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FUNCTIONAL, ADAPTIVE, AND EVOLUTIONARY IMPLICATIONS

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THE JOINTS OF THE TARSUS IN THE STREPSIRHINE PRIMATES: FUNCTIONAL, ADAPTIVE, AND EVOLUTIONARY IMPLICATIONS

by

MARIAN DAGOSTO

A dissertation submitted to the Graduate Faculty in Anthropology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York.

1986

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Abstract

THE JOINTS OF THE TARSUS IN THE STREPSIRHINE PRIMATES: FUNCTIONAL, ADAPTIVE, AND EVOLUTIONARY IMPLICATIONS

by

Marian Dagosto

Adviser: Professor Frederick S. Szalay

The purpose of this project is to analyze the functional, adaptive, and phylogenetic aspects of the tarsal joints in extant and extinct strepsirhine primates. Joint surfaces are described in linear dimensions, aspects of curvature, orientation, their placement in the MacConaill joint classification system, and other nonmetrical aspects of form. Functional attributes of joints are analyzed based on these components of form.

Form-function complexes of joints are related to particular aspects of positional behavior by comparing the distribution of such traits with the distribution of differences in presence or frequency of positional behaviors. However suggestive these lines of evidence may be, the hypothesis of a relationship between a morphological feature and an aspect of positional behavior is considered weak unless the functions deriving from the form of the feature allow the organism to fulfill the selective demands of the behavior. Causal arguments are the only valid tests of these kinds of hypotheses.

Not unexpectedly, leaping, climbing, and grasping have the most impact on the form of the tarsus. Leaping and climbing exert opposing selective forces leading to antithetical morphological adaptations.

Since both behaviors are performed by almost all strepsirhines, some interesting compromises exist, especially in indriines and galagines.

The notharctine primates are most similar to the extant lemurids in tarsal morphology and presumed locomotor behavior, but adapins are best reconstructed as quadrupedal climbers. The tarsals of the subfossil *Varecia insignis* and archaeolemurines evidence some committment to terrestriality. *Megaladapis*, however, was predominantly arboreal.

A phylogenetic analysis of the tarsus corroborates accepted phylogenetic hypotheses of primate and strepsirhine relationships. Two synapomorphies unite Adapiformes and Lemuriformes into a monophyletic Strepsirhini. Extant Lemuriformes form two natural groups. The Lemuroidea (Lemuridae and Indriidae) are united by pedal features related to large body size and increased use of vertical supports. The Lorisoidea (Cheirogaleidae and Lorisidae) are the more primitive group postcranially and are not defined by any derived pedal features. Within this group, some cheirogaleids share extensive pedal synapomorphies with the Galaginae. *Daubentonia* has a very primitive tarsus suggesting an early split between it and other Lemuriformes.

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CHAPTER I: INTRODUCTION

I. Description and aims of the study. The postcranial skeleton, like any other aspect of an organism, can be studied from many perspectives. On one hand, a knowledge of the osseous and muscular anatomy of an animal in conjunction with the study of its locomotor behavior allows us to develop hypotheses concerning the causal and historical relationships among structure, function, and behavior. These relationships, in living species, if well established, form the necessary framework for the reconstruction of the behavior of extinct species for which we may know morphology, but can never observe behavior. On the other hand, postcranial features provide an extensive amount of data which can be used to test hypotheses of phylogenetic relationships that have traditionally been based on characters of the dentition and skull. Although these two approaches, the functional and the phylogenetic, have often been investigated independently, they need not be pursued as if they had mutually exclusive goals. Functional information is often useful in elucidating the polarity of character states in a morphocline (Szalay, 1981b, 1984), and the recognition of derived character states in a group, no matter what bodily system they may be from, immediately brings up the question of the adaptational significance of those characters. Many have successfully combined the functional and phylogenetic approaches (Schaeffer, 1947; Robinette and Stains, 1970; Maglio, 1972; Szalay, 1977b, 1980; Szalay and Decker, 1974; Szalay et al., 1975; Lewis, 1980c).

Most studies of primate postcranial morphology have been functionally oriented and little emphasis has been placed on the taxonomic value of the postcranial features studied. In fact, it has sometimes been claimed that features of the postcranium in particular can have little taxonomic significance because functional demands on morphology will often overshadow any phylogenetic input, a curious distinction between tooth and bone. At various taxonomic levels, numerous postcranial features, in most orders of mammals, and particularly in the primates, have been recognized as synapomorphies, e.g. the elongated calcaneus and navicular of the Galaginae, the prehensile tail of the Atelini, and the shoulder-thorax complex of the Hominidae (sensu Szalay and Delson, 1979), but there have been very few systematic studies of any musculo-skeletal region directed towards generating primarily phylogenetic rather than functional groupings. That such studies are likely to be useful and enlightening is demonstrated by the success of Mivart's (1867) overview of the primate postcranium; the work of Szalay (1977b, 1980), Szalay and Dagosto (1980), Szalay and Drawhorn (1980), and Novacek (1980) which used postcranial morphology to test and develop hypotheses of therian relationships, and Ford's (1980) use of postcranial characters to investigate platyrrhine relationships.

This project aims to provide a systematic assessment of mechanical, adaptive, and phylogenetic aspects of the morphology of the articular surfaces of the tarsal bones in the strepsirhine primates. To this end the variation in the shapes and orientations of the articular surfaces are delineated and defined, the mechanical implications of these features are analyzed, the relationship between structural features and observed differences in positional behavior is examined, and the importance of the distribution of features for elucidating phylogenetic relationships is investigated. On the basis of the relationships between patterns of tarsal morphology and patterns of positional behavior in living strepsirhines, hypotheses are developed concerning the probable positional behavior of extinct strepsirhines. Thus, an overview of the evolution of tarsal structure in the Strepsirhini is generated.

The tarsus is investigated for several reasons. It is likely that the foot responds primarily to the demands of the characteristics of the substrates habitually used by the animal, and the mechanical requirements of its positional behavior, thus it reflects these demands perhaps more faithfully than any other part of the skeleton. The tarsal bones comprise a complex functional unit with many features available for analysis and interpretation. Tarsal bones are associated with many extinct strepsirhines so that the results of this study, based primarily on living forms, can easily be extended to include analysis of the fossil groups.

II. Theoretical issues. There have been surprisingly few comprehensive attempts to analyze the evolution of overall positional behavior, or of specific morphological areas of the postcranium in primates. Those that have been made (e.g. Mivart, 1867; Gregory, 1920; Morton, 1924; Napier, 1967; Simons, 1967; Lewis, 1980c) may suffer from several problems, especially 1) lack of theoretically sound hypotheses relating morphology and behavior; 2) lack of information on fossil primates; and 3) unsound phylogenetic analyses. Each of these problems is discussed in detail below.

The lack of theoretically sound hypotheses relating morphology and behavior. Several factors are at work here, the most serious being the lack of detailed studies of locomotor behavior in free ranging animals, and theoretical problems in relating morphology to behavior. In any study such as this one in which an attempt is made to relate morphology and behavior, the quality of both the morphological and behavioral data is critical. The specificity of the conclusions reached is limited by the specificity of the data sets. In other words, solid morphological-behavioral hypotheses cannot be generated or tested if behavior or morphology are only described in vague general ways. Morphological features examined should be chosen to reflect functionally important variables. In many cases, however, the operational problems in obtaining such data are tremendous (e.g. the axis of joint rotation), and such variables are ignored or estimated. In terms of locomotor behavior, animals are often placed in broadly defined locomotor categories without detailing the different kinds of postures and locomotions used, their rates and durations of use, and the contexts in which they occur.

This study is of course greatly constrained by the lack of such data. For example, a major hindrance to interpreting aspects of distal foot morphology is the absolute dearth of any information concerning grasping postures or support size choice in strepsirhines. In fact, aside from the work of Charles-Dominique (1977) on East African lorisids and Tattersall (1977) on *Lemur fulvus*, there has not been a single field study of locomotion in a strepsirhine primate which gives detailed information on general aspects of locomotion such as frequencies of different locomotor behaviors, support size, and support orientation. Gebo (1986) has collected some such information on prosimians at the Duke Primate Research Center and has generously made these data available to me. These data have the disadvantage of being collected under somewhat artificial conditions, but have the great advantages of 1) being based on a large number of observations, and 2) having been collected by a single researcher, which greatly facilitates interspecific comparisons. Dykyj (1980) has published similar information for *Nycticebus coucang*. In addition to these studies, general accounts of strepsirhine locomotor behavior are given in Walker (1974, 1979) and Petter *et al*. (1977).

Although strepsirhine primates may be conveniently grouped as arboreal quadrupeds, vertical clingers and leapers, or slow climbers (Napier and Napier, 1967), it is apparent that all prosimians use a wide range of locomotor and postural behaviors (Stern and Oxnard, 1973; Walker, 1974; Petter, *et al*., 1977; Gebo, 1986). Within each broad locomotor category there may be great differences in the actual frequency with which various behaviors are performed, and the relative importance of "secondary" locomotor behaviors (Stern and Oxnard, 1973; Mittermeier and Fleagle, 1976). For instance, both *Lemur fulvus* and

Cheirogaleus major may be classed as arboreal quadrupeds, but *L. fulvus* leaps considerably more than *C. major*. Small differences in substrate use or the compromising demands of other aspects of behavior or ecology among animals classed in the same locomotor group can produce very different locomotor or postural repertoires and ultimately, distinct morphological differences (Stern and Oxnard, 1973). This has been demonstrated in species of galagines and lorisines (Charles-Dominique, 1977), in lemurs (Ward and Sussman, 1979) in *Tarsius* (Niemitz, 1979), in *Macaca* (Rodman, 1979) and in *Presbytis* (Fleagle, 1977 a,b).

Considering these problems, this study will not concentrate on the rather sterile exercise of trying to identify features which are correlated with locomotor groups. Rather, the relationship between morphology and more specific aspects of positional behavior (leaping, climbing, vertical clinging) is assessed. These components of postural behavior have more clearly defined consequences for morphology which must be understood before more general relationships can be examined.

This is not to say that such descriptive categories of locomotor behavior are useless. A parallel can be drawn between the descriptive locomotor categories of Napier and Napier (1967) or Szalay and Dagosto (1980) and descriptive dietary categories. No one would argue that calling two primates "insectivores" implies that they both eat only insects, or that they both eat the same kind of insects, or that both have identical dentitions. Nor would anyone argue that because two animals classed as insectivores have different secondary dietary preferences, or eat totally different kinds of insects, or have vastly different dentitions, that the descriptive term "insectivore" is useless. Vertical clinging and leaping is a perfectly apt description of the positional behavior of *Indri*, *G. senegalensis*, and *Tarsius*, despite the fact that each taxon differs in its morphological solution to the mechanical demands of this behavior. Indeed, the demands themselves may be quite different given the different phylogenetic "starting points" from which each taxon adopted the behavior. Finding that there are no morphological features which are exclusively shared by all vertical clingers and leapers does not negate the value of the term in describing the positional behavior of an animal.

The nature of the relationship between morphology and behavior is extremely complex as it involves a multiplicity of factors. These include the potentially conflicting demands of all behaviors affecting a particular region of the body; the phylogenetic history of the animal, which may furnish a starting point morphology that constrains the paths adaptation to a particular behavior may take; the fact that multiple morphological solutions to particular problems are often available; and the effects of body size, which may limit available avenues of morphological change.

This complexity of factors is in part the reason for the failure to find morphological features exclusively shared by all members of particular locomotor groups, as discussed above. Previous attempts to do this have often assumed that all or many of the postcranial features of a species have been molded only by presently experienced demands and have ignored the influence of the factors listed above (Szalay, 1981a). Thus, these studies searched for similar morphological solutions to presumed similar problems posed by the behavior, ignoring the fact that different morphologies may be able to solve the same problem (paradaptations, see Bock 1977), or that the problems may not even be the same, even though the behavior is. This is the reason why exceptions to correlations between morphology and behavior do not always negate the applicability of general "rules".

Two main methods exist for ascertaining the correspondance between morphology and behavior and the related problem of using these correlations to infer, from their morphology, the behavior of extinct animals, or animals where behavior is unknown. These methods (or lines of reasoning) are direct analysis and the comparative method (Bock, 1977). Studies of primates have generally relied most heavily on the comparative method (but see Fleagle, 1979 and Preuschoft, *et al.* 1979 for discussions of direct approaches), using analogies to reconstruct probable behavior from morphology. Kay and Cartmill (1977) and Szalay (1981a) have discussed in detail the logic of analogy arguments, although they disagree on the criteria for constructing the best analogy.

There are, however, problems with the comparative method (Bock, 1977). On a basic level, there are problems with identifying relevant variables. Bock and von Wahlert (1965) have attempted to remedy this situation by carefully defining terms referring to aspects of the organism and environment relevant to such analyses. The Bock and von Wahlert framework can be summarized as follows: A feature is defined as any trait or character of an organism, be it morphological, behavioral, or biochemical. Each feature has two aspects to it: its form (shape, configuration, appearance) and its function, which is the physical, mechanical, or chemical property(ies) which necessarily follow from the form. A single feature may have several functions associated with it. The combination of a form and a function of a feature is called a faculty. If a feature has several functions, then it also has several faculties. The faculty, and not simply the form alone, is what is subject to natural selection. If a feature has many faculties its form may have to be a compromise, due to the conflicting selective demands on it.

A single feature can have many faculties, but not all of them may be utilized by the organism. The actual activity(ies) performed by the animal in its natural environment, with the feature is called the biological role(s) of that feature. In the Bock and von Wahlert model there is a critical distinction between the concepts of function and biological role. While function may be assessed by laboratory experimentation or theoretically deduced from the laws of physics or chemistry, biological role can only be determined by field observations. Biological role "...cannot be predicted with any certainty from the study of the form and function of the feature..." (Bock and von Wahlert, 1965:278); "these two aspects of the feature have a definite relationship to one another, but they are not equivalent or interchangeable..." (Bock and von Wahlert, 1965:279).

Comparative method arguments are usually variants of analogy by enumeration taking the form: All *observed* As are Bs, therefore *all* As are Bs. Animal X is (has) A, therefore it also is (has) B. For example: All observed vertical clingers and leapers have an intermembral index lower than 67. *Notharctus* has an intermembral index lower than 67. Therefore, *Notharctus* was a vertical clinger and leaper (Napier and Walker, 1967). Obviously, these arguments are purely inductive and the conclusion cannot be logically derived from the premises (i.e. it is not deducible from them). This would only be valid if there were a covering law of uniformity of the relationship between morphology and behavior; Bock (1977) has shown the fallacy of such an assumption.

Even if one were willing to accept inductive inference as valid[1], any exceptions to the general rule "All As are Bs" could easily be explained away by resorting to the kinds of *ad hoc* hypotheses listed above (different phylogeny, body size, paradaptation). In many cases these additional hypotheses are perfectly valid; but they are so pervasive that it is almost always possible to rescue a favored hypothesis from apparent falsification by invoking them. Another drawback of the analogy method is that such arguments are useless for elucidating the biological roles of animals with unique morphology.

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[1] W. Salmon (1967) discusses in general, and Binford (1967), M. Salmon (1975, 1976), and Smith (1977) with particular reference to historical reconstruction in archaeology, a discipline with many of the same problems of inference as historical biology, the issue of choice between competing unfalsified hypotheses.

Most authors have recognized these problems of using analogy by enumeration and have suggested ways to improve our confidence in the inductive inference in the confirmation of hypotheses, or in the validity of the inference. One such criterion is the comprehensivity of the analogy. If the original conclusion is based on one feature, will the same biological role hypothesis account for other features of the organism which are related to this biological role? The specificity of the analogy is increased if all known As are Bs and all known Bs are As. I.e. all organisms with the biological role have the trait, and all organisms with the trait have the biological role.

In the special case of studying organisms with unique phylogenetic histories, confidence in our assessment of biological role is enhanced if we rely more on recently acquired derived features of an organism than a general assessment of its total morphology (Szalay, 1981a).

An analogy will be more likely to be successful if: "the initial resemblances are such that the inferred property would account for the resemblances" (Binford 1967:2, paraphrasing Stebbing, 1961); "All the features specified in the definition of T (traits) have some functional relationship to F (function)" (Kay and Cartmill, 1977:21); it is based on "two or more morphologically and functionally convergent derived features which are causally explicable and exclusively correlated with the same biological roles.." (Szalay, 1981:167). All of these statements invoke a causality criterion. Even if there were a 100% perfect correlation between a feature and a biological role, the argument should be recognized as weak if there is no causal, i.e. "functional" relationship between the feature and the biological role. The correlation may well be spurious. We must discover the mechanisms underlying the association, which allow us to say "All observed As are Bs because A (or some aspect of A) necessitates B. Therefore all As must be Bs.

This important criterion changes an inductive analogic argument into a deductive inference. If causal relationships are known, there is in fact no need to make an analogy at all (Hesse, 1966). The inference may be made independently of the observation of co-occurrence. For example, one could make an analogy between the earth and the moon. The earth has an atmosphere and it has life. The moon has no atmosphere, therefore it has no life. Although the conclusion is correct, the analogy is not needed. A much stronger causal argument could be constructed from a knowledge of the universal laws of nature dealing with the necessary conditions for life and the properties of the moon. The properties of earth are irrelevant to this argument. Thus, causality arguments do not belong to the comparative method, but are part of direct analysis.

Direct analysis involves studying the properties of form and function of the feature, identifying the biologial role from study of the organism in its natural environment, and identifying the selective forces on the organism arising from that biological role. The degree of goodness of fit between the feature and the biological role is judged by a criterion of energy efficiency (Bock and von Wahlert, 1965).

Although direct analysis does not suffer from the logical problems of the comparative method, there are some operational problems. This method requires detailed observations of animals in their natural environment. For this study, as noted above, the available data are sparse. How are features and biological roles to be defined? Can we consider an entire mode of locomotion as a biological role, or should we confine our analysis to more specific aspects of it? At what level are features related to biological roles? Can something be a biological role at one level of analysis, but a feature in another? For example, we can obviously relate specific features of the postcranium to a mode of locomotion, but can we take the mode of locomotion as a feature, and relate it to other aspects of the animal's ecology, such as resource distribution and availability, forest structure, etc. These are also relationships which we want to understand. How does one determine function from form? How do we know when we have identified all the relevant functions? How does one determine selective forces? In some cases the answers to these problems are simple--models are available [e.g. Cartmill's (1974) model of forces acting on a vertically clinging clawless mammal, or MacConaill's (1973) derivation of joint function from form] or laws of chemistry or physics will apply. But in other cases the derivation of forces or functions is not so obvious.

The criterion of goodness of fit between a feature and a biological role is also operationally problematic. How well does the faculty have to match the selective force before we accept the relationship? How badly does the mismatch have to be before we reject the relationship? This is not a critical problem in extant species where we can observe the animal, and thus see whether or not the feature is used in the performance of a particular biological role. If we know by observation that it is used, even if the fit is not good, the relationship must be accepted. If it is not used, then no matter how good the fit, the relationship must be rejected. There are problems, however, in defining criteria for use in the analysis of fossils. It is difficult to see how an energy efficiency criterion could work as an accept-reject criterion unless only zero or negative energy efficiency is grounds for rejection, and any positive relationship is grounds for acceptance. This seems to allow almost any relationship to qualify. Perhaps its value lies in its use as a comparative criterion. That is, the feature seems to be more energy efficient in terms of one biological role than any other.

The problem we are left with is this. If inductive, analogic approaches are logically invalid, and direct approaches require observation of animals in their natural environment, how are we to ascertain the biological roles of fossils? According to Bock (1977) we simply cannot--there is no way to deduce biological role from morphology. However, perhaps the problem we should be concerned with is whether our hypotheses of biological role in fossils are falsifiable in the sense of Popper (1959). If they are, then they are valid scientific hypotheses.

According to Popper, an hypothesis is falsifiable if there are empirically observable implications deduced from the hypothesis such that if H (the hypothesis) is true, then I (the implication) must be true. If the implication is found on observation to be false, then the hypothesis must also be false. The opposite however, is not true. If the implication is true, it does not mean that the hypothesis is true; the implication could theoretically be deduced from some other hypothesis as well. All one can say if the implication is true is that the hypothesis has passed one test: it is corroborated.

