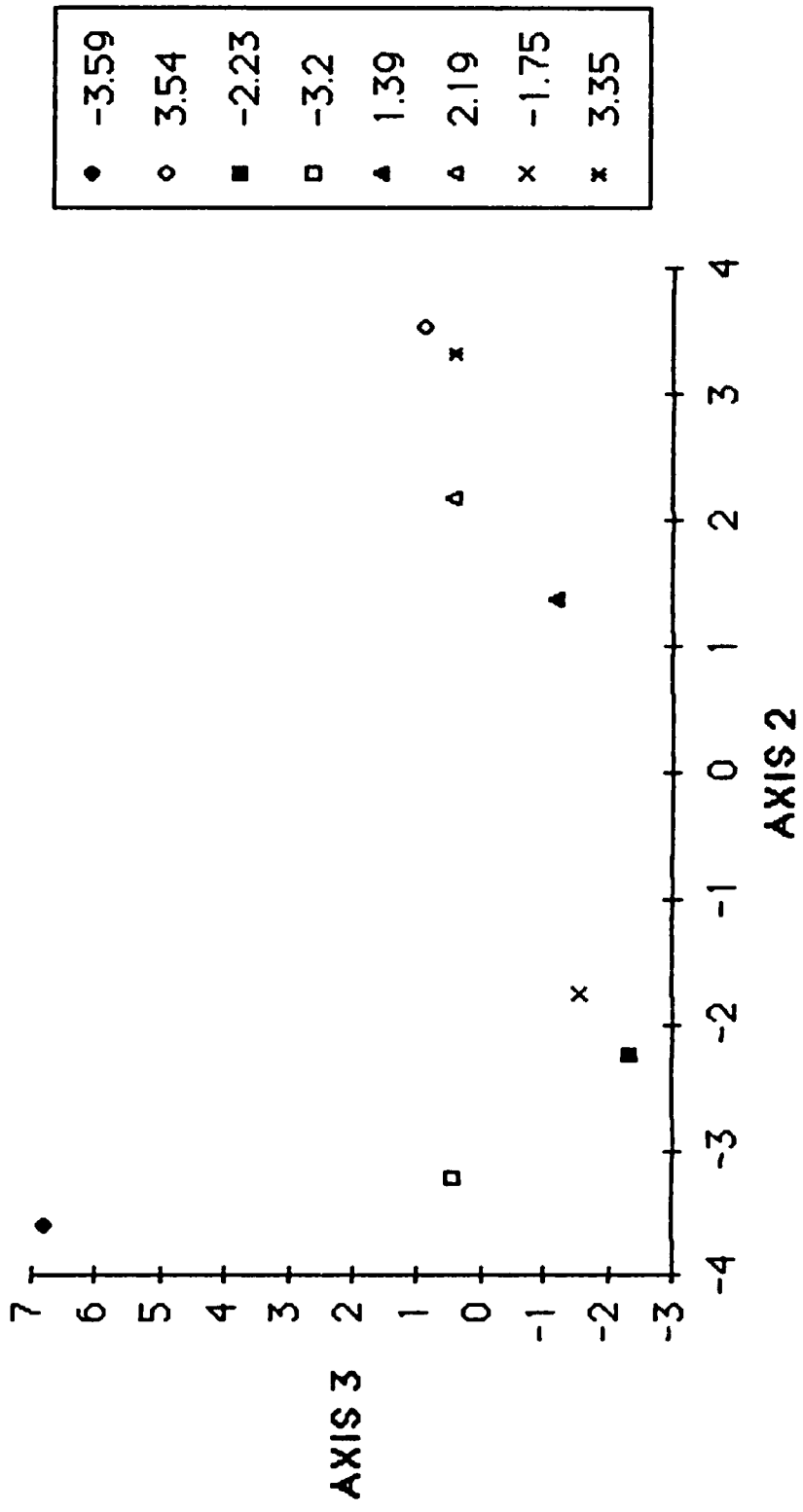
Plot 34. Discriminant Axes 1 and 2. Femoral Log Data.



Plot 35. Discriminant Axes 1 and 3. Femoral Log Data.



Plot 36. Discriminant Axes 2 and 3. Femoral Log Data.



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1982 "Functional analysis of the galago tarsus."
Amer. J. Phys. Anthrop., 57:167 (abstract).
1983 "The femur among prosimian primates." Am.
J. Phys. Anthrop., 60:170 (abstract).
1983 "Prosimian Anatomy", Review of "An Atlas
and Source Book of the Lesser Bushbaby,
Galago senegalensis" by J.L. Stevens, V.R.
Edgerton, D.E. Haines and D.M. Meyer. 1981,
CRC Press. Amer. J. Primatol., 4:193-194.