As an example consider the following hypothesis. The postcranium of *Adapis parisiensis* is morphologically similar to that of the lorisine primates. Therefore, the biological role of the postcranium of *Adapis parisiensis* is the type of locomotion observed in the lorisine primates which we call slow-climbing quadrupedalism. What test implications could be deduced from this hypothesis?

1. If we could observe *Adapis* in its natural environment, we would see it using slow-climbing quadrupedalism as its mode of locomotion.

2. If there were a covering law principle that similarity of morphology equals similarity of biolgical role, we could falsify the hypothesis by showing non-similarity of morphology, or corroborate it by showing similarity of morphology.

3. We could falsify the hypothesis by a demonstration that the selective forces of the biological role could not be met by the faculties of the form-function complex.

Obviously option 1 is not available to us. Bock (1977) has shown the invalidity of using any covering law principle. Implication 3 is the only one available to us; however, it does involve additional hypotheses related to correctly identifying selective forces and faculties.

The type of approach outlined in 3 is similar to the paradigm approach advanced by Rudwick (1964). In this approach a biological role is proposed; its optimum form (its paradigm) is specified based on engineering priciples; the paradigm or expected morphology is compared to the actual observed specimen; and a judgement is made as to the goodness of fit. This approach is compatible with the Bock and von Wahlert model. Instead of constructing the actual paradigm, one could use the principles which would guide the construction of the paradigm as a clue to the selective demands of the biological role.

The advantage of this approach is that it involves a deductive relationship between the biological role proposed and the morphology used to test it, and thus provides a criterion for falsification. Also, in a purely comparative approach the range of our biological role inferences about fossils is limited by the range of biological roles possessed by extant organisms. In the paradigm approach our biological role inferences are limited only by our understanding of the problems of engineering.

The problems with this approach are similar to those discussed above with the Bock and von Wahlert model. How do we determine the rules for paradigm construction? How do we know when we have identified all the relevant selective demands? If a feature has several biological roles, the resulting morphology may not resemble any paradigm, or its faculties may not fit the selective demands of any one biological role well. Is it possible to model such compromises? If so, how can we know when we have identified all the relevant biological roles acting on a feature? What about other factors affecting morphology besides biological role? Can we model in phylogenetic constraints, or those due to growth patterns? How do we know when we have identified all the other relevant factors? What if the demands of the biological role are not met by the faculties of one feature but were met by another? How many features should we consider in our analysis? How do we deal with functional complexes? And finally, do we understand biomechanics well enough to be able to have clear criteria for falsifying biological role hypotheses?

Analogy arguments are invalid for inferring biological role in fossils. These observations are helpful in suggesting hypotheses to be tested [they establish prior probablility (Salmon (1967)], but are not themselves sufficient to test or corroborate such hypotheses. At the present time hypotheses as to biological role in fossils are theoretically falsifiable by two criteria, but operationally only by one. And this one is quite difficult to put into practice. Most biological roles of primates we are interested in, like locomotor behaviors and diet, are not discrete phenomena; types grade into one another in a way which makes falsification on the grounds of impossibility of performance difficult. When can we say it was impossible for a primate to leap or to have eaten leaves? One may be able to infer that one biological role was more likely than another on energetic grounds, but this of course assumes that animals always do the things they are best suited to do. Are there any grounds for choosing between the following three hypotheses? *Adapis* was not a leaper; *Adapis* was a bad leaper; the postcranium of *Adapis* performed no biological role. Given our current knowledge of biomechanics, it would be difficult to know if hypothesis one or two were closest to the truth (i.e. we cannot falsify either one, and corroborative evidence would likely be similar for both cases). I know of no way the third hypothesis could be operationally falsified (it could be falsified by direct observation). We can narrow the spectrum of possibilities considerably, but we will always be left with more than one unfalsified hypothesis.

The second problem in analyzing the evolution of the postcranium is the lack of information on fossil primates. This cannot be attributed solely to the rarity of fossil postcranial remains, but primarily to the scarcity of analyses on the fossils which do exist. Certainly there are large gaps in our knowledge, but known postcranial material of notharctines, adapines, and omomyids has gone uncatalogued and undescribed for decades. Thus, the variation in form and behavior among the fossil taxa is sometimes unappreciated, and analysis relies too heavily on the few described taxa.

A third critical problem results from unsound analyses of phylogeny. The value of a reconstruction of the path of evolution of any morphological system depends on the strength of the phylogeny on which it is based (Eldredge and Tattersall, 1975; Delson, Eldredge and Tattersall, 1977; Delson, 1977). If phylogenetic relationships are not considered, or if the phylogeny is faulty, or if it is constructed on false premises, obviously the interpretation based on it will be flawed. Scenarios of locomotor evolution based on an assumed [i.e. an untested vertical comparison (Bock, 1977)] "stage of evolution" approach where specific taxa are chosen as representatives of different "stages" in the sequence, usually based on a phylogeny reconstructed from another character complex, are good examples of this problem. For example, Morton (1924) chose *Notharctus* as representative of the primitive primate stage of foot evolution, Lewis (1980c) used *L. catta*, and Martin (1972) used *Microcebus murinus*. In each of these cases, the choice of the representative was based on the (stated or unstated) perception that "lemurs" are more primitive than higher primates or that small nocturnal animals are more likely to be primitive than large, diurnal ones. While these perceptions may be true, it does not necessarily follow that all aspects of foot structure of these animals will also be primitive. The success of analyses based on this approach, of course, lies in choosing representative types which differ least from the actual ancestor. However in these studies there is usually no rigorous attempt (a character analysis as outlined below) to discover what this ancestor was like. In some studies contemporary forms are treated without appropriate justification as if they were unchanged relics of past stages. The mistake is no less serious when fossil forms are treated in this way. In other studies, a judgement is made as to which is the most "generalized" animal. The basis on which this assessment is made is often unclear.

The approach I espouse is briefly outlined below. An hypothesis of relationships of taxa is constructed for the group under discussion. This hypothesis must accomodate all relevant evidence on relationships, not just the features (here tarsal morphology) one is attempting to analyze. There are several schools of thought on the best way to construct such an hypothesis; my theoretical orientation derives from the method developed by Hennig (1966). Taxa are grouped only on the basis of shared-derived similarities, not ancestral retentions, parallelisms, convergences, or general phenetic resemblance. The reasoning behind this method of phylogenetic inference has been discussed numerous times (e.g. Brundin, 1968; Nelson, 1970) and, as its tenets have been accepted by most systematists, its use will not be justified further here.

The major problems in applying this method lie in determining 1) homology from homoplasy, and 2) the polarity of character states. In this work I have generally followed the guidelines of Simpson (1961) for the recognition of homology. The determination of primitive from derived character states is based on several lines of reasoning: 1) the distribution of characters in primates and in other mammals; 2) a consideration that the morphology of an early representative of a group is more likely to be primitive than that of a later member; 3) covariance of postcranial characters with previously determined polarities for cranial and dental features; 4) information from functional studies is used in the testing of hypotheses of homology and polarity (Bock, 1981; Fisher, 1981; Szalay, 1981b, 1984, 1985), and in the determination of the relative weight given to different features (Hecht and Edwards, 1977). Functional analysis is also useful in the recognition of new features, and in understanding the relationships between features (and thus the probable coevolution of features). Ontogenetic information may also be useful for determining polarity, but is unavailable for virtually all of the features discussed in this thesis.

The results of the phylogenetic analysis are presented in a cladogram, "...a diagram of relationships which has no true time axis, but represents only a sequence of branching events along each lineage involved " (Delson 1977:435). Each branching event is indicated by a "node" representing the unknown ancestor of the group. The suite of features characterizing this ancestor is the reconstructed morphotype of the taxa descended from that ancestor. In some rare cases a known species may be recognized as the probable real ancestor of the group. Criteria for ancestor recognition are outlined in Delson (1977) and Szalay (1977a).

The course of evolution of the particular character complex under consideration is best traced through changes in the morphotypes of supraspecific taxa, not by directly comparing the morphology of species which may or may not resemble these morphotypes (see fig. 1).

The advantage of this approach, that of constructing hypothetical morphotypes to represent ancestral stages, is that it allows one to put together a conglomerate of features that *must* have been present in an ancestor, but *may* no longer be found in any extant (or known extinct) animal. Thus, although I might agree with Morton (1924) that the foot structure of *Notharctus* is *close* to that of the morphotype euprimate, it does exhibit many features which I would not expect to find in this animal. Similarly, *Microcebus murinus* is simply too morphologically specialized to be a good structural ancestor for Malagasy lemuriforms [contra Martin (1972)].

A related problem in these analyses is the failure to separate the concepts of the ancestral primate, the ancestral euprimate, the ancestral strepsirhine, and the ancestral lemuriform. To my mind, these are all very different animals, and to jumble them together (especially the middle two) results in a muddled analysis and erroneous conclusions. For example, no known extant or fossil strepsirhine is a perfect model for the common ancestor of strepsirhines and haplorhines. All strepsirhines have features which distinguish them from this ancestor. They are (at least in some aspects of the tarsus) *more* specialized than haplorhines, not less.

III. Plan of the study. The following chapter discusses previous studies concerned with foot morphology of strepsirhine primates. and establishes the definitions of bones, joints, joint motion, and taxonomy used in the remainder of the thesis. Chapter three describes the materials used in the study and the methods used to collect data and analyze it. Chapters four to seven describe the morphology of joint surfaces in the upper ankle, subtalar, transverse tarsal, and intertarsal joints. The form of these joints is described usually at the family or subfamily level; any significant departures from the norm are noted. The mechanical significance of variations in joint structure is discussed, and hypotheses as to the relationship between joint structure and positional behavior are presented. In Chapters eight and nine the joint structure of Eocene strepsirhines and subfossil lemurs is analyzed. Chapter ten synthesizes the information of the previous six chapters by construction of a genealogy of strepsirhines based on features of the tarsus, and the probable adaptational significance of transformations in tarsal structure.

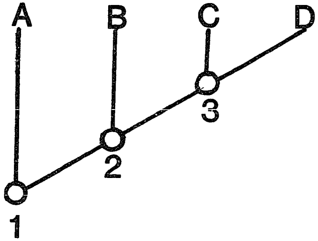

Figure 1. The difference between a representative taxon or "stage of evolution" approach (SE) and tracing transformations in morphotypes (TM). To reconstruct the changes leading to taxon D, TM compares changes between ancestral nodes 1, 2, and 3. SE reconstructs paths of change by comparing taxa at A, B, and C. Obviously, 1-2-3 is the "real" path of evolutionary change. A-B-C is an attempt to represent 1-2-3. Its success depends on how closely A=1, B=2, and C=3. If these endpoint taxa have autapomorphies not present in the ancestor, the results of A-B-C will not mirror 1-2-3. SE analyses are often biased by unwarranted preconceptions that endpoint taxa to the left of the cladogram are more primitive in every way than taxa to the right.

CHAPTER 2: PREVIOUS WORK AND CURRENT DEFINITIONS.

II. General remarks on the morphology of the strepsirhine foot.

A. Osteology.

1. Previous studies. The comparative osteology of the foot, and especially of the joint surfaces is the main subject matter of this thesis, and is discussed in detail in the chapters to follow. However, some general remarks will be made here, including a brief account of other relevant studies. The comparative osseous anatomy of the extant strepsirhine primates has been treated in several broadly comparative works. DeBlainville (1839) observed the shortness of the calcaneus in lorisines, and noted the lengthening of the tarsal region in cheirogaleids. Mivart (1867) described and compared aspects of the foot skeleton of many sterepsirhine genera in his treatise on the skeleton of primates. Lamberton (1939) utilized metrical data on a broad spectrum of living lemurs in his work evaluating the morphology of the foot in the subfossil Malagasy primates. Volkov (1903-4) considered several prosimians in his comprehensive treatise on the foot of primates.

Foot proportions in primates have been studied by Lessertisseur and Jouffroy (1973), Jouffroy and Lessertisseur (1979), Schultz (1963), and Volkov (1903-4). Their results are equivocal in terms of the relationship between morphological patterns and locomotor or functional groups. All lorisines share a shortened tarsal region, as in other primate climbers (e.g. _Pan_, _Alouatta_), but so do the leaping indriids and _Daubentonia_. A long tarsal region is found in many vertical clingers and leapers (galagines, *Tarsius*, *Lepilemur*) but not in the indriines. Relatively long tarsals are also characteristic of the Cheirogaleidae, who display a variety of locomotor behaviors.

Hafferl (1932) and Decker (ms) have both concentrated on the varieties of form of the articular surfaces in strepsirhines. The structure of the articular surfaces of some prosimians has also figured in the analysis of the evolution of the human foot presented by Lewis (1980 a,b,c). Differences between strepsirhines in myological and osteological adaptations for grasping are discussed by Gebo (1985).

In addition to these comparative works, there are several excellent papers on particular problems in selected animals. Hafferl (1929), Hall-Craggs (1965, 1966) and Walker (1970) have all commented on the relationship between tarsal elongation and mechanisms of tarsal rotation to leaping ability. Grand's (1967) work on *Nycticebus* stressed the relationship between the reorganization of the crural and tarsal joints which allow increased ranges of motion, and the peculiar mode of locomotion in these primates. Similar insights were reached by Decker (ms), and Hafferl (1932) in their studies of tarsal articulations, by Mackenzie's (1931) comparison of foot myology in *Lemur* and *Perodicticus*, by Forster (1922a,b, 1923, 1934) in his series of papers which included discussions of the myology and osteology of *Nyticebus*, *Perodicticus*, and *Lemur*, and by Wrobel's (1960) detailed dissections of the foot musculature of lorisines.

Some aspects of the foot structure of fossil strepsirhine primates have also been studied. Matthew (1915) and Rose and Walker (1985) have described foot bones of *Cantius*; Gregory (1920) has discussed the foot structure of *Notharctus*; Decker and Szalay (1974), Von Koenigswald (1979) and Dagosto (1983) described and analyzed the adapine primates.

The approaches, goals, and results of these studies are too varied and numerous to be succinctly summarized here. Particular aspects of these works are discussed in the body of the thesis where they are relevant to the discussion.

2. General osteology. Strepsirhines have the normal mammalian complement of seven tarsal bones, five metatarsals, and three phalanges for each digit, except the hallux, which has only two (fig. 2). There is no prehallux. There are normally two sesamoid bones at all the metatarso-phalangeal joints; sometimes the two bones may be fused into a single structure. There is sometimes a sesamoid in the tendon of peroneus longus as it crosses the cuboid. In *Perodicticus*, as has long been known (van Campen, 1859), there is an accessory bony piece lateral to the entocuneiform, called the os ventrum (fig. 3). I have observed similar ossifications in the foot of *Arctocebus*, *Galago senegalensis*, and *Varecia*. Wrobel (1960) and Grand (1967) report very thickened cartilage in this region in *Nycticebus* and *Loris*. This suggests that such thickened pieces of cartilage or ossifications in this region of the foot may be fairly common among strepsirhines, although they may not always be preserved in dried museum specimens.

Dissections of fresh specimens are necessary to determine the extent of such a phenomenon in the strepsirhines. Wrobel (1960) has offered an explanation for this structure. He believes that this piece serves to plantarly close a tunnel for the long flexor tendon to the hallux in order to channel the tendon so that its line of action is at right angles to the line of action of the long flexor tendons for the other digits. This is supported by Grand's (1967, fig. 7) work on *Nycticebus*. In pottos, this structure also serves as a site of attachment for several intrinsic foot muscles.

In the living lemuriforms, the calcaneus extends more distally than the astragalus even in eversion (fig. 2). Thus, there is never any astragalo-cuboid contact (which is the definition of an "alternating" tarsus). However, the foot is not strictly of the serial type (with the possible exception of the indriids, *Daubentonia*, and lorisines), since the proximal extension of the lengthened calcaneus results in a stepped arrangement of the proximal tarsals. This may be called a "reverse alternating" condition (Lewis, 1980a). In some taxa there may be contact facets betwen the navicular and the calcaneus (Chap 7). Other intertarsal articulations are discussed in the following chapters.

B. Myology. The muscular anatomy of the strepsirhine foot is known from the descriptive accounts of individual species, e.g. Owen's (1863) and Oudeman's (1890) work on *Daubentonia*, Van Campen (1859) and Forster (1934) on the potto, Milne Edwards and Grandidier (1875) on indriines, Beddard (1901) on *Hapalemur*, Kingma (1855) on *Galago* *demidovii*, Mivart and Murie (1865) on *Nycticebus*, and Wrobel (1960) on the lorisines. Murie and Mivart (1872) described and compared several species of *Lemur*, *Varecia*, *G. crassicaudatus* and *G. alleni.* Fischer (1804) also described several species. Much of this early material is summarized in Hill (1953), but Jouffroy's (1962) monograph remains the most comprehensive comparative account of strepsirhine myology. Information from these works was used to construct the table of muscle arrangement (Table 1). It should be noted that not all workers are in total agreement on all points [compare the descriptions of the intrinsic foot muscles of the potto in Van Campen (1859), Forster (1934), and Wrobel (1960)], but not all disagreements are noted. Future, more detailed work on the foot myology of prosimians (Gebo, 1986) may resolve some of these issues.

It is apparent from these works that although there is some minor variation regarding the presence of smaller muscles and in the sites and extents of some origins and insertions, the major differences between groups lie in the relative sizes of the muscle masses. Unfortunately, this area of comparison has received very little attention aside from the qualitiative observations of Jouffroy (1962), and the papers of Wrobel (1960), Grand (1967), Jolly and Gorton (1974), and Ward and Sussman (1979). Two other areas of potentially fruitful research, comparative muscle fiber histology and electromyography are only beginning to be applied to strepsirhine primates (e.g. Jungers *et al.*, 1980; Anapol and Jungers, 1986).

The lorisines are the most distinctive strepsirhines in terms of leg and foot myology. They are distinguished from other strepsrihines by the absence of peroneus digiti quinti, peroneus digiti quarti (sometimes), plantaris (sometimes), and the superficial head of flexor digitorum brevis; the lesser development of gastrocnemius and soleus; and the greater development of flexor tibialis. These differences have been related to the distinctive slow-climbing mode of locomotion and powerful grasp employed by lorisines (MacKenzie, 1931; Wrobel, 1960; Grand, 1967; Jolly and Gorton, 1974).

II. Definitions. In the study of the foot perhaps no problem is more vexing than that of the terminology for the joints, joint surfaces, and joint motions. Many authors have used similar terms for different things; inversion, eversion, supination, and pronation are often interchanged. Conversely, there are often several names for the same thing (i.e., the lower ankle joint and the subtalar joint). While I have no desire to add to the general confusion by creating new names or redefining old ones, it is very difficult to engage in an unambiguous discussion of foot morphology and function without first defining for the reader exactly what I mean when I refer, for example, to the movement of inversion. I do not mean to imply that this is the best use of these terms; I merely wish to inform the reader of my concept of their meaning.

A. The bones. The bones of the foot are illustrated in figure 2. The abbreviations used for them are given in Table 2. In this work the word "foot" refers to all the bones distal to the tibia and fibula. In discussions of the function of the foot it is useful to have a term to refer to the unit consisting of the calcaneus plus the remainder of the foot, in other words, the foot minus the astragalus. MacConaill and Basmajian (1969) have coined the term "lamina pedis" for this portion of the foot.

B. The joints and joint surfaces. Each articular unit is given a name based on the two bones involved in the articulation, i.e. the calcaneocuboid joint. Every unit is given a specific abbreviation (Table 2). If two bones articulate at more than one location, each of these units is given a separate name (e.g. the anterior astragalocalcaneal joint, the posterior astragalocalcaneal joint). Each unit is made up of two corresponding facets, one on each bone of the articular pair. For the sake of clarity (if not ease) of discussion, I have found it necessary to have a way to refer to each facet of the pair, e.g. the calcaneo-cuboid facet on the calcaneus; the calcaneo-cuboid facet on the cuboid. These unwieldy terms are avoided in the text by a method of abbreviation based on that of Szalay (1982). In this method, the abbreviation for the joint is followed by the abbreviation for the bone (in parentheses) on which the surface under consideration is. For example, the calcaneocuboid facet on the calcaneus is abbreviated as CCu(C); the calcaneocuboid facet on the cuboid is abbreviated as CCu(Cu). These abbreviations are listed in Table 2.

The upper ankle joint is a compound joint made up of four articulations. The tibia articulates with the astragalus dorsally and medially; it is convenient for clarity of discussion if these two articulations are given separate names. The medial astragalotibial joint (ATiM) is the articulation for the medial malleolus of the tibia with the medial side of the astragalus (fig. 4). The articulation of the inferior surface of the tibia with the dorsal surface of the astragalus is called the lateral astragalotibial joint (ATiL). The astragalus also articulates with the fibula at the astragalofibular joint (AFi). Finally, the tibia and fibula articulate at the inferior tibiofibular joint. No strepsirhines have calcaneofibular contact.

In this work I will adopt the convention of Shephard (1951), who included in his concept of the subtalar joint (sometimes referred to as the lower ankle joint) the posterior astragalocalcaneal articulation (a.k.a. the ectal facets) and the astragalocalcaneal part of the astragalocalcaneonavicular joint (a.k.a. the sustentacular facets). This has the disadvantage of breaking up the astragalocalcaneonavicular articulation, which is a single morphological entity within the same joint capsule, into two parts, one considered here as part of the subtalar joint, and the other (the astragalonavicular joint) as part of the transverse tarsal joint. The advantage of this scheme lies in the ease of description --only two bones and two surfaces need be considered. The facets of the STJ are illustrated in figure 5.

The transverse tarsal joint consists of the articulations between the astragalus and navicular and the calcaneus and cuboid. These are illustrated in figure 5.

The remaining intertarsal articulations are self expanatory, and their abbreviations are listed in Table 2.

C. Joint motions. As pointed out by Lewis (1980b) there is a certain amount of confusion concerning the terminology for movements of the foot. The following conventions will be adopted in this paper. A reference position of the foot is defined with the foot plantigrade, and midway between dorsiflexion and plantarflexion at the upper ankle joint. Three axes of the foot are defined (note that these axes have *nothing to do* with joint motion axes). Axis one runs proximodistaly through the foot (the long axis of the foot), axis two runs mediolaterally at right angles to the first, and axis three runs dorsoplantarly at right angles to the first two (fig. 6). This last axis is parallel to the long axis of the tibia. Motions of the *foot* (and the bones of the foot) around these axes are defined as follows: first axis, pronation and supination; second axis, plantarflexion and dorsiflexion; third axis, abduction and adduction (fig. 6).

Motions at the foot are rarely pure rotations about any one of these axes. However, it is often useful to consider the separate contributions about each axis when analyzing a particular joint motion. Much work on the primate foot has stressed the importance of inverted and everted positions of the foot. As has been shown (e.g. Lewis, 1980b), inversion and eversion are complex movements involving displacements with respect to all three reference axes. Moving the foot into the inverted position (which takes place at the subtalar and transverse tarsal joints) involves concurrent supination, plantarflexion, and adduction; the combination of these movements is referred to in this work as inversion. Eversion involves concurrent pronation, dorsiflexion and abduction. Inversion and eversion are <u>not</u> synonyms for supination and pronation.

In addition to rotations, bones may also translate along these axes. Translation along axis one will be called protraction and retraction; along axis two, medial and lateral slides; along axis three, dorsal and plantar slides.

D. Types of bone and joint displacement. The following discussion is adapted from MacConaill (1966, 1973). Bone movement can be of two types, swing and spin. A spin (fig. 7) is a simple rotation around the long axis of a bone. All other movements are called swings and they may be pure (involving no concurrent spin), or impure where some spin is also taking place. Swings always involve a movement of the long axis of a bone from one point to another. At the joint, this means that one surface slides across the other. A joint surface can move across its opposing surface by either of two paths. A chordal path is defined as the shortest distance between two points, while an arcuate path is any other path which is not the chordal path. A chordal movement on a joint surface will result in a pure swing, and an arcuate movement will result in an impure swing. The spin which accompanies arcuate movements is termed conjunct rotation. Conjunct rotation must be distinguished from adjunct (or independent) rotation, which can be carried out as an independent spin movement (e.g. pronation and supination at the humeroradial joint). Conjunct rotation may occur whether or not the articulating pair allows independent (or adjunct) rotation of the bones. It will always occur as a result of any arcuate swing or diadochal movement. This phenomenon is important to take into account when analyzing joints, as it does affect the final relationship between the articulating bones after an arcuate movement. MacConaill's observations of most of the joints of the human body show that the habitual movement at any joint is arcuate and therefore associated with a conjunct rotation. The probable reason for this is that arcuate movements are thought to minimize joint attrition (MacConaill, 1946, 1953).

I will introduce one new term, concomitant displacement, for those movements which are necessary adjuncts to major motions at a joint, and which change the spatial relationships of the articulating pair of bones, but which are not the result of conjunct rotations. These concomitant displacements are usually the result of the axis of joint motion (which results from several aspects of joint shape) not being purely parallel or perpendicular to the reference axes of the foot, so that displacement, even in a pure swing, involves displacement in more than one plane. The discussions of UAJ and STJ motion in Chapters 4 and 5 illustrate this point.

Concomitant displacement may also be the result of helical orientations of facets, yielding concomitant translations along the joint motion axis.

E. Axes. In this work the word axis is used in three different senses. First, there are the "reference" axes of the foot referred to above. Second, there are "long" axes of joint faces, which simply refer to the longer of the two dimensions of a facet. I also discuss "joint motion" axes of the UAJ and STJ. These are the functional axes of those joints, i.e. the line defined by points around which no motion occurs during displacement at the joint.

F. Taxonomy. Morphological descriptions of taxa are given at the family or subfamily level. The classification of strepsirhine taxa used in this study is presented in Table 3. It differs from that of Szalay and Delson (1979) and Tattersall (1982) in the recognition of a taxon Lemuroidea containing only lemurids and indriids, and an uncertain position for *Daubentonia* and *Lepilemur* (which is described with lemurids). A family Cheirogaleidae is recognized despite problems with this collection of taxa (see Chapter 10). Olson's (1979) classification of galagos is used. The reasons for these decisions are discussed in Chapter 10.

Table 1. Muscles acting on the foot of strepsirhine primates. Mainly from Jouffroy, 1962. Other references: 1. Nayak (1933); 2. MacKenzie (1931); 3. Wrobel (1960); 4. Kingma (1855); 5. Beddard (1901); 6. Forster (1934); 7. Rosenfeld (1898); 8. Hill (1951); 9. Jolly and Gorton (1974), 10. Gebo(1985). O=origin, I=insertion.

MUSCLE	GENERAL CONDITION	VARIATIONS
CRURAL MUSCLES		
TIBIALIS ANTERIOR	O. Antero-lateral side, upper 2/3 of tibia by two heads. I. medial border of entocuneiform (medial head), and first metatarsal (lateral head).	Cheirogaleines, lorisines, and *Tarsius* have no metatarsal I insertion (no abd. hallucis longus).
EXTENSOR HALLUCIS LONGUS	O. antero-medial side of distal 1/2 of fibula, interosseous membrane, and lateral face of tibia. I. distal phalanx, digit I.	no fibular origin in galagines, lorisines, or *Tarsius* (1). well-developed in *Perodicticus* (Jouffroy), weak in *Perodicticus* (2)
EXTENSOR DIGITORUM LONGUS	O. superior lateral part of tibia, interosseous membrane, and superior one third of fibula I. splits into 3 tendons to supply lateral 4 toes.	no tendon for digit 2 in *Perodicticus* or *Nycticebus* (3)
PERONEUS LONGUS	O. lateral condyle of tibia, superior 1/3 lateral border of fibula I. base of metatarsal 1.	
PERONEUS BREVIS	O.inferior 1/2 of antero-lateral face of the fibula I. base of metatarsal 5.	insertion to cuboid in *Perodicticus* (2)
PERONEUS DIGITI QUINTI	O. superior 1/2 of the lateral side of the fibula. I. joins with tendon of ext. dig. brevis for MT5.	inconstant in Lorisiformes

(continued)

Table 1, continued.

PERONEUS DIGITI QUARTI	O. inferior 1/2 of fibula I. base of metatarsal 5.	absent in Lorisiformes, (but reported by Wrobel)
GASTROCNEMIUS	O. from fabellae or femoral shaft above femoral condyles I. heel of calcaneus	less developed in lorisines, fabellae are absent. Well-developed in *Tarsius*, *Galago*, *Microcebus*, *Cheirogaleus*, *Propithecus*.
SOLEUS	O. fibular head I. heel of calcaneus	more extensive fibular origin in *Loris*, *Galago*
PLANTARIS	O. lateral fabella or femoral shaft above lateral condyle I. heel of calcaneus	well developed in *Tarsius*, *Galago* less developed in cheirogaleids, *Daubentonia*, poorly developed or absent in lorisines, absent in *G. demidovii* (4), absent in *Hapalemur* (5)
TIBIALIS POSTERIOR	O. medial border of fibula I. tuberosity of navicular, entocuneiform	inserts only on navicular in the potto (6); inserts also on the 2nd and 3rd metatarsal bases in *Loris* (7)
FLEXOR FIBULARIS	O. posterior surface of the fibula and inferior half of the external posterior face of the tibia I. sends tendons (mixed with those of fl. tibialis) to digits 1-4, sometimes 5	tendons only to 1, 2 in *Propithecus* no tibial origin in *Galago* (8) relatively larger part of crural musculature in lorises (9)

(continued)

Table 1, continued

FLEXOR TIBIALIS	O. superior 2/3 of posterior face of the tibia, lateral border, tibial head. I. sends tendons (mixed with those of fl. fibularis) to digits 1-5	may be double or triple headed in lorises; relatively larger part of crural mesculature in lorises (3,9)
INTRINSIC FOOT MUSCLES		
EXTENSOR DIGITORUM BREVIS	O. dorso-lateral face of calcaneum I. usually 4 tendons for lateral 4 digits, sometimes a tendon for digit 1.	variable, tendons to to digits 1 or 5 are most often absent lorises may have a well developed ext. hallucis brevis
FLEXOR DIGITORUM BREVIS	O. by two heads, a superficial head from the deep face of the plantar aponeurosis, and the tuberosity of the calcaneum; and a deep head from the plantar face of the tendon of fl. tibialis. I. superficial--tendons to digits 2,3; deep--tendons to digits 3-5	In lorisines, the superficial head may be absent; if present (3) it arises only from the plantar fascia in *Loris* and *Nycticebus*
LUMBRICALS	O. from the long flexor tendons I. medial border of corresponding distal phalanx	very little variation; often the first will be absent in lorises
CONTRAHENTES	O. and I. very variable, in addition to an add. hallucis (arising from the 4th metatarsal), there are 2 adductors on the 5th and 4th digits and abductors on 2,3,4	no abductor for digit 3 in *Daubentonia*, *Propithecus*

(continued)

Table 1, continued

ADDUCTOR HALLUCIS	O. by two heads usually from MT 4 I. MT 1	very large in *Lemur* and *Propithecus* and the two heads are fused (10)
INTEROSSEI	O. and I. variable; usually 5 plantar and 4 dorsal arranged around an axis of the 4th digit	dorsal of 2nd digit is large in lemurids and indriids (10)
ABDUCTOR DIGITI MINIMI	O. plantar medial surface of the calcaneus or plantar aponeurosis I. base of proximal phalanx of digit V.	an accessory muscle exists in *Loris* and *Perodicticus* (2,3) especially large in lemurids and indriids (10)
ABDUCTOR HALLUCIS (BREVIS)	O. deep face of plantar fascia and from abd. dig. min. I. medial border of proximal phalanx of digit 1 (and sesamoids).	originates on navicular in Lorisiformes and *Tarsius* and on os ventrum in *Perodicticus* two headed origin in indriids; one from the posterior extremity of the calcaneus, one from a sesamoid bone situated immediately behind the base of metatarsal I.
FLEXOR HALLUCIS (BREVIS)	O.navicular, entocuneiform, base of metatarsal 1. I. base of proximal phalanx, digit 1.	
FLEXOR DIGITI MINIMI BREVIS	O. base of metatarsal 5. I. base of proximal phalanx, digit 5.	

Table 2. Abbreviations used in this study. See also figures 2, 4 and 5.

Abbreviations:

Bones:
- Tibia (Ti)
- Fibula (Fi)
- Astragalus (A)
- Calcaneus (C)
- Navicular (N)
- Cuboid (Cu)
- Ectocuneiform (Ec)
- Mesocuneiform (Me)
- Entocuneiform (En)
- First Metatarsal (MT1)
- Second Metatarsal (MT2)
- Third Metatarsal (MT3)
- Fourth Metatarsal (MT4)
- Fifth Metatarsal (MT5)

Upper ankle joint (UAJ):

AFi (astragalofibular joint)
- AFi(A) joint surface for the AFi on the astragalus
- AFi(Fi) joint surface for the AFi on the fibula

ATiL (lateral astragalotibial joint)
- ATiL(A) joint surface for the ATiL on the astragalus
- ATiL(Ti) joint surface for the ATiL on the tibia

ATiM (medial astragalotibial joint)
- ATiM(A) joint surface for the ATiM on the astragalus
- ATiM(Ti) joint surface for the ATiM on the tibia

Subtalar joint (STJ)

pAC posterior astragalocalcaneal joint
- pAC(A) joint surface for the pAC on the astragalus
- pAC(C) joint surface for the pAC on the calcaneus

aAC anterior astragalocalcaneal joint
- aAC(A) joint surface for the aAC on the astragalus
- aAC(C) joint surface for the aAC on the calcaneus

Transverse Tarsal Joint (TTJ):

AN astragalonavicular joint
- AN(A) joint surface for the AN on the astragalus
- AN(N) joint surface for the AN on the navicular

CCu calcaneocuboid joint
- CCu(C) joint surface for the CCu on the calcaneus
- CCu(Cu) joint surface for the CCu on the cuboid

continued

Table 2 continued.

Intertarsal Articulations

CuN	cuboideonavicular joint
CuN(Cu)	joint surface for the CuN on the cuboid
CuN(N)	joint surface for the CuN on the navicular
CuEc	cuboid-ectocuneiform joint
CuMe	cuboid-mesocuneiform joint
NEc	navicular ectocuneiform joint
NEc(N)	joint surface for the NEc on the navicular
NEc(Ec)	joint surface fot the NEc on the ectocuneiform
NMe	navicular mesocuneiform joint
NMe(N)	joint surface for the NMe on the navicular
NMe(Me)	joint surface for the NMe on the mesocuneiform
NEn	navicular entocuneiform joint

Table 3. Classification of strepsirhine primates adopted for this study. Only fossils mentioned in the text are included.

- Order Primates
  - (Taxon) Euprimates
    - Suborder Strepsirhini
      - Infraorder Adapiformes
        - Family Adapidae
          - Subfamily Notharctinae
            - *Cantius*
            - *Notharctus*
            - *Smilodectes*
          - Subfamily Adapinae
            - Tribe Adapini
              - *Adapis*
              - *Leptadapis*
              - *Caenopithecus*
      - Infraorder Lemuriformes
        - Superfamily Lemuroidea
          - Family Lemuridae
            - *Lemur*
            - *Hapalemur*
            - *Varecia*
          - Family Indriidae
            - Subfamily Indriinae
              - *Indri*
              - *Avahi*
              - *Propithecus*
            - Subfamily Archaeolemurinae
              - *Archaeolemur*
              - *Hadropithecus*
            - Subfamily incertae sedis *Mesopropithecus*
          - Family incertae sedis *Lepilemur*, *Megaladapis*
        - Superfamily Lorisoidea
          - Family Cheirogaleidae
            - *Cheirogaleus*
            - *Phaner*
            - *Microcebus*
            - *Mirza*
          - Family Lorisidae
            - Subfamily Galaginae
              - *Galago*
              - *Galagoides*
              - *Otolemur*
            - Subfamily Lorisinae
              - *Perodicticus*
              - *Arctocebus*
              - *Loris*
              - *Nycticebus*

continued

Table 3, continued.

Superfamily incertae sedis *Komba*, *Progalago*

Infraorder incertae sedis *Daubentonia*

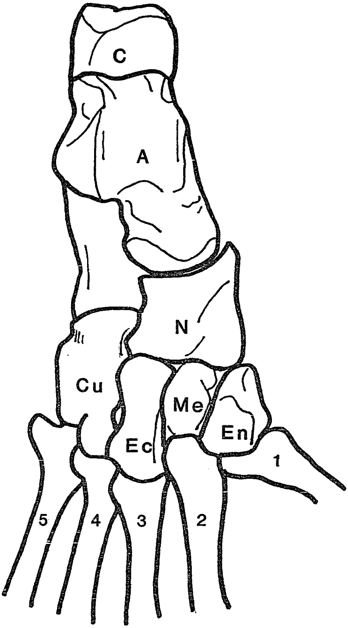

Figure 2. Bones of the right foot in <u>Propithecus verreauxi</u>. Abbreviations as in Table 2.

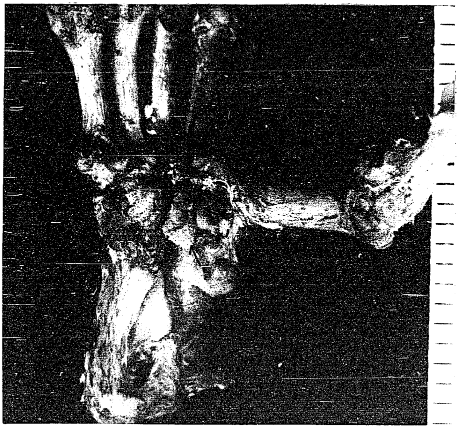

Figure 3. Plantar view of foot of Perodicticus potto (AMNH 200232). Arrow points to the os ventrum.

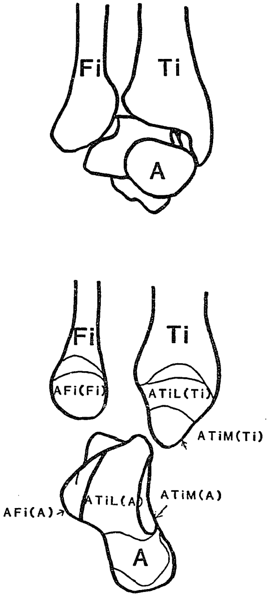

Figure 4. Bones and joint surfaces of the upper ankle joint in *Lemur fulvus* (right foot). Abbreviations are explained in Table 2.

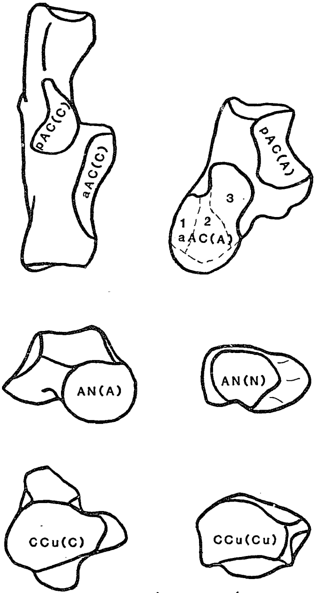

Figure 5. Joint surfaces of the STJ (top) and TTJ (middle and bottom) in the right foot of Lemur fulvus. In the aAC(A) the numbers 1,2, and 3 illustrate the extent of the area articulating with the plantarcalcaneonavicular ligament at all times (1); and in eversion (1+2). In inversion areas 2 and 3 articulate with the aAC(C).

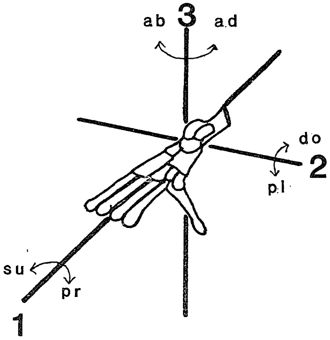

Figure 6. Right foot indicating reference axes of the foot and movements that take place around them. su, supination; pr, pronation; do, dorsiflexion; pl, plantarflexion; ab, abduction; ad, adduction.

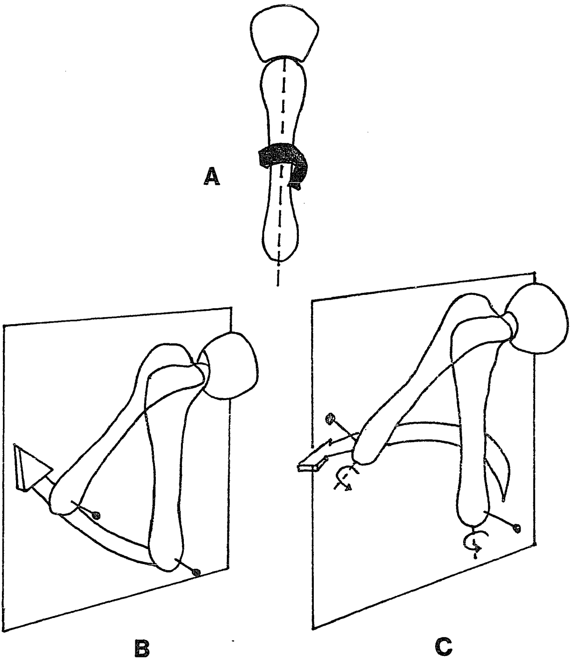

Figure 7. Joint motions. A, a spin (axial or adjunct rotation) around the axis of a bone. B, a pure (chordal) swing. The bone stays in a single plane and undergoes no conjunct rotation. C, an impure (arcuate) swing. The bone moves out of the plane and then returns to it, acquiring a conjunct rotation. This movement can be broken down into its components of a spin plus a pure swing. After Warwick and Williams (1973).

CHAPTER 3: MATERIALS AND METHODS

Measurements and observations were made on osteological and paleontological specimens in museum collections; a list of the specimens examined is presented in Table 4. For fossils and subfossils see Chapters 8 and 9. Only adult animals were measured, age being judged by degree of closure of all bone epiphyseal junctions. It was, of course, not possible to judge age in this manner for fossil specimens without associated long bones and teeth. If the bone appeared to be fully ossified, it was measured, even though full ossification of foot bones often preceeds complete long bone growth. I preferred to measure only animals collected in the wild in order to minimize possible variation in morphology resulting from confinement. Casual inspection of zoo animals reveals that they can have postcranial morphologies which are somewhat different from their free ranging conspecifics. The shape of joint surfaces can be particularly affected (Szalay and Dagosto, 1980). In humans, it is hypothesized that forces acting on a joint during an individual's lifetime can have a great effect on the ultimate shape and orientation of a joint surface (Inman, 1976). It has also been shown that animals with basically similar morphology, but slight differences in substrate preferences often exhibit distinctive joint morphologies (e.g. Fleagle, 1977b). Whether this is due to underlying genetic differences, ontogenetic and/or environmental effects on bone growth or muscle-bone interactions is not yet clear. Therefore, without knowing exactly how genetically determined morphology is affected by the qualities of the substrates travelled during life, it seemed best to limit this study to specimens collected in the wild in order to eliminate, as far as is possible, the effects of extreme variability of habitat within each species. Unfortunately, it was not possible to achieve this goal for several reasons. In some museum collections, locality data is poor, and in particular, it is often not clear if the animal was received from the wild or from a zoo. Secondly, a few taxa (e.g. *Lemur catta*, *Varecia variegata*) are mainly represented in collections by zoo animals. Without including zoo animals in the study these taxa would only have been represented by one or two specimens. In any case, when zoo animals were measured, they (as were free ranging animals) were carefully inspected for evidence of disease, breakage, or deformity, and were not included in the study if they showed any pathological conditions. In *L. catta* and *V.variegata* I did not include zoo specimens in which I could observe significant qualitative differences in joint structure. Unfortunately, I had no species with large enough samples of both zoo and free ranging individuals to systematically examine differences between them.

The series of measurements taken on each specimen is detailed in Table 5. In addition to these measurements, note was taken of other features such as the size and position of various muscle and ligament attachments, and the nature of intertarsal articulations. Three types of measures were taken: linear, angular, and measures of joint curvature. All linear measurements were taken with sliding calipers and measured to the nearest .1 millimeter, with the exception of very small specimens which were measured using the measuring reticle of a Wild stereoscopic microscope. Angles were measured by protractor from camera lucida tracings of bones. This kind of data involves some subjectivity, since the long axes of the surfaces were determined by eye. As Table 7 shows, angle measures have higher errors than linear measures. The problem is exacerbated in small angles (less than 30 degrees), since a difference of only 5-10 degrees (which is probably the range within angles can be accurately measured by this method) can increase the percent difference between the minimum and maximum measures much more than in larger angles.

Skeletal trunk length (STL; see Biegert and Maurer 1972) is closely correlated with body weight in strepsirhines (Jungers, 1979), and thus was used as a normalizing variable in the construction of some indices. Actual body weight would be an even better variable to use (Jungers, 1985), but is unavailable for virtually all of the specimens used in this study. Dr. W.L. Jungers has measured STL on the majority of specimens used in this study and has kindly made these data available to me.

In any study of the functional anatomy of an area, it is extremely important to be able to accurately characterize the joint surfaces, since the shapes of the articular surfaces directly control the amount and direction of movement. In this project, articular pairs were classified using the MacConaill (1973) classification system. In this system, there are only four articular shapes, each associated with a set of allowable movements and a number of degrees of freedom (Table 6). According to MacConaill, there are only two basic joint shapes, the ovoid and the sellar. An ovoid surface is either concave or convex in all directions, and always articulates with another ovoid surface of the opposite curvature (e.g. the shoulder joint). A sellar surface is concave in one direction, but convex at right angles to this. It always articulates with another sellar surface (e.g. the upper ankle joint). These two types of surfaces have different functional properties derived from the geometry of their curvatures. Three differences exist: no adjunct rotation (also called axial rotation or independent rotation) is allowed at a sellar joint; a clockwise movement on an ovoid results in a clockwise conjunct rotation, but the reverse is true for a sellar joint; arcuate movements of a given length on a sellar surface produce more conjunct rotation than does the same movement on an ovoid.

Ovoid and sellar joints have been further divided by MacConnaill into modified and unmodified subclasses, each of which has its own unique functional properties. Every sellar surface is bordered by a pair of convex margins and a pair of concave margins. It is thus divisible into a central part and two marginal parts. If all of these parts are sellar, the surface forms an unmodified sellar unit (e.g. the trapezium-metacarpal I joint). If on one of the sellar surfaces, the two margins are convex in all directions, and on the other these margins are concave, but the central part is sellar shaped, the surface is a modified sellar unit (e.g. the human upper ankle joint). On an ovoid surface there are two principal curvatures measured at right angles to one another. If the difference between these two is great enough to prevent adjunct rotation, the joint is a modified ovoid unit (e.g. the posterior astragalo-calcaneal joint). If the difference between the principal curvatures is not enough to prevent adjunct rotation, the unit is an unmodified ovoid unit (e.g. the human shoulder joint). These are the four structural types of articular units .

MacConaill has also shown that there are only four types of functional articular units based on the kinds of motion permitted at the joint. One type of functional unit allows only an arcuate slide, the second type allows a bichordal (two slides at right angles to each other) and an arcuate slide, the third type allows both bichordal and biarcuate slides, and the fourth type allows bichordal slides, biarcuate slides, and adjunct rotation. Examination of all the joints in the human body has allowed MacConaill to correlate the four structural types of joints with the four functional types of joint movements. This correlation is based on observation only, not on experimental or theoretical proofs (MacConnail, 1973). The correlation is as follows (see Table 6): modified sellars allow only an arcuate slide; unmodified sellars allow one arcuate slide and bichordal slides; modified ovoids allow both biarcuate and bichordal slides; unmodified ovoids allow biarcuate and bichordal slides and independent rotation. Some of the permitted movements may be enhanced or limited by the muscular and ligamentous arrangement of the joint, the extent of the articular surfaces, or by details of joint structure such as bony processes acting as stops to movement. In addition, each of the four structuro-functional classes is associated with a specific number of degrees of freedom. There is a rough inverse correlation between the number of degrees of freedom and the stability of the joint.

This correlation allows comparison to be made between joints not only in form, but in function as well. By classing each joint examined into the structuro-functional classification, and comparing the homologous joints of different species, differences in possible movements and in stability/mobility can be noted, and hopefully related to documented differences in locomotion or posture.

From a preliminary survey of the tarsal bones of primates, it is apparent that joints rarely change in form from one structuro-functional classification to another. Most variation in joint structure takes the form of variation in details of shape and amount of curvature within a class. An attempt was made to document these types of differences as well. One important aspect of joint form is the degree of curvature of the surface, since the maximum amount of angular displacement allowed at a joint is related to this factor. Therefore, an attempt was made to measure the curvatures of some joint surfaces. The curvature of a joint surface was traced from the bone using a drawing tube attached to a Wild stereomicroscope. The recorded arc was then matched as closely as possible to a circle by visually matching the arc to drawn templates of circles graduated by 1 mm. of radius. If an appropriate circle was located, the center of this circle was determined and drawn on the sketch of the arc traced from the bone. By using this center, the degree measurement of the arc could be determined. In addition to the radius of curvature (corrected, of course, for the magnification), and the degree measure of the arc, the length of the arc path was determined by the formula:

Length of arc=(degree measure of arc / 180) * radius * π

This method of measuring arcs suffers from several defects. First of all it must be assumed that all the curvatures to be measured will form parts of true circles. This is almost never true, but in practice the agreement is usually close enough to allow this simple method to be used. It has been successfully used by Inman (1976) in his study of the human ankle joint. In any case, any serious deviations from circularity were noted. The medial and lateral arcs of the astragalar trochlea were almost always easily matched to circles. The curvature of the astragalo-navicular joint, however, was often difficult to analyze, since it tended to flatten out or assume an irregular outline in some groups. A related problem occurred in arcs of small angles (less than 90°). Arcs of this type could easily be matched to several circles, increasing the error involved in determining their radius and degree values. Both arcs of this type (the medio-lateral arc of the posterior astragalocalcaneal joint and the dorsoplantar arc of the AN joint) were, for this reason, not analyzed in this study. A second flaw in this method derives from the fact that the investigator must make subjective judgements on several levels. First, when making a tracing from the bone, care must be taken to orient the bone properly, or at least to orient it in a homologous way in each specimen. This was not always easy to do given the extensive variations in tarsal form which characterize the Strepsirhini. Ideally, the curve should be traced in a position where it is at right angles to the axis of joint movement. Otherwise, the arc may appear ellipsoid rather than circular for the simple reason of parallax (Inman, 1976). This, according to Inman, is the reason Barnett and Napier (1952) found that the lateral arc of the human tibial trochlea was not circular. Inman could match the lateral arc to a circle in 80% of humans if the astragalus was oriented in the proper position.

In theory Inman is correct, but it is extremely difficult to put this idea into practice. To properly orient each bone, one would first have to determine the axis of the joint for each specimen, but no simple nor non-subjective method exists for doing so. I found, however, that it was not inordinately difficult to orient the bones in the same way, and the fact that most traced arcs were fairly close to circularity suggests that it is not impossible to approach the correct orientation without knowing the exact location of the joint axis. Orientations for tracing each particular arc are described with the measurements in Table 5.

Subjective judgments also had to be made as to the circle of best fit, and to the angle of the arc. Another drawback of this method is that it can't be used to measure "negative" arcs, that is, arcs which are formed by depressions in bones (e.g. the distal end of the tibia), unless casts are made of the depressions.

Several checks were made to insure that measurement error was not too great. First, one specimen of medium size (Lepilemur, AMNH 170558) was measured at six different times during the course of the study; an evaluation of the margins of error for each measurement based on this study is presented in Table 7. Secondly, in a small subset of the sample, the circle of best fit was redetermined. Very little discrepancy was observed; although it was common to differ from the original determination by +/- 1mm radius, it was only in rare cases (<3%) that the values differed by more than this. Thirdly, in a small subset of the total sample, the actual length of the traced arc was determined with a map-measure, and compared to the value derived from the formula based on determined radius and angle; in no case did this length vary by more than 20%.

The shape of the measured arc and the degree of the arc are, of course, only indications of the direction and possible range of motion at a joint. First of all, only the bony surface of the joint is measured, not the cartilage on which the movement actually takes place. It is assumed in this study that the smooth facets on bones accurately reflect the extent of the joint cartilage, but this assumption was not tested directly. Other studies have shown, however, that the cartilage of the upper ankle joint in a series of animals is fairly thin (Simon, 1970; 1971), distributed uniformly over the surface of the joint (Wynarsky and Greenwald, 1982) and at least one study has favorably compared the cartilaginous joint surface to the bony joint surface, again in the upper ankle joint (Ziemer and Palfrey, 1979). Secondly, allowances must be made for the overlap of joint surfaces in determining the actual range of motion. Thus, the degrees of curvature presented in this study should not be read as equivalent to the degree of angular displacement. They are only indications of maximum possible displacement.

Although this way of measuring joint curvatures is obviously not ideal, being painstaking, time-consuming, somewhat subjective, and not directly related to any functional attribute, it has many advantages over previous studies of primate postcrania in which joint surfaces were analyzed (e.g. Corrucini et al., 1975; Lisowski et al., 1974). These studies rarely considered the curvatures of joint surfaces, or even the structuro-functional class of the joint. Rather, linear measures of chordal length and breadth were used to characterize joints. This treatment of joint surfaces is very superficial and misses much of the important information contained in the curvatures. In contrast, studies such as Ziemer's (1978) and Inmans's (1976) which analyzed shape and curves of joints have contributed much to our knowledge of joint function.

The position of the axis of joint motion in three dimensional space yields important clues to the direction of movements taking place at a joint. There is no general agreement as to the best method of doing this. Most workers have used a rather simple method in which one member of the articulating pair is held stationary while the other is moved through the range of motion. A point is then located on one side of the moving bone around which no motion occurs. The procedure is repeated on the other side of the bone. These two points define a line which corresponds to the axis of motion of the joint. This method was used by Manter (1941) and Inman (1976). Another method, that of the instantaneous centers of rotation (Sammarco _et al._, 1973) may be preferable, but it depends on obtaining X-rays from living animals.

In this study I attempted to determine the axis of motion for the upper ankle joint and the subtalar joint using the first method outlined above. Although reasonably similar results were obtained in subsequent trials, this method is fairly subjective. It is also virtually impossible to apply it to anything smaller than _Lemur_, since the actual displacements are so small, and the tiny bones are difficult to handle. Only the results for lemurids and indriids are discussed in this work. I have no doubt that significant interfamilial and perhaps even interspecific differences in axis orientations exist, but this method is not sensitive enough to detect them.

Basic statistics (mean, standard deviation, observed range) were derived for each measurement and for indices constructed from those measurements. The statistics were calculated using a Kaypro personal computer and Microplan spreadsheet software.

Table 4. List of specimens of extant primates used in this study.

Lemur fulvus	20
Lemur mongoz	3
Lemur rubriventer	1
Lemur macaco	3
Lemur coronatus	3
Lemur catta	9
Varecia variegata	14
Hapalemur griseus	14
Hapalemur simus	1
Lepilemur mustelinus leucops	13
Daubentonia madagascariensis	6
Avahi laniger	10
Indri indri	11
Propithecus verreauxi	7
Propithecus diadema	11
Microcebus murinus	14
Mirza coquereli	2
Cheirogaleus medius	5
Cheirogaleus major	8
Phaner furcifer	1
Galago senegalensis	6
Galago moholi	9
Galago gallarum	2
Galago elegantulus	16
Galago matschei	1
Galagoides demidovii	9
Galagoides zanzibaricus	1
Galagoides alleni	5
Otolemur crassicaudatus	6
Otolemur garnetti	3
Perodicticus potto	16
Arctocebus calabarensis	11
Nycticebus coucang	12
Loris tardigradus	6
TOTAL	259

Table 5. List of measurements. These are illustrated in Figures 8 and 9.

Astragalus

1. Linear measures.

A1. Length of astragalus. The astragalus is oriented so that the medial and lateral tubercles are flush against one arm of the calipers, and the head of the astragalus is against the other.

A2. Breadth of astragalus. The breadth is taken from the most lateral point of the astragalo-fibular facet (including the entire extent of the lateral projection of this facet, if any) to the most medial point of the astragalo-tibial facet.

A3. Chordal length of trochlea (ATiL(A)). The distance between the most proximal and most distal points of the articular surface for the tibia. Includes the "squatting" facet if any, and full extent of articular surface on the posterior trochlear shelf. The line defining these points is usually oblique to A1.

A4. Chordal width of tibial trochlea [ATiL(A)]. The distance between the most medial and most lateral points of the trochlear crests. Taken at the widest point (in the majority of strepsirhines the two sides are parallel; there is very little wedging of the body of the astragalus). This line is approximately at right angles to A3.

A5. Chordal length of astragalar neck and head. The distance between the most distal point of the tibial trochlea and the most proximal point of the astragalar head. Taken oblique to A1.

A6. Chordal breadth of astragalar head. The distance between the most medial and lateral points of the astragalar head.

A7. Medial height of the astragalus. The bone is oriented in the following manner. The plantar side of the bone is placed atop a glass microscope slide of 1mm. thickness. The lateral side of the bone and both the medial and lateral tubercles lay on the slide (i.e., in the same plane). A thin layer of glue or clay may be used to hold the bone in place. The height is then measured as the distance between the bottom of the glass slide and the most cranial point of the medial trochlear crest; 1 mm. is subtracted from the measurement to compensate for the thickness of the slide.

A8. Lateral height of the astragalus. Same orientation as in A7. Measured as in A7, but from the bottom of the slide to the most cranial point of the lateral trochlear crest.

continued

Table 5, continued.

A9. Chordal length of posterior astragalo-calcaneal facet [pAC(A)]. The distance between the most postero-medial and antero-lateral points of this facet, along the long axis of this facet.

A10. Chordal breadth of posterior astragalo-calcaneal facet. The distance between the most medial and lateral points of this facet. Taken perpendicular to A9.

2. Angular measures.

A11. Astragalar neck angle. Astragalus is oriented as in A1. The astragalar neck angle is formed by the intersection of the long axis of the tibial trochlea and the long axis of the neck of the astragalus. The long axis of the tibial trochlea is estimated as a line drawn from the midpoint of the posterior edge of the trochlea to the midpoint of the anterior edge of the trochlea. The determination of this line is complicated by the slight curvature of the tibial trochlea which exists in strepsirhines. The long axis of the astragalar neck is estimated as a line drawn between the midpoints of the proximal and distal edges of the neck (including the astragalar head). This is the same line along which A5 is taken.

A12. Astragalar head torsion angle. The angle between a line connecting the most cranial points of the medial and lateral trochlear crests and the medio-lateral axis of the astragalar head. Complications arise when the astragalar head approaches circularity, since it then becomes impossible to determine a long axis.

A13. Offset angle of the pAC(A) facet. The angle between a line representing the long axis of the tibial trochlea and a line representing the long axis of the pAC(A) facet.

3. Measures of joint curvature.

A14. Medial trochlear arc. The astragalus is oriented in the following manner. The lateral edge of the bone is pushed into a bed of clay to steady it, and the bone is adjusted until the surface of the tibial facet is more or less parallel to the platform of the microscope. The arc is then traced from its most anterior to its most posterior points as defined by contact with the tibia. Two caveats: In fossil specimens (or extant specimens) without articulating tibiae, the extent of tibial contact was estimated by the extent of the facetted surface. From studying specimens with articulating tibiae, it is obvious that this is an accurate method. Secondly, this arc sometimes flattens out at its anterior end, especially if a "squatting" facet is present. This anterior extension was ignored in the calculations.

continued

Table 5, continued.

A14a. radius of curvature
A14b. degree of curvature
A14c. length of arc

A15. Lateral trochlear arc. The astragalus is oriented in the following manner. The medial side of the bone is pushed into clay to steady it, and the bone is adjusted until the upper part of the fibular facet is approximately parallel to the platform of the microscope. The arc is then traced from its most anterior to its most posterior points as defined by contact with the tibia.
A15a. radius of curvature
A15b. degree of curvature
A15c. length of arc

Calcaneus

1. Linear measures.

C1. Length of calcaneus. The long axis of the calcaneus is parallel to the line of measurement. The distance between the most proximal and most distal points of the bone.

C2. Breadth of calcaneus. Measured from the most lateral tip of the bone to the most medial point of the sustentaculum tali.

C3. Chordal length of posterior astragalo-calcaneal facet [pAC(C)]. The distance between the most proximal and the most distal points of the facet. Slightly oblique to C1.

C4. Chordal breadth of the posterior astragalo-calcaneal facet. The distance between the most medial and most lateral points of the facet, measured at its widest point (generally the distal end). At right angles to C3.

C5. Chordal breadth of cuboid facet. Distance between the most plantar-medial and dorso-lateral points of the cuboid facet.

C6. Chordal height of cuboid facet. The distance between the most dorsal and most plantar points of the cuboid facet. Line of measurement is at right angles to C5.

C7. Heel length. Same orientation as in C1. The distance between the most proximal point of the calcaneus and the most proximal point of the posterior astragalo-calcaneal facet. Generally parallel to C1, but may deviate plantarly, especially in lorisines.

continued

Table 5, continued.

2. Angular measures.

C8. Offset angle of the pAC(C) facet. The angle between the line representing the long axis of the calcaneus and the long axis of the pAC(C) facet.

C9. Cuboid facet angle. The angle between the line representing the long axis of the CCu(C) facet and the horizontal.

3. Measures of joint curvature.

C10. Proximo-distal arc of the posterior astragalo-calcaneal facet. The bone is oriented in the following manner. The lateral side of the calcaneus is pushed into a bed of clay, and the bone is adjusted so that the proximo-distal axis of the facet is parallel to the microscope platform. This usually involves pushing the distal end of the bone further into the clay than the proximal end, since the facet is at a slight angle to the long axis of the calcaneus. The arc is then traced from its most proximal to its most distal points, which are clearly marked by the extent of the facet, but can be double checked by articulating the astragalus.

C10a. radius of curvature
C10b. degree of curvature
C10c. length of arc

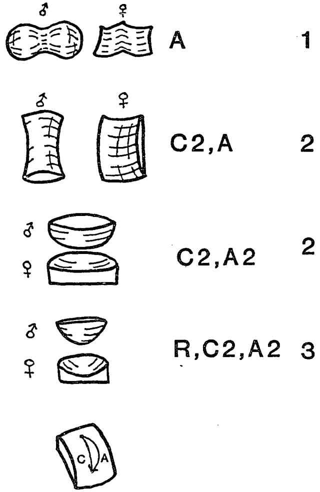

Table 6. The MaConaill structurofunctional classification of joints. After Ziemer (1978). Male and female opposing surfaces are illustrated. Row 1, modified sellar unit. Row 2, unmodified sellar unit. Row 3, modified ovoid unit. Row 4, unmodified ovoid unit. First column, illustration of unit. Column 2, types of motion possible. Column 3, degrees of freedom. A, arcuate slide in one plane; A2, arcuate slides in two planes; C, chordal slide in one plane; C2, chordal slides in two planes; R, independent axial rotation.

Table 7. Results of six-fold measures on *Lepilemur mustelinus*, AMNH 170558. MIN=minimum, MAX= maximum, SD=standard deviation, %DIFFERENCE= [MAX-MIN] * 100/MAX.

MEASURE	MIN	MAX	MEAN	SD	%DIFFERENCE
A1	12.9	13.3	13.2	.15	3.00
A2	7.6	7.8	7.7	.08	2.56
A3	6.0	6.2	6.12	.10	3.23
A4	4.1	4.4	4.23	.12	6.82
A5	6.1	6.8	6.6	.25	10.29
A6	4.6	4.9	4.82	.12	6.12
A7	5.9	6.4	6.08	.17	7.81
A8	5.2	5.7	5.4	.17	8.77
A9	5.1	5.7	5.47	.22	10.53
A10	2.8	3.3	3.07	.02	15.15
A11	15.0	32.0	25.33	5.89	53.13
A12	14.0	20.0	16.83	2.48	30.00
A13	16.0	25.0	21.50	3.33	36.00
A14A	3.17	3.67	3.48	.19	13.63
A14B	160.0	190.00	168.00	7.90	15.79
A14C	9.95	10.51	10.20	.20	5.33
A15A	3.34	3.67	3.50	.15	8.99
A15B	180.0	200.0	189.0	7.0	10.00
A15C	11.0	12.8	11.58	.72	14.06
C1	20.5	20.9	20.78	.15	1.91
C2	6.5	6.9	6.68	.13	5.79
C3	4.6	5.6	5.00	.36	17.86
C4	2.5	2.8	2.65	.10	28.57
C5	4.6	4.9	4.77	.12	6.12
C6	3.3	3.9	3.72	.21	15.38
C7	4.6	5.9	4.97	.47	22.03
C8	11.0	18.0	14.17	2.64	38.89
C9	9.0	14.0	11.83	1.72	35.71
C10A	2.67	3.00	2.78	.13	11.00
C11B	142.0	155.0	149.0	4.0	8.39
C11C	6.89	7.85	7.22	.42	12.23

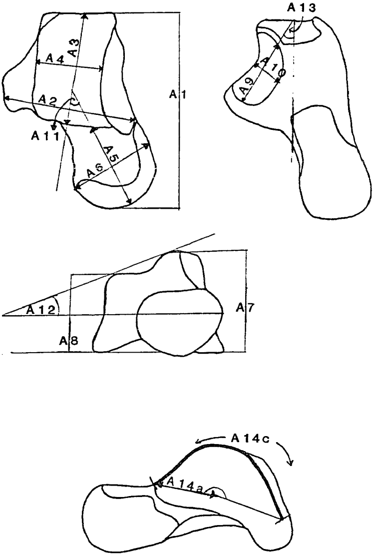

Figure 8. Measurements of the astragalus. See Table 5 for description.

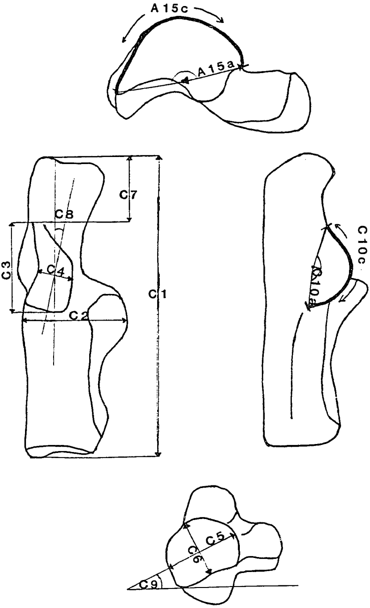

Figure 9. Measurements of the astragalus and calcaneus. See Table 5 for description.

CHAPTER 4: THE UPPER ANKLE JOINT

I. General Remarks. As noted in Chapter 2, the UAJ is a compound articulation between three bones, the astragalus, the tibia and the fibula. But, obviously, the forms of the different articulations dictate motions which complement each other. Movements at the UAJ in primates have been recently analyzed by Lewis (1980a) and Dagosto (1985). The displacements involved are fairly complex as a result of joint shape and orientation.

In all strepsirhines (and indeed in most eutherians; Szalay, 1984) the ATiL is a modified sellar unit. In the MacConaill system this means that only one movement is possible: a single arcuate slide. The main component of this slide is the movement of plantarflexion to dorsiflexion (or vice-versa). The conjunct rotations which necessarily accompany this arcuate slide are medial and lateral rotation of the tibia (relative to a stationary astragalus). Considering a stationary tibia and a moving astragalus, plantarflexion at the UAJ results in an adducted astragalus and dorsiflexion results in an abducted astragalus (Lewis, 1980a; Dagosto, 1985). The relative medial and lateral rotation of the tibia or abduction and adduction of the astragalus are enhanced in strepsirhines by the curvature of the tibial trochlea (ATiL(A)) itself, which arcs medially as it progresses distally (Hafferl, 1932; Lewis, 1980a; Dagosto, 1985). Thus, the ATiL is a section of a helix. Part of the medial rotation of the tibia results from its translating medially along the axis of rotation at the UAJ.

Relative rotation of the tibia (=abduction\adduction of the astragalus) is also reflected in the position of the axis of motion at the UAJ. The axis of rotation at the UAJ was determined in a lemur and a sifaka (fig. 10). In both, the axis is inclined dorsomedially and posterolaterally as in humans. There was no evidence for separate dorsiflexion and plantarflexion axes as Barnett and Napier (1952) found in humans. The inclination of the joint motion axis means that it is not identical or parallel to any of the reference axes of the foot. Thus, motion around this axis cannot be purely around any of the reference axes, but must involve concomitant displacements in all three planes. Perhaps this is best understood by examining separately the effects of different axis placement (see fig. 11).

If the joint motion axis were identical to reference axis 2, motion around the axis would be pure plantar- and dorsiflexion (fig. 11b). If the axis were identical to reference axis 3, motion around the axis would yield abduction and adduction (fig. 11c). If the axis were identical to reference axis number 1, pure supination and pronation would be the result (fig. 11a).

The dorsomedial orientation of the axis may be thought of as the resultant of a combination of the pure flexion-extension axis and the pure abduction-adduction axis (fig. 12a). Thus, motion around this resultant axis is a combination of both flexion-extension and abduction-adduction. In this particular case, (dorsomedial orientation), dorsiflexion is combined with abduction and plantarflexion with adduction (considering a stationary tibia and a moving astragalus).

In Lemur and Propithecus the resultant axis is not strongly dorsomedially inclined (30-45°); the flexion-extension component is dominant to the abduction-adduction component. Thus, the flexion-extension component of motion is more obvious than the abduction-adduction component.

Similarly, the posterolateral inclination of the axis is a resultant of the flexion-extension axis and the pronation-supination axis (fig. 12b). In this case, dorsiflexion is accompanied by concomitant pronation; plantarflexion with concomitant supination. Again, the flexion-extension component is dominant to the pronation-supination one; the amount of concomitant pronation-supination must be small.

The combination of both the dorsomedial and posterolateral inclinations of the axis result in motion such that dorsiflexion (of the foot at the UAJ) gives concomitant displacements of abduction and pronation; plantarflexion is combined with adduction and supination fig 12c). Considering a stationary astragalus and a moving tibia, dorsiflexion at the UAJ yields a medially rotated and laterally angled tibia; plantarflexion a laterally rotated and medially angled one.

If the lamina pedis is considered as a passive appendage to the astragalus during UAJ motion, it must become relatively pronated during dorsiflexion, as a result of the orientation of the UAJ axis. This would appear to be disadvantageous to animals which need to have supinated feet (in order to grasp a branch) regardless of UAJ position. Of course, any concomitant or conjunct pronation that occurs during dorsiflexion (or supination during plantarflexion) can be compensated for (or enhanced) by movement between the astragalus and the lamina pedis at the transverse tarsal and subtalar joints. It appears that motion at the UAJ and the other two joints is relatively independent. Thus, the lamina pedis (but not the astragalus) can be pronated or supinated regardless of UAJ position. In fact, putting the astragalus into an everted position (as happens in dorsiflexion) actually opens up room for full inversion of the lamina pedis at the STJ and TTJ. In full dorsiflexion, the astragalus close packs into the tibia, and functionally becomes part of the leg; the lamina pedis is free to move around it. It should also be noted that all muscles capable of working the UAJ cross the TTJ and STJ as well, and can either pronate or supinate the foot.

Relative abduction\adduction movements of the astragalus during dorsiflexion and plantarflexion are determined by three factors. One, the conjunct rotation demanded by arcuate motion at a modified sellar joint; two, the helical nature of the ATiL(A) facet relative to the joint axis; and three, the concomitant displacement due to the dorso-medial orientation of the UAJ axis. It is difficult to determine the relative significance or interrelatedness of these factors.

Movements at the ATiM and AFi joints complement those at the ATiL. The ATiM is an ovoid articulation; the surface on the astragalus (ATiM(A)) is concave; the surface on the tibia (ATiM(Ti)) is convex. Like the ATiL(A), the ATiM(A) is curved; it swings medially as it progresses distally and thus ends in a cuplike depression on the posterior aspect of the astragalar neck. The ATiM(Ti) is likewise medially rotated; it faces approximately 20°-40° from the sagittal plane (Dagosto, 1985; Table 8a). This curvature and orientation of the ATiM allow the medial side of the astragalus to rotate around the medial malleolus of the tibia during dorsi- and plantarflexion at the UAJ, reflecting the conjunct and concomitant abduction and adduction of the astragalus which are necessary components of these movements. In full dorsiflexion the medial malleolus fits snugly into the ATiM(A) cup, locking the tibia and astragalus into the close packed position (Lewis 1980; Dagosto, 1985).

The actual displacements of the fibula relative to the astragalus during dorsi- and plantarflexion are very difficult to analyze from disarticulated bones, since they appear to be very slight. Similar problems have plagued the study of the human AFi, and there is still no general agreement as to the relative motions of the fibula. Although most authors agree that some combination of tibiofibular separation, fibular rotation, and\or dorsoplantar displacement of the fibula must occur, the relative importance of, and actual combination of movements occurring is the subject of some debate [see Inman (1976) and Reimann and Anderhuber (1980) for discussion].

The most obvious disagreement concerns the axial rotation of the fibula. Most authors (Barnett and Napier, 1952, 1953; Lewis, 1980a) state that during dorsiflexion the fibula rotates laterally about its own long axis. Kapandji (1970), however, finds that it rotates medially. Both kinds of rotation were reported for humans by Reimann and Anderhuber (1980).

In strepsirhines it seems that the motion of the fibula relative to the astragalus and tibia is fairly complex. If maximum congruence between the astragalus and fibula is maintained throughout a course from full plantarflexion to full dorsiflexion, it appears that the fibula first rotates medially, then reverses midway to begin a lateral rotation. In full dorsiflexion, then, the fibula *is* laterally rotated relative to its original plantarflexed position, although this rotation is not continuous throughout its course of motion. This sinuous path is a result of the complex shape of the AFi(A) which posteriorly is an ovoid surface (but fairly flat), but anteriorly is sellar shaped. As MacConaill has demonstrated (1946, 1966, 1973), the sense of conjunct rotations at ovoids and sellars is different. Thus, if swing in a particular direction on an ovoid surface results in a clockwise conjunct rotation, travel in the same direction on a sellar surface will result in a counterclockwise conjunct rotation.

In addition to this factor of joint shape, joint orientation also affects the relative movement of the tibia. Hafferl (1932) noted that only the medial edge of the ATiL(A) curves medially; the lateral edge is nearly straight, or may (rarely) flare laterally. This would force the tibia to rotate medially *more* than the fibula. Thus, even if *both* the tibia and fibula rotate medially, *relative* to the tibia, the fibula would appear to have laterally rotated.

Whether actual lateral rotation of the fibula occurs, or if the tibia rotates medially more than the fibula, it is obvious that some relative motion between the tibia and fibula must occur in full dorsiflexion. This is accommodated by the synovial joint between the distal ends of the tibia and fibula (Carleton, 1941; Dagosto, 1985).

In all strepsirhine taxa examined, the close packed position for the ATiL, the ATiM, and probably the AFi joints is that of dorsiflexion. The astragalus appears to be remarkably loose in the mortise formed by the tibia and fibula in any other position.

II. Variations among extant strepsirhines in the UAJ. (figs. 13-19).

A. Lemuridae. The ATiL(A) is a modified sellar surface. The lateral crest is usually slightly sharper than the medial, but the crests are of approximately equal height. The depth of the surface is variable, but generally moderately deep. Anteriorly, the ATiL(A) ends in a flat "squatting facet" on the neck of the astragalus; this articulates with a facet on the anterior face of the distal tibia in extreme dorsiflexion. Posteriorly, the ATiL(A) extends onto the posterior astragalar shelf which is of moderate extent in lemurids. The length of the ATiL(A) is about 50% of total astragalar length (Table 9a).

The ATiL(A) tapers posteriorly so that it appears to extend further medially than laterally. This is a result of the rotations undergone by the astragalus and tibia during plantarflexion, so that in the plantarflexed position, the lateral edge of the tibia becomes posteromedially angled.

The ATiL(Ti) is quadrangular. The anterior and posterior edges diverge from each other laterally. The anteroposterior dimension of this facet exceeds the mediolateral, reflecting the longer than wide ATiL(A) (Dagosto, 1985; Table 8b). The divergence of the anterior and posterior edges of the ATiL(Ti) reflects the longer lateral edge of the ATiL(A).

In all taxa the ATiM(A) is an ovoid joint which curves medially. This curvature is much less marked in *Lepilemur* and to a lesser extent in *Hapalemur*, as is common in other primates where leaping is emphasized (Dagosto, 1985). The medial malleolus [ATiM(Ti)] of lemurids faces 12-40° from the sagittal plane (Table 8a). *Lepilemur* exhibits lower rotation values than do other lemurids, as do many specialized leapers (Dagosto, 1985).

Lepilemur has a higher angle of curvature ($p < .01$), a higher astragalar body ($p < .001$), and a longer ATiL(A) arc than lemurids.

There are no significant variations in the shape of the AFi(A) or AFi(Fi) among lemurids.

B. Indriinae. The general shape of the ATiL(A) is like that of lemurids. The trochlea is moderately deep in *Indri* and *Propithecus*, but very shallow in *Avahi*. The most striking difference from lemurids is the greater development (posterior extension) of the posterior trochlear shelf. The posterior rather than plantar extension of the shelf might slightly reduce the degree of plantarflexion possible.

Extant indriines also have a marked medio-plantar twisting of the shelf (fig. 14). Theoretically this would increase the degree of lateral rotation of the tibia which accompanies plantarflexion. Also as a result of this twisting, the groove for fl. hall. long. is plantarmedially angled in indriines rather than transverse as in lemurids; and the pAC(A) facet is lifted dorsally. This may indicate that the posterior part of the astragalus is more strongly buttressed in the inverted rather than everted position, and is possibly related to the vertically clinging positon, although other vertical clingers (bushbabies, *Lepilemur*) do not share this feature.

The purpose of the posterior trochlear shelf is obscure. Some development is probably a primitive character for all euprimates (Decker and Szalay, 1974). An especially large posterior trochlear shelf is found in all extant indriines and notharctines, although the latter taxa do not share the twisting of the process. Reduction or loss of the shelf is characteristic of lorisids, most omomyids, and *Tarsius*. Distribution alone provides no clue to its function. Dagosto (1983) suggested that the shelf provides a buttress for a plantarflexed foot in push off, but the absence of a shelf in galagids and *Tarsius* weakens this hypothesis. The extent of the posterior trochlear shelf also serves to elongate the pAC(A) (Szalay and Decker, 1974) and flatten it somewhat, matching the attenuated flattened pAC(C) (see Chapter 5).

The ATiM(A) of indriines is perhaps slightly less medially curved than in lemurids. They also have somewhat less malleolar rotation than lemurids, as do other frequent leapers like *Lepilemur* and galagines (Table 8a). These two features suggest that UAJ dorsi- and plantarflexion are accompanied by less conjunct and concomitant rotation than in lemurids. Indriines have higher radii of curvature, ATiL(A) arc lengths, and higher astragalar bodies than lemurids (Tables 10b; 11a,b).

The shape of the AFi(A) and AFi(Fi) facets are the same as in lemurids, suggesting that the same types of motions occur. The AFi(A) in somewhat less laterally protrusive in indriines than in lemurids.

C. *Daubentonia*. *Daubentonia* has some very distinctive features which distinguish this genus from all other extant strepsirhines. It is the only strepsirhine in which the ATiL(A) is noticeably wedged; it is narrower proximally than distally (Hafferl, 1932). *Daubentonia* is also unique in the extremely low relief of the ATiL(A); only *Avahi* approaches it in this trait. The joint thus approaches an ovoid. This has two probable mechanical consequences. The UAJ of *Daubentonia* would tend to be less stable than that of other strepsirhines, possibly allowing some medio-lateral rocking within the ankle mortise. The flattened surface of the ATiL(A), along with the lesser curvature of this facet and the ATiM(A), make it likely that *Daubentonia* has less concomitant abduction-adduction or supination-pronation accompanying flexion and extension at the UAJ. This is somewhat puzzling, as except for the shallow ATiL(A), this is morphology and mechanics that one would be more likely to expect in a committed leaper than in a climber like *Daubentonia*.

The posterior trochlear shelf of *Daubentonia* is moderately extensive posteriorly. It is not twisted as in indriines.

D. Cheirogaleidae. There are no major differences from lemurids. *Microcebus* has a reduced posterior trochlear shelf compared to *Cheirogaleus* major. Cheirogaleids do exhibit shorter ATiL(A) lengths relative to astragalar length (Table 9a). However, their ATiL(A) lengths are not different when compared to STL (Table 9b). This suggests that cheirogaleids have relatively longer astragali than other strepsirhines, and that this increased length is due to a relatively longer astragalar neck.

E. Galaginae. The general morphology of the ATiL(A) is similar to that of lemurids. The posterior trochlear shelf is very reduced; remaining largest in *Galago elegantulus*. The anterior process of the tibia is more distally extensive in galagines. Correspondingly, the pit for its articulation at the distal end of the ATiL(A) is deeper, providing a stable lock in dorsiflexion. In galagines, the ATiL(A) and ATiM(A) curve less, and the lateral flare of AFi joint is reduced.

In galagines, the body of the astragalus is higher relative to STL than in other strepsirhines (Table 10b). This is partly the result of a higher radius of curvature at the UAJ (Table 11a). Indriines are the only strepsirhines with higher radii of curvature. The angle of curvature at the UAJ is significantly higher ($p < .001$) in galagines.

F. Lorisinae. Hafferl (1932) correctly recognized that lorisines exhibit the strongest medial curvature of the ATiL(A) and ATiM(A) facets, and have the most marked cupping of the ATiM(A). The AFi(A) projects further laterally than in other strepsirhines. The rotation of the medial malleolus is greater than in non-lorisines. Thus, the amount of abduction\adduction accompanying dorsi- and plantarflexion is likely to be greater in lorisines than in other strepsirhines. As in galagos the posterior trochlear shelf is absent. The groove for fl. fibularis is not posterior to the ATiL(A), but is shifted laterally in all lorisines. The ATiM(A) is deeper than in other strepsirhines. It tends to be strongly concave for its entire length, as opposed to only anteriorly.

The proportions of the astragalus are distinctive in lorisines (Dagosto, 1983). The ATiL(A) is longer relative to astragalar length (Table 9a) and the body is higher (Table 10a). If STL is used as the normalizing variable, however, ATiL(A) length is actually shorter in lorisines (Table 9b), and the body of the astragalus is relatively low (Table 10b). This results from the fact that lorisines have a very different relationship between STL and astragalar length than other strepsirhines (fig. 20). For a given body size, a loris will have a shorter astragalus than will another strepsirhine. The lesser height of the body is partly the result of a lower radius of curvature at the UAJ (Table 11a).

Lorisines exhibit lower angles of UAJ curvature than other strepsirhines, averaging 153° compared with 170°. This, along with the lower radius of curvature at this joint, explains the relatively smaller length of arc (Table 11b) in lorisines.

III. Summary of UAJ features (see Table 12).

The form of the UAJ in strepsirhine primates is a result of two conflicting selective pressures: mobility, which permits the foot to adopt variable orientations; and stability, which is necessary for weight support (in pronograde positions) and to conserve energy in leaping. Given the constraints to mobility at the UAJ dictated by the tenon-mortise form of the primitive eutherian ankle joint (Szalay, 1984), strepsirhine primates could only increase mobility at the UAJ by developing the curvatures and rotations of the ATiL, ATiM, and AFi joints (Dagosto, 1985). These features allow curvilinear astragalar motion, which adds conjunct and concomitant displacements to the main motion of dorsiflexion and plantarflexion. Lewis (1980a) has related this suite of features specifically to grasping. The increase in attainable abduction of the foot is certainly important for the grasping posture of the foot. However, I believe that there is a more general relationship to the requirements of the arboreal milieu. Such a morpho-functional complex is well suited for allowing the foot to attain variable orientations; the dorsiflexed-abducted-pronated position of the astragalus allows for the full range of motion of the lamina pedis at the STJ and TTJ.

Among strepsirhines the slow-climbing lorisines exaggerate these conditions, increasing the amount of conjunct and concomitant displacements accompanying UAJ motion. The greater lateral flare of the AFi joint provides support for an astragalus which attains a more pronated position due to exaggerated UAJ, STJ, and TTJ motion. Actual displacement at the UAJ is probably less in lorisines than in other strepsirhines given the lower angle of displacement, smaller radius of curvature, and lower arc length at the UAJ.

Strepsirhines which leap frequently (Lepilemur, indriines, galagines) exhibit completely opposite trends. The curvature of the ATiL, ATiM, and the rotation of the medial malleolus are all less than in lorisines or in other strepsirhines like lemurids. These features tend to limit dorsi-and plantar flexion to a more purely parasagittal plane. The AFi(A) is more vertical, again reflecting the more parasagittal motion of the UAJ. The angle of displacement is generally higher in these leapers than in other strepsirhines; indriines are an exception with angles similar to those of lemurids. Assuming that the overlap of the ATiL(A) and ATiL(Ti) is similar in the two groups of strepsirhines, as it appears to be, the range of motion at the UAJ is increased in leapers. The increased angle of curvature at the UAJ plus the higher radius of curvature evidenced in leapers, yields a relatively greater length of arc. The benefit provided by a greater radius of curvature, however, is not clear.

Table 8. Indices and measurements of the upper ankle joint. For this and following tables, top row of each species is mean, standard deviation; bottom row is observed range, number of individuals.

	A		B		C	
	Rotation of Tibial Malleolus		ATiL(Ti) AP/ML		angle of lateral ATiL(A) [A15b]	
Lemur fulvus	34.27	3.4	124.59	7.6	178.10	9.5
	30-37	11	109.00-135.00	12	165-190	17
Lemur mongoz			122.22	-	142.00	-
			-	1	-	1
Lemur macaco			129.68	-		
			-	1		
Lemur rubriventer					180.00	-
					-	1
Lemur coronatus	35.00	-	123.64	-	155.00	-
	-	1	-	1	135-180	3
Lemur catta	30.00	-	127.75	-	162.00	16.2
	-	1	115.79-139.70	2	150-190	5
Varecia variegata	37.00	-	126.92	-	180.18	9.1
	-	1	126.44-127.40	2	169-193	11
Hapalemur griseus	34.67	4.0	128.28	12.4	178.78	11.7
	30-37	3	114.3-145.80	5	155-190	9
Hapalemur simus					170.00	-
					-	1
Lepilemur mustelinus	24.46	6.9	116.21	8.4	187.75	5.7
	12-35	13	103.6-135.5	14	180-19	12
Daubentonia madagascariensis	45.00	-	140.56	-	172.40	5.3
	-	1	127.14 153.97		165-180	5
Avahi laniger	28.00	-	112.24	-	172.22	11.3
	-	1	107.69-116.18	3	147-180	9
Propithecus verreauxi	31.00	-	124.41	-	171.00	6.1
	29-37	3	119.76-128.75	3	160-180	7

Table 8, continued.

	A		B		C	
	Rotation of Tibial Malleolus		ATiL(Ti) AP/ML		angle of lateral ATiL(A)	
Propithecus	22.00	-	117.65	-	175.11	6.7
diadema	-	1	-	1	170-190	9
Indri indri	32.00	-	128.30	-	174.64	11.2
	-	1	-	1	160-195	11
Microcebus	29.25	4.6	133.88	13.5	184.27	8.9
murinus	22-36	12	115.00-160.00	13	173-200	15
Mirza coquereli					180.00	-
					-	1
Cheirogaleus					178.33	-
medius					175-180	3
Cheirogaleus	44.00	-	123.68	-	181.25	6.3
major	-	1	-	1	175-190	4
Galago	25.00	-	131.58	-	184.00	13.5
senegalensis	-	1	-	1	168-200	5
Galago moholi	28.80	1.9	115.90	7.7	183.57	8.0
	26-31	5	107.69-124.33	5	175-195	7
Galago gallarum	25.00	-	118.92	-	190.00	-
	-	1	-	1	-	1
Galago	25.00	-	114.29	-	181.33	12.2
elegantulus	-	1	-	1	170-200	12
Galago					185.00	-
matschei					-	1
Galagoides	26.00	5.1	114.34	8.3	184.43	7.0
demidoff	20-30	5	100.00-120.00	5	175.196	7
Galagoides			121.88	-	195.00	-
zanzibaricus			-	1	-	1
Galagoides			104.54	-	186.25	7.7
alleni			-	1	175-192	4

Table 8, continued.

	A		B		C	
	Rotation of Tibial Malleolus		ATiL(Ti) AP/ML		angle of lateral ATiL(A)	
Otolemur	32.00	-	123.70	-	180.00	0
crassicaudatus	30-34	2	123.61-126.09	3	180	5
Otolemur					183.33	2.3
garnetti					180-185	3
Perodicticus	35.83	4.17	139.85	17.14	153.57	16.7
potto	30-42	6	111.32-161.90	7	120-180	14
Arctocebus	48.00	-	147.00	-	141.88	13.8
calabarensis	-	1	144.00-150.00	2	123-160	8
Nycticebus	37.00	-	136.10	-	160.10	16.0
coucang	-	1	130.00-140.00	3	128-180	10
Loris	49.00	-	138.09	-	161.40	10.2
tardigradus	42-56	2	123.53-150.00	3	145-170	5
Lemuridae*	34.05	3.4	125.89	8.4	174.60	14.1
	30-37	18	109.46-145.80	24	135-190	48
Indriinae	29.17	5.0	119.48	7.4	173.44	9.2
	22-37	6	107.69-128.75	8	147-195	36
Cheirogaleidae	30.38	6.0	133.15	13.2	182.78	7.8
	22-44	13	115.00-160.00	14	173-200	23
Galaginae	27.64	3.4	117.41	8.6	183.30	8.9
	20-34	14	100.00-126.09	15	168-200	43
Lorisinae	39.80	7.6	139.70	12.96	153.87	16.2
	30-56	10	111.32-161.90	15	120-180	37

*Lemuridae does *not* include *Lepilemur* in this or any other table.

Table 9. Indices and measurements of the upper ankle joint. Conventions as in Table 8.

	A ATiL(A) length/ astragalar length [A3/A1]*100		B ATiL(A) length/ STL [A3/STL]*100	
Lemur fulvus	53.79	4.4	3.26	.17
	43.83-61.69	20	2.75-3.45	13
Lemur mongoz	49.79	4.8	2.73	-
	43.95-55.07	4	2.70-2.76	2
Lemur macaco	53.80	4.3	3.34	-
	49.70-58.33	4	3.28-3.39	2
Lemur	50.58	-	3.41	-
rubriventer	-	1	-	1
Lemur	48.54	5.1	2.70	-
coronatus	43.08-53.24	3	2.50-2.90	2
Lemur catta	51.67	2.8	3.15	.09
	47.31-55.00	7	3.06-3.28	8
Varecia	53.65	3.9	3.13	.32
variegata	47.02-59.18	11	2.64-3.56	8
Hapalemur	54.12	3.3	3.39	.27
griseus	48.85-61.11	10	3.12-3.73	6
Hapalemur	50.85	-	3.39	-
simus	-	1	-	1
Lepilemur	48.20	4.7	3.46	.38
mustelinus	38.21-58.55	14	2.72-4.34	13
Daubentonia	54.26	6.9	3.63	.38
madagascariensis	44.44-60.95	5	3.11-4.01	5
Avahi laniger	55.11	3.6	4.43	.43
	49.02-61.59	10	3.73-5.06	9
Propithecus	50.38	3.9	3.56	.45
verreauxi	44.44-56.93	7	3.23-4.33	5

continued

Table 9, continued.

	A		B	
	ATiL(A) length/ astragalar length		ATiL(A) length/ STL	
Propithecus diadema	54.97 47.62-64.68	4.7 10	4.05 3.70-5.00	.41 9
Indri indri	52.72 46.01-60.80	5.6 11	4.08 3.58-4.58	.38 10
Microcebus murinus	44.7 36.67-52.08	5.1 14	3.15 2.88-3.42	.19 6
Mirza coquereli	53.74 52.53-54.95	- 2	3.56 -	- 1
Cheirogaleus medius	54.64 49.04-59.02	3.8 5	2.93 2.73-3.20	- 3
Cheirogaleus major	52.52 48.82-55.67	2.8 5	3.10 2.74-3.47	.30 4
Phaner furcifer	49.04 -	- 1	3.68 -	- 1
Galago senegalensis	50.03 47.73-51.56	- 6	3.99 3.67-4.13	.22 4
Galago moholi	53.94 49.35-60.81	3.8 9	3.99 3.69-4.29	.26 5
Galago gallarum	57.61 55.95-59.26	- 2		
Galago elegantulus	46.62 39.00-51.11	3.5 16	3.30 2.85-3.64	.27 10
Galago matschei	56.10 -	- 1	4.64 -	- 1
Galagoides demidoff	53.17 46.67-56.25	3.1 8	3.66 3.50-3.88	.14 6
Galagoides zanzibaricus	54.43 -	- 1	4.24 -	- 1

continued

Table 9, continued

	A		B	
	ATiL(A) length/ astragalar length		ATiL(A) length/ STL	
Galagoides	51.59	5.1	3.99	.39
alleni	45.00-59.09	5	3.66-4.57	5
Otolemur	56.02	1.4	3.73	-
crassicaudatus	54.30-57.93	6	3.63-3.82	2
Otolemur	52.46	-	3.92	-
garnetti	50.75-53.91	3	3.82-4.00	3
Perodicticus	63.37	5.5	3.37	.20
potto	51.35-70.69	15	3.08-3.54	8
Arctocebus	62.70	3.3	2.43	.20
calabarensis	56.06-67.14	9	2.15-2.81	8
Nycticebus	62.76	5.7	3.16	.23
coucang	49-73.45	11	2.68-3.35	7
Loris	62.20	3.7	3.13	.23
tardigradus	56.52-65.82	6	2.86-3.41	5
Lemuridae	52.84	4.1	3.19	.27
	43.83-61.69	62	2.50-3.45	41
Indriinae	53.51	4.8	4.09	.48
	44.01-64.68	38	3.23-5.06	33
Cheirogaleidae	48.82	6.0	3.15	.29
	36.67-59.02	27	2.73-3.68	15
Galaginae	51.48	4.6	3.75	.39
	39.00-60.81	57	2.85-4.64	37
Lorisinae	62.88	4.7	3.01	.43
	51.35-73.45	41	2.15-3.54	28

Table 10. Indices and measurements of the upper ankle joint. Conventions as in Table 8.

	A				B			
	lateral height/ astragalar length [A8/A1]*100				lateral height/ STL [A8/STL]*100			
Lemur fulvus	43.04	1.8	40.57-46.58	12	2.58	.09	2.41-2.71	8
Lemur mongoz	40.98	-	34.78-47.17	2				
Lemur macaco	38.46	-	-	1				
Lemur rubriventer	44.19	-	-	1	2.98	-	-	1
Lemur coronatus	43.17	-	-	1				
Lemur catta	43.90	1.8	41.98-46.25	5	2.58	.08	2.47-2.66	4
Varecia variegata	45.23	1.7	43.64-48.28	8	2.64	.07	2.53-2.75	7
Hapalemur griseus	43.71	1.6	41.22-45.52	10	2.69	.09	2.56-2.80	6
Hapalemur simus	43.50	-	-	1	2.91	-	-	1
Lepilemur mustelinus	40.30	1.7	38.46-43.90	14	2.91	.15	2.67-3.12	13
Daubentonia madagascariensis	42.67	-	42.13-43.20	2	2.91	-	2.88-2.93	2
Avahi laniger	38.37	1.4	36.24-40.52	6	3.10	.19	2.86-3.42	6
Propithecus verreauxi	39.77	2.1	37.62-43.17	5	2.86	-	.83-2.90	3

Table 10, continued.

	A			B		
	LH/AL			LH/STL		
Propithecus	41.96	-		3.16	-	
diadema	40.08-44.26		3	3.01-3.42		3
Indri indri	40.57	2.6		3.14	.21	
	36.16-43.54		7	2.82-3.40		7
Microcebus	37.91	4.1		2.59	.24	
murinus	29.69-44.23		14	2.46-3.03		6
Mirza coquereli	40.66	-				
	-		1			
Cheirogaleus	39.55	-				
medius	38.57-40.54		2			
Cheirogaleus	43.33	.90		2.57	.13	
major	42.11-44.23		4	2.39-2.62		4
Galago	43.02	-		3.42	-	
senegalensis	-		1	-		1
Galago moholi	40.58	2.1		3.21	-	
	39.33-43.42		6	3.20-3.22		2
Galago gallarum	43.65	-				
	42.86-44.44		2			
Galago	40.12	-		2.97	-	
elegantulus	38.30-41.94		2	-		1
Galagoides	42.37	-		3.13	-	
demidoff	-		1	-		1
Galagoides	40.51	-		3.16	-	
zanzibaricus	-		1	-		1
Galagoides	42.05	-		3.25	-	
alleni	-		1	-		1
Otolemur	44.46	1.6		2.96	-	
crassicaudatus	42.57-56.21		4	2.90-3.01		2

Table 10, continued.

	A		B	
	LH/AL		LH/STL	
Otolemur	45.74	-	3.41	-
garnetti	-	1	-	1
Perodicticus	47.83	5.0	2.50	.20
potto	43.40-55.45	9	2.24-2.77	7
Arctocebus	58.12	5.3	2.23	.25
calabarensis	46.38-63.34	10	1.80-2.53	9
Nycticebus	44.77	3.3	2.33	.17
coucang	40.37-48.67	6	2.23-2.59	4
Loris	45.05	2.4	2.34	.13
tardigradus	43.48-48.68	4	2.16-2.47	4
Lemuridae	43.56	2.4	2.65	.12
	34.78-48.28	41	2.41-2.98	27
Indriinae	39.95	2.31	3.09	.20
	36.16-44.26	21	2.82-3.42	19
Cheirogaleidae	39.23	4.0	2.59	.19
	29.69-44.23	21	2.46-3.03	6
Galaginae	42.25	2.4	3.17	.17
	38.30-46.21	19	2.90-3.42	10
Lorisinae	50.37	7.3	2.34	.23
	40.37-63.34	29	1.80-2.77	24

Table 11. Indices and measurements of the upper ankle joint. Conventions as in Table 8.

	A		B	
	Radius UAJ/ STL [A15a/STL]*100		Arc length UAJ/ STL [A15c/STL]*100	
Lemur fulvus	1.81	.15	5.63	.40
	1.54-1.98	12	5.17-6.34	12
Lemur mongoz	1.71	-	4.35	-
	-	1	-	1
Lemur rubriventer	2.19	-	6.89	-
	-	1	-	1
Lemur coronatus	1.78	-	5.39	-
	1.76-1.79	2	4.16-6.62	2
Lemur catta	1.94	.10	5.26	.22
	1.79-2.04	4	4.97-5.46	4
Varecia variegata	1.72	.06	5.46	.26
	1.62-1.82	9	5.08-5.80	9
Hapalemur griseus	1.88	.27	5.67	.60
	1.49-2.21	6	4.90-6.06	6
Hapalemur simus	2.00	-	5.96	-
	-	1	-	1
Lepilemur mustelinus	1.82	.15	6.02	.46
	1.56-2.06	12	5.56-6.70	10
Daubentonia madagascariensis	2.07	.07	6.20	.31
	1.95-2.14	5	5.90-6.72	5
Avahi laniger	2.41	.16	7.17	.33
	2.24-2.69	9	6.85-7.79	9
Propithecus verreauxi	2.14	.18	6.30	.40
	1.95-2.34	5	5.92-6.88	5
Propithecus diadema	2.09	.21	6.39	.67
	1.86-2.46	10	5.53-7.80	9

Table 11, continued.

	A		B	
	Radius UAJ/ STL		Arc length UAJ/ STL	
Indri indri	2.18	.21	6.62	.90
	1.84-2.46	10	5.31-8.34	10
Microcebus	1.65	.11	5.12	.40
murinus	1.53-1.71	6	4.56-5.67	6
Mirza coquereli	1.78	-	5.55	-
	-	1	-	1
Cheirogaleus	1.58	-	4.60	-
medius	1.53-1.61	3	4.43-4.71	3
Cheirogaleus	1.55	.12	4.85	.46
major	1.37-1.63	4	4.24-5.34	4
Galago	2.18	.19	7.25	-
senegalensis	1.89-2.30	4	6.65-7.39	3
Galago moholi	2.27	-	7.37	.37
	2.23-2.26	3	7.08-7.91	4
Galago	1.99	.13	6.25	.33
elegantulus	1.79-2.10	8	5.71-6.79	8
Galago	2.32	-	7.57	-
matschei	-	i	-	1
Galagoides	1.93	.10	6.20	.34
demidoff	1.79-2.06	6	5.84-6.75	6
Galagoides	2.07	-	7.01	-
zanzibaricus	-	1	-	1
Galagoides	2.05	.10	6.66	.16
alleni	1.95-2.20	4	6.43-6.81	4
Otolemur	2.08	-	6.50	-
crassicaudatus	2.07-2.08	2	6.49-6.51	2
Otolemur	2.06	-	6.65	-
garnetti	1.86-2.20	3	5.92-7.27	3

continued

Table 11, continued.

	A		B	
	Radius UAJ/ STL		Arc length UAJ/ STL	
Perodicticus	1.89	.28	5.08	.80
potto	1.35-2.20	8	3.84-6.01	8
Arctocebus	1.34	.20	3.36	.37
calabarensis	.95-1.49	7	2.86-4.02	7
Nycticebus	1.53	.31	4.17	.78
coucang	1.41-2.06	6	3.41-5.57	6
Loris	1.42	.22	3.94	.42
tardigradus	1.17-1.71	5	3.45-4.31	5
Lemuridae	1.82	.17	5.55	.57
	1.49-2.21	36	4.16-6.89	36
Indriinae	2.21	.22	6.66	.71
	1.84-2.69	33	5.31-8.34	33
Cheirogaleidae	1.61	.11	4.96	.43
	1.37-1.71	14	4.24-5.67	14
Galaginae	2.07	.16	6.64	.56
	1.79-2.32	33	5.71-7.91	33
Lorisinae	1.57	.33	4.19	.90
	.95-2.20	26	2.86-6.01	26

Table 12. Summary of distribution of features of the UAJ.

TAXON	
LEMURIDAE	moderate medial curvature of ATiL(A)
	moderate medial curvature of ATiM(A)
	rotation of medial malleolus 30-37°
	moderate flaring of AFi(A)
	angle of curvature of UAJ 175°
	radius of curvature of UAJ/STL 1.82
	ATiL(A) length /STL 3.19
	height of astragalus/STL 2.65
	arc length UAJ/STL 5.55
INDRIINAE	reduced medial curvature of ATiL(A)
	reduced medial curvature of ATiL(M)
	rotation of medial malleolus 22°-37°
	reduced flaring of AFi(A)
	angle of curvature of UAJ 174°
	radius of curvature of UAJ/STL 2.21
	ATiL(A) length/STL 4.09
	height of astragalus/STL 3.09
	arc length of UAJ/STL 6.66
CHEIROGALEIDAE	moderate medial curvature of ATiL(A)
	moderate medial curvature of ATiM(A)
	rotation of medial malleolus 22-44°
	moderate flaring of AFi(A)
	angle of curvature of UAJ 183°
	radius of curvature of UAJ/STL 1.61
	ATiL(A) length/STL 3.15
	height of astragalus/STL 2.59
	arc length of UAJ/STL 4.96
	relatively longer astragalar necks
GALAGINAE	reduced medial curvature of ATiL(A)
	reduced medial curvature of ATiM(A)
	rotation of medial malleolus 20-34°
	reduced flaring of AFi(A)
	angle of curvature of UAJ 183°
	radius of curvature of UAJ/STL 2.07
	ATiL(A) length /STL 3.75
	height of astragalus/STL 3.17
	arc length of UAJ/STL 6.64

continued

Table 12, continued

LORISINAE	increased medial curvature of ATiL(A)
	increased medial curvature of ATiM(A)
	rotation of medial malleolus 30-56°
	increased lateral flaring of AFi(A)
	angle of curvature of UAJ 154°
	radius of curvature of UAJ/STL 1.57
	ATiL(A) length/STL 3.01
	height of astragalus/STL 2.34
	arc length of UAJ/STL 4.19

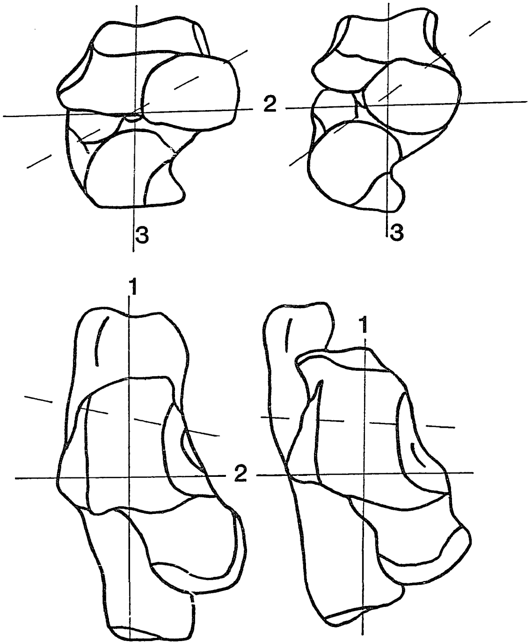

Figure 10. Position of UAJ motion axis in Lemur fulvus (left) and Propithecus diadema (right). Upper pair, proximal view of astragalus and calcaneus; lower pair, dorsal view. The dashed lines indicate the motion axis; the solid numbered lines are reference axes as in figure 6.

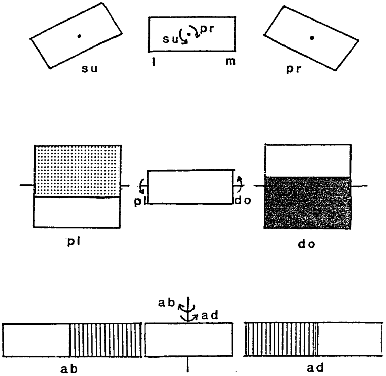

Figure 11. Effect of different positions of UAJ joint motion axis on ultimate displacement of right foot (represented by the box). The foot is viewed from the front; the central figure in each line is the foot in reference position. White, front of foot; black, sole of foot; stipple, dorsum of foot; lines, sides of foot; gray, back of foot. A. rotation of +/- 30° around reference axis 1 yielding supination (su) and pronation (pr). B. rotation of +/- 30° around reference axis 2, yielding plantarflexion (pl) and dorsiflexion (do). C. rotation of +/- 30° around reference axis 3 yielding abduction (ab) and adduction (ad). l= lateral, m= medial.

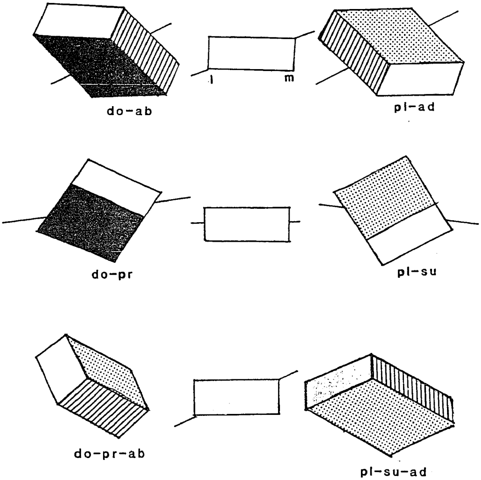

Figure 12. Effect of different position of UAJ joint motion axis on ultimate displacement of right foot. Conventions as in fig. 11. A. rotation around combined axes 2 and 3 yielding dorsiflexion-abduction and plantarflexion-adduction. B. rotation around combined axes 2 and 1 yielding dorsiflexion-pronation and plantarflexion-supination. C. rotation around combined axes 1, 2, and 3, yielding dorsiflexion-abduction-pronation and plantarflexion-adduction-supination. l=lateral, m=medial.

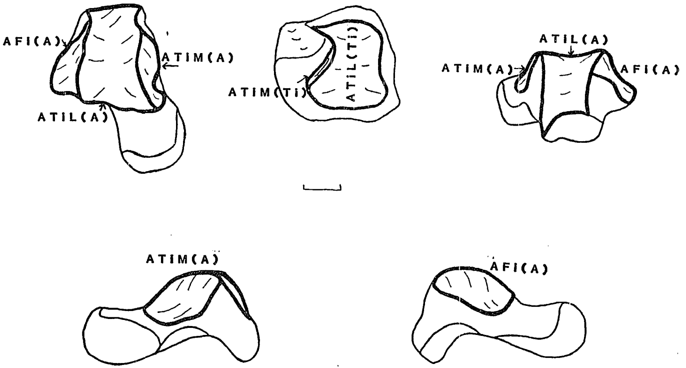

Figure 13. Upper ankle joint features of Hapalemur griseus. Top row, right to left, dorsal view of astragalus, inferior view of tibia (pictured as if it has been rolled away from articulation with the dorsal astragalus), posterior view of astragalus. Bottom row, medial and lateral views of the astragalus. Scale is 5 mm.

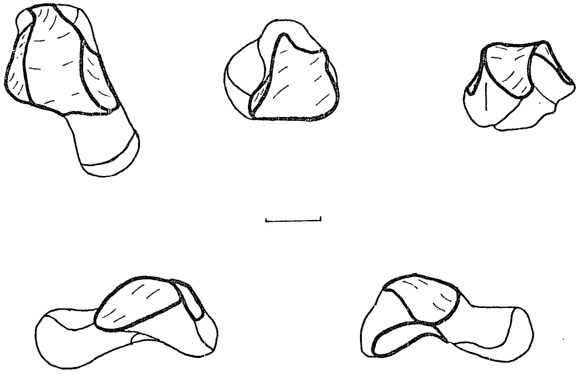

Figure 14. Upper ankle joint features of <u>Avahi laniger</u>. Views as in fig. 13. Scale is 5 mm.

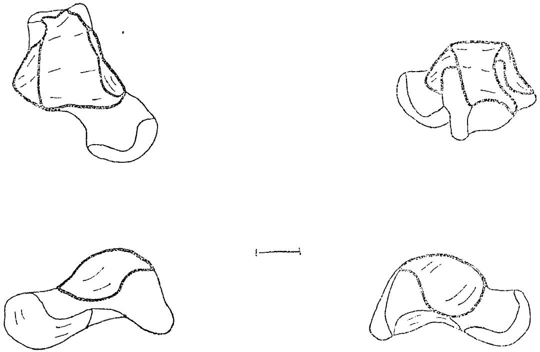

Figure 15. Upper ankle joint features of *Daubentonia madagascariensis*. Views as in fig. 13. Scale is 5 mm.

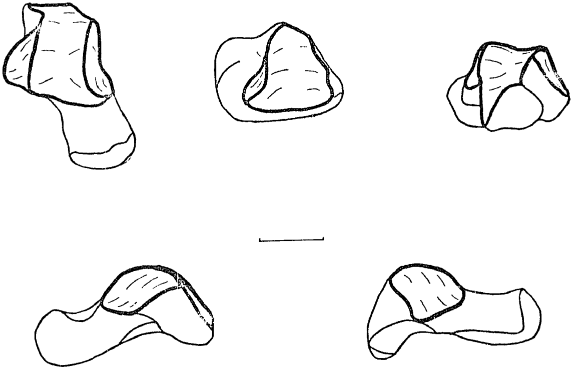

Figure 16. Upper ankle joint features of Cheirogaleus major. Views as in fig. 13. Scale is 2 mm.

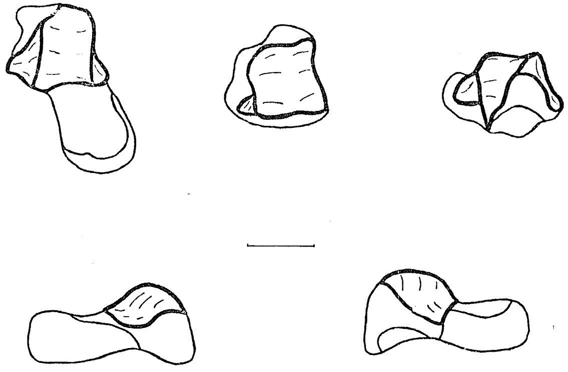

Figure 17. Upper ankle joint features of <u>Microcebus</u> <u>murinus</u>. Views as in fig. 13. Scale is 1 mm.

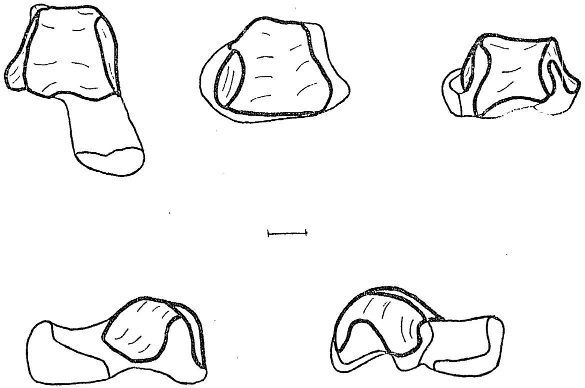

Figure 18. Upper ankle joint features of *Galago senegalensis*. Views as in fig. 13. Scale is 2 mm.

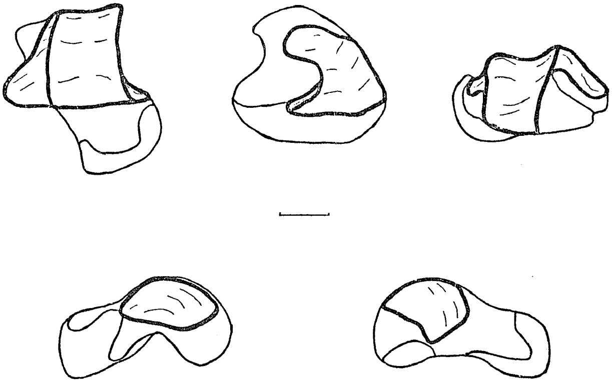

Figure 19. Upper ankle joint features of Arctocebus calabarensis. Views as in fig. 13. Scale is 2 mm.

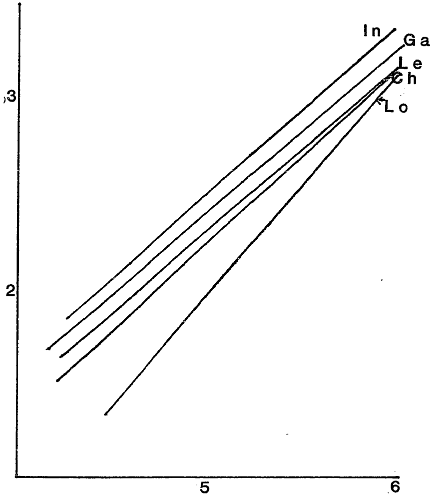

Figure 2 0. Relationship between log astragalar length (y axis) and log skeletal trunk length (x axis) in strepsirhines. In, indriines; Ga, galagines; Le, lemurids; Ch, cheirogaleids; Lo, lorisines.

Taxon	intercept	slope	r
Lemuridae	-2.125	.8815	.90
Indriinae	-2.031	.9016	.99
Cheirogaleidae	-2.223	.8953	.93
Galaginae	-2.009	.8794	.98
Lorisinae	-4.090	1.2039	.85

CHAPTER 5: THE SUBTALAR JOINT

I. General Remarks. The STJ consists of the two articulations between the astragalus and the calcaneus, the posterior astragalocalcaneal joint (pAC) and the anterior astragalocalcaneal joint (aAC) (fig. 5). The subtalar joint (STJ) and the transverse tarsal joint (TTJ) are functionally related and thus some of the description of joint function in Chapter 6 is relevant. They are discussed in separate chapters in this work merely as a matter of convenience of description. The two joints work as a unit during the movements of inversion and eversion of the forefoot. The details of relative astragalar and calcaneal motion during inversion and eversion are discussed in Chapter 6. To summarize the relevant information for the STJ here, the calcaneus adducts, supinates, and plantarflexes relative to a stationary astragalus during inversion. It abducts, pronates, and dorsiflexes during eversion. The way pAC and aAC shape influence these motions is discussed below. Morphology and movements at the subtalar joint in primates is also discussed by Hafferl (1932), Szalay and Decker (1974) and Lewis (1980b).

II. The posterior astragalocalcaneal joint (pAC). General remarks. Motions at the pAC, like at the UAJ and the TTJ, are quite complex and involve displacements in all three planes. Relative motions of the bones involved in the subtalar articulation are the result of several factors; the shapes of the joint facets and the relationships of the joint facet axis to the joint motion axis being the most important. The orientation of the joint motion axis in three dimensional space reflects the complex nature of motion at this joint.

The calcaneal facet [pAC(C)] is part of a cone. The long axis of this cone is not quite perpendicular to the long axis of the calcaneus, but is tilted slightly anteriorly in most taxa. This causes the long axis of the pAC(C) to be laterally offset from the long axis of the calcaneus (fig. 21a). It is also tilted significantly plantarmedially from the horizontal (fig. 21b). The estimated axis of motion at the subtalar joint is also inclined anteriorly, but slightly dorsad (fig. 22). Thus, the axis of motion at the subtalar joint is not perpendicular to the long axis of the pAC(A) or pAC(C) facets. There are almost certainly interspecific differences in the exact degrees to which tilting in the subtalar axis occurs, but the methods used in this study to determine the joint axis are not accurate enough to demonstrate this unambiguously.

It is these aspects of facet and joint axis orientation which give the important concomitant displacements to movements at the subtalar joints, which allow the calcaneus to follow the motions of the navicular and cuboid at the TTJ during inversion and eversion of the fore part of the foot (Chapter 6).

The axis of motion at the STJ is posterolaterally and dorsomedially inclined, like the UAJ axis, so the same combinations of motions apply (see figs. 11 and 12). To review, if the subtalar joint motion axis were perpendicular to the long axis of the calcaneus, rotations of the lamina pedis (relative to a stationary astragalus) would simply involve either dorsiflexion with a resultant upward tilt of the lamina pedis, or plantarflexion with a resultant downward tilt. If the axis were purely parallel to the long axis of the foot, then motion at the subtalar joint would involve pronation and supination of the lamina pedis. The posterolateral tilt of the axis means that the compromise axis is a combination of the pure flexion-extension and pure pronation-supination axes, thus concomitant lateral (supination) and medial (pronation) displacements are added to flexion and extension at the joint. In strepsirhines the motion axis is midway between the pure pronation-supination axis and the flexion-extension axis, therefore pronation-supination and flexion-extension are equal components of motion. In dorsiflexion the calcaneus (and lamina pedis) pronates, in plantarflexion it supinates. The subtalar axis also has a slight dorsal tilt, though not nearly as much as in humans (Lewis, 1980b). Rotation about a purely vertical axis would yield pure abduction and adduction of the lamina pedis. Thus, as Inman (1976) has shown, the dorsal tilt of the axis contributes concomitant abduction-adduction displacements to motion at the subtalar joint. Dorsiflexion is accompanied by abduction, plantarflexion by adduction. However, the more horizontal the axis (as in strepsirhines), the more supination and pronation are emphasized over abduction and adduction. Thus, in strepsirhines a great deal of supination can take place with only a moderate degree of adduction.

The position of the long axis of the pAC relative to the subtalar joint axis also affects movement at this joint. Because the two axes are not the same, helical motion is imparted to the calcaneus and forefoot during motion at the subtalar joint. The lamina pedis not only rotates around the joint axis, but also translates along the axis. In dorsiflexion-pronation the calcaneus translates laterally (abducts) and retracts, in plantarflexion-supination it translates medially (adducts) and protracts (Lewis, 1980b). Thus, the end result of movement at the subtalar joint is a lamina pedis which, relative to a stationary astragalus, is plantarflexed, supinated, adducted, and protracted (=inverted) or dorsiflexed, pronated, abducted, and retracted (=everted). These movements complement those occurring between the astragalus and navicular and calcaneus and cuboid at the transverse tarsal joint (see Chapter 6). Figures 23-28 illustrate calcaneal repositioning in inversion and eversion in several strepsirhines.

III. Variations in the posterior astragalocalcaneal joint in strepsirhines (see figs. 29-30).

A. Lemuridae. The pAC is a modified ovoid joint theoretically allowing two chordal slides and two arcuate slides. The chordal slides are in an anteroposterior direction (giving the primary motion of dorsiflexion and plantarflexion) and in a mediolateral direction (giving abduction and adduction). The first slide is very important, and is in fact the main (and probably only) kind of motion occuring at this joint. The second slide is not very important, if it occurs at all. The extent of the two allowed arcuate slides is limited because of the small amount of mediolateral sliding possible.

The calcaneal facet [pAC(C)] is convex in both directions (but more so in the proximodistal than in the mediolateral); the astragalar facet [pAC(A)] is concave in both directions. On the calcaneus the facet is longer (proximodistally) than wide (mediolaterally). The long axis of the facet is offset 10-20° from the long axis of the calcaneus (Table 14a). The average angle of curvature of the pAC(C) is 154°, but with a wide range (Table 13c).

The pAC(A) is configured to match the pAC(C). It is a concave surface, whose long axis is offset 10-30° from the long axis of the astragalus (which is parallel to the long axis of the calcaneus in a neutral position) (Table 14b). It is also offset plantarmedially to match the orientation of the pAC(C).

There is little variation among lemurids in the major features of this joint. Varecia and Lemur macaco have a lower angle of curvature than other lemurids.

B. Indriinae. Indriines share the basic shapes of the pAC(A) and pAC(C) outlined above for lemurids. They are distinguished by relatively longer, and thus apparently narrower facets (Table 13a,b). The facet is long compared to either calcaneal length or STL. The facet tends to flatten out posteriorly, making the pAC less perfectly circular than in lemurids, limiting the degree to which the lamina pedis plantarflexes and supinates during inversion. There is also slightly less lateral offset of the facets (Table 14a,b), but the difference is not statistically significant. This would increase the amount of translation along the joint axis, increasing the abduction and adduction and protraction-retraction accompanying dorsiflexion and plantarflexion [assuming that the joint motion axis is in a similar position as in lemurids, as it appears to be (fig. 22)]. The difference in actual degree of motion between lemurids and indriines appears, however, to be very small.

C. *Daubentonia*. *Daubentonia* resembles indriines in the length and narrowness of the facets, and in the lesser offset of the facets. However, the apparent increased length of the pAC(C) may simply be an artefact of a relatively short calcaneus, as pAC length relative to STL is significantly lower than in indriines. The pAC(C) does not, however, share the posterior flattening of the pAC typical of indriines. Thus, one would expect *Daubentonia* to have a slightly greater range of motion at the STJ than lemurids or indriines. This seems to be borne out by comparing the relative displacement of the calcaneus in inversion and eversion in *Daubentonia* and other taxa (fig. 25). *Daubentonia* has a relatively low angle of curvature at the pAC joint.

D. Cheirogaleidae. Cheirogaleids are essentially lemurid-like in all aspects of this joint. *Microcebus* exhibits less angulation of its pAC(C) and pAC(A) facets than does *Cheirogaleus* or lemurids, but not as little as indriines.

E. Galaginae. In galagines, the details of facet morphology are not very different from lemurids. *G. moholi* exhibits a lower offset angle of the pAC facets than does *O. crassicaudatus*. Like indriines, galagines have pAC(C) facets which are long relative to STL, but in galagines the posterior part of the facet is not flattened. Galagines generally have higher angles of curvature at the pAC joint than other strepsirhines. G. elegantulus and O. crassicaudatus have the lowest angles of curvature of all galagines.

F. Lorisinae. The pAC(C) is cone-shaped as in other strepsirhines, but is very constricted proximodistally. The plantar medial angle of the pAC(C) axis is more marked than in other strepsirhines. This contributes to the "inverted set" (Grand, 1967) of the lorisine foot, by orienting the calcaneus in a more supinated and adducted position relative to the astragalus. Although very variable, lorisines in general exhibit higher lateral offset angles than do other strepsirhines. This probably means that the degree of helical motion at this joint is decreased somewhat in lorisines, and that the joint motion axis is more anteroposteriorly placed, resulting in a higher inversion component to STJ motion.

The pAC(A) is modified to match the pAC(C), with a more marked plantarmedial angle. This facet is very short proximodistally, overlapping less than 50% of the pAC(C). This would theoretically allow a greater range of motion at this joint, but as noted below (Chapter 6), the position of full eversion in the lorisine foot is very unstable. From manipulating bones, it is obvious that congruence and stability at the STJ is only attained in the inverted position of this joint. The angle of curvature varies greatly in lorisines. It is very low in Perodicticus and Arctocebus, but high in Loris and Nycticebus.

IV. The anterior astragalocalcaneal articulation. General remarks. The aAC(A) and aAC(C) provide a platform to facilitate the sliding movements of the astragalus and calcaneus during the complex movements into inversion and eversion at the STJ and TTJ. The surfaces of the aAC are in general fairly flat modified ovoid surfaces. The facet on the calcaneus [aAC(C)] is usually slightly concave; the facet on the astragalus [aAC(A)] is slightly convex. In all taxa the aAC(A) is confluent with the AN(A) and spring ligament facets. The aAC(C) is a comma shaped facet which forms the sustentaculum of the calcaneus. Viewed from the medial side, its proximal part slopes plantad at a fairly marked angle, then flattens out for the rest of its extent, angling slightly dorsad at its distal end. These angulations are mirrored in the form of the aAC(A). The bony part of the sustentaculum is supplemented medially by the plantar-calcaneonavicular or "spring" ligament. In an inverted position at the STJ the aAC(A) rests almost entirely on the bony part of the sustentaculum. In the everted position the spring ligament supports almost all of the astragalar neck and head. Figures 29-30 illustrate the part of the aAC(A) facet supported by the spring ligament in the inverted and everted positions.

V. Variations in the anterior astragalocalcaneal joint in strepsirhines. (see figs. 29-30).

A. Lemuridae. The shape of the aAC facets is essentially identical to the one given above. The aAC(C) does not extend all the way to the distal end of the calcaneus (except in *Varecia*), reflecting the reverse alternating condition of the tarsus. *Lemur catta* has a more medially extensive proximal part of the sustentaculum, perhaps providing more astragalar support in eversion. *Lemur catta* is also distinguished by a greater invasion of the aAC(A) surface by the interosseous ligaments. This is also probably a stabilization mechanism. In members of the genus *Lemur* and sometimes in *Hapalemur* the proximal part of the joint hooks over the bony sustentaculum. This provides a bony lock for the joint in eversion, preventing any further retraction of the calcaneus. *Lepilemur* exhibits the strongest plantad bend to the sustentaculum than any other lemurid. This is a feature which it shares with indriines.

B. Indriinae. The aAC(C) extends to the distal end of the calcaneus, reflecting the serial condition of the tarsus. The entire facet is bent plantad so that its surface lies more on the medial side of the bone than on its dorsal side. This is probably related to the more marked dorsolateral orientation of the astragalar head (Chapter 6). The angle of the aAC must accomodate this angulation of the astragalus. This probably provides greater support for the astragalar head in the inverted position, and may be related to vertical clinging with the feet strongly inverted, but other vertical clingers (bushbabies, *Tarsius*) do not share this trait.

C. *Daubentonia*. There are no significant differences from lemurids, except for a slightly more marked dorsad slope to the distal end of the aAC(C).

D. Cheirogaleidae. All cheirogaleid genera are quite lemurid-like in all aspects of this joint. Some individuals show the hooking over of the sustentaculum found in members of the genus *Lemur*.

E. Galaginae. Obviously, due to the extreme length of the calcaneus the aAC(C) only extends partly down the bone. The posterior part of the facet is the more emphasized, the anterior part is relatively small.

F. Lorisinae. The sustentaculum is broader than in other strepsirhines. The sustentaculum is oriented more plantarly than in other strepsirhines (except indriines), but for a very different reason. In lorisines, the plantad slope reflects the more marked plantad angle of the axis of the pAC(C). Thus, in lorisines, the angle of the aAC is parallel to the axis of the pAC(C), while in indriines it is not.

In all lorisines, the aAC(A) is restricted to the lateral side of the astragalus. This is due to the strong dorsomedial angle of the astragalar head (Chapter 6) which lifts the medial side of the astragalus away from the sustentaculum and spring ligament.

VI. Summary. Important features of the subtalar joint are summarized in Table 15. The articulations of the STJ provide a platform around which the calcaneus and the remaining part of the lamina pedis reorient relative to the astragalus during inversion and eversion. These motions complement those occurring at the TTJ.

Indriines are perhaps the most distinctive strepsirhine taxon in the construction of the STJ. The increased length of their pAC(C) facets might seem to indicate a greater range of motion, but the flattening of the posterior part of the facet would in fact limit the degree of inversion and its components.

Indriines also exhibit the least lateral offset of the pAC facets of any strepsirhine. Assuming that the joint motion axis is similarly placed, this would increase helical motion (lateral-posterior/medial anterior translations) along the joint motion axis during eversion and inversion respectively. It should be noted, however, that any ultimate difference in bone displacement between indriines and other strepsirhines is likely to be small.

Galagines, like indriines, have relatively long pAC(C) facets, which may act as stable weight bearing platforms in these leapers. Both taxa also appear to have greater overlap between the pAC(A) and pAC(C) facets which would tend to reduce motion at the subtalar joint, despite the high angle of curvature exhibited by galagines. This also adds stability to the STJ. However, this stability is gained at the expense of subtalar mobility. To maintain the capability of inversion and eversion of the forefoot, modifications are made in more distal joints of the tarsus in both galagines and indriines (Chapter 6). Hall-Craggs (1966) has also correctly argued that reduction of STJ mobility is necessary in galagines due to the angle of the STJ motion axis and the length of the calcaneus, both of which would tend to amplify the concomitant flexion and extension of the calcaneus to ridiculous proportions.

Lorisines also exhibit some interesting modifications of the STJ. The pAC(C) and pAC(A) facets are quite plantarmedially angled, contributing to the naturally inverted position of the tarsal bones. Their rather anteriorly-posteriorly compressed pAC(C) facets, the high offset of the pAC(C) facet, and low overlap betweeen the pAC(C) and pAC(A) facets allows a great range of inversion and eversion of the lamina pedis. The everted position is, however, very unstable.

Table 13. Indices and measurements of the subtalar joint. Conventions as in Table 8.

	A		B		C	
	pAC(C) length STL [C3/STL]*100		pAC(C) length/ Calcaneus length [C3/C1]*100		pAC(C) arc C10b	
Lemur fulvus	2.35	.18	26.91	2.2	162.47	11.3
	1.94-2.64	13	20.75-30.67	21	140-185	19
Lemur mongoz	1.82	-	24.15	3.0	153.33	-
	1.74-1.99	2	20.42-27.27	4	137-173	3
Lemur macaco	2.84	-	29.43	2.0	133.00	-
	2.80-2.89	2	27.58-31.58	3	128-138	2
Lemur rubriventer	2.97	-	29.68	-	150.00	-
	-	1	-	1	-	1
Lemur coronatus	2.16	-	26.99	4.5	169.00	-
	1.84-2.49	2	20.29-30.39	4	152-180	3
Lemur catta	2.60	.11	26.98	2.5	159.50	-
	2.41-2.71	6	23.64-30.47	10	140-170	4
Varecia variegata	2.61	.23	31.72	2.6	141.63	10.9
	2.26-2.89	9	27.27-35.56	12	130-163	11
Hapalemur griseus	2.57	.13	27.83	1.8	148.67	11.2
	2.34-2.69	6	25.37-31.09	11	130-170	9
Hapalemur simus	2.64	-	28.34	-	140.00	-
	-	1	-	1	-	1
Lepilemur mustelinus	2.63	.15	23.52	1.2	156.25	16.3
	2.38-2.93	12	21.46-25.13	12	135-175	12
Daubentonia madagascariensis	2.82	.20	30.51	1.9	135.8	11.9
	2.56-3.03	5	27.78-32.38	5	115-145	5
Avahi laniger	3.34	.35	30.93	2.9	158.75	14.4
	2.83-3.96	5	26.77-36.41	10	150-180	4
Propithecus verreauxi	2.95	.13	31.08	1.4	166.67	11.3
	2.80-3.17	5	29.74-32.68	6	155-185	6

continued

Table 13, continued.

	pAC(C) length STL		pAC(C) length/ Calcaneus length		pAC(C) arc	
Propithecus	3.07	.19	31.84	2.0	150.4	15.4
diadema	2.78-3.10	10	28.78-34.97	11	127-170	5
Indri indri	3.40	.23	33.78	2.0	149.33	12.6
	3.06-3.78	9	30.33-36.34	9	135.165	9
Microcebus	2.32	.26	18.46	1.5	153.78	15.11
murinus	2.04-2.77	6	16.04-21.88	15	125-180	14
Mirza coquereli	2.87	-			158.00	-
	-	1			-	1
Cheirogaleus	2.46	-	29.11	1.7	160.00	-
medius	2.13-2.60	3	26.37-31.00	5	140-180	2
Cheirogaleus	2.39	.12	26.95	.99	154.75	9.0
major	2.25-2.56	5	26.20-28.37	5	142-162	4
Phaner furcifer	2.31	-	16.33	-		
	-	1	-	1		
Galago	3.18	.34	11.64	1.4	170.00	12.3
senegalensis	2.88-3.71	5	9.32-12.84	6	155-180	4
Galago moholi	3.11	.15	11.58	.6	176.67	6.0
	2.91-3.30	5	10.71-12.59	9	165-180	6
Galago gallarum			10.57	-		
			-	1		
Galago	2.83	.32	17.09	2.7	154.8	16.6
elegantulus	2.41-3.34	10	10.88-23.58	16	130-190	10
Galago	3.63	-	13.38	-	150.00	-
matschei	-	1	-	1	-	1
Galagoides	2.96	.17	10.81	.72	161.71	10.9
demidoff	2.78-3.24	6	9.68-11.88	9	150-180	7
Galagoides	3.06	-	12.55	-	170.00	-
zanzibaricus	-	1	-	1	-	1

continued

Table 13, continued.

	pAC(C) length STL		pAC(C) length/ Calcaneus length		pAC(C) arc	
Galagoides	2.88	.18	13.52	.94	179.60	4.3
alleni	2.70-3.16	5	12.07-14.63	5	73-185	5
Otolemur	2.85	-	16.67	.76	164.75	10.8
crassicaudatus	2.81-2.88	2	15.76-17.59	4	155-180	4
Otolemur	2.94	-	15.04	.35	175.00	-
garnetti	2.89-3.01	3	14.75-15.43	3	170-180	3
Perodicticus	2.40	.50	34.34	6.7	144.00	8.5
potto	1.86-3.40	8	26.45-48.15	16	135-160	6
Arctocebus	1.60	.25	31.18	5.3	148.00	11.1
calabarensis	1.22-2.02	10	25.53-42.86	11	136-164	7
Nycticebus	2.17	.19	31.30	2.9	171.80	21.6
coucang	1.91-2.24	7	.80-35.71	11	3-194	5
Loris	2.26	.53	33.49	7.7	169.33	-
tardigradus	1.48-2.67	5	21.68-42.07	6	120-196	3
Lemuridae	2.49	.28	27.57	4.4	153.66	14.8
	1.74-2.89	42	20.29-35.56	67	128-185	53
Indriinae	3.16	.27	32.05	2.4	155.46	14.3
	2.78-3.93	34	26.77-36.41	3	127-180	24
Cheirogaleidae	2.40	.24	22.34	4.9	154.76	14.7
	2.04-2.77	16	16.04-31.00	27	125-180	21
Galaginae	2.98	.28	14.00	3.1	166.50	14.1
	2.41-3.71	38	9.32-23.58	55	130-190	41
Lorisinae	2.06	.49	32.77	5.7	155.57	22.0
	1.22-3.40	30	21.68-48.15	44	120-196	21

Table 14. Indices and measurements of the subtalar joint. Conventions as in Table 8.

	A		B	
	offset of pAC(C) facet C8		offset of pAC(A) facet A13	
Lemur fulvus	12.8	2.8	17.1	5.8
	9-19	12	9-30	12
Lemur coronatus	6.0	-	16.00	-
	-	1	-	1
Lemur catta	18.7	2.3	19.33	4.5
	16-20	3	15-24	3
Varecia variegata	17.5	-	14.5	-
	17-18	2	14-15	2
Hapalemur griseus	9.7	2.1	20.0	7.0
	13-27	3	9-12	3
Lepilemur mustelinus	12.8	2.5	15.2	6.6
	8-16	13	6-23	13
Daubentonia madagascariensis	5.0	-	18.0	-
	-	1	-	1
Avahi laniger	10.0	-	0	-
	-	1	-	1
Propithecus verreauxi	8.8	1.7	4.0	4.8
	7-11	4	4-14	4
Propithecus diadema	7.0	-	6.0	-
	-	1	-	1
Indri indri	8.0	-	0	-
	-	1	-	1
Microcebus murinus	11.7	3.3	12.07	2.9
	7-15	13	5-16	13
Cheirogaleus major	23.0	-	18.00	-
	-	1	-	1

continued

Table 14, continued.

	offset of pAC(C) facet		offset of pAC(A) facet	
Galago moholi	14.8	3.4	7.6	3.0
	10-18	5	4-12	5
Galago elegantulus	14.0	-	10.0	-
	-	1	-	1
Galagoides demidoff	10.0	-	12.00	-
	-	1	-	1
Otolemur crassicaudatus	22.50	-	20.00	-
	20-25	2	15-25	2
Perodicticus potto	17.8	6.4	17.80	4.6
	10-27	6	12-25	6
Arctocebus calabarensis	24.00	-	14.00	-
	-	1	-	1
Nycticebus coucang	18.00	-	35.00	-
	-	1	-	1
Loris tardigradus	22.50	-	22.50	-
	17-28	2	21-24	2
Lemuridae	12.15	5	16.6	5.9
	6-20	34	9-30	34
Indriinae	8.57	1.5	5.71	5.3
	7-11	7	0-14	7
Cheirogaleidae	12.5	4.4	12.5	3.2
	7-23	14	5-18	14
Galaginae	15.89	4.9	11.11	6.2
	10-18	9	4-25	9
Lorisinae	19.40	6.0	20.10	6.7
	10-28	10	14-35	10

Table 15. Summary of distribution of characters of the subtalar joint.

TAXON	pAC	aAC
LEMURIDAE	modified ovoid pAC(C) offset 6-20° pAC(A) offset 6-30°	proximal hook-over present in some
INDRIINAE	modified ovoid post. flattening of pAC facets pAC(C) offset 7-11° pAC(A) offset 0-14°	aAC(C) facet bent plantad
DAUBENTONIA	modified ovoid pAC(C) offset 5° pAC(A) offset 18° low angle of curvature	
CHEIROGALEIDAE	modified ovoid pAC(C) offset 7-23° pAC(A) offset 5-18°	
GALAGINAE	modified ovoid high angle of curvature pAC(C) offset 10-25° pAC(A) offset 4-25°	posterior part of facet emphasized, anterior reduced.
LORISINAE	modified ovoid pAC(C) offset 10-28° pAC(A) offset 12-35°	broader sustentaculum plantad orientation of aAC(C)

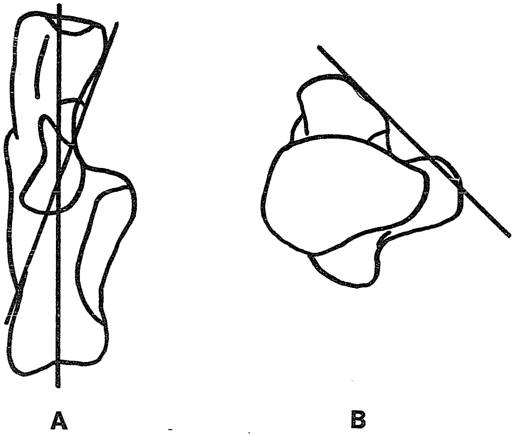

Figure 21. A. The relationship of the long axis of the pAC(C) facet to the long axis of the clacaneus. The angle between the two lines is the "offset" angle of the pAC(C). B. the plantar-medial tilt of the pAC(C).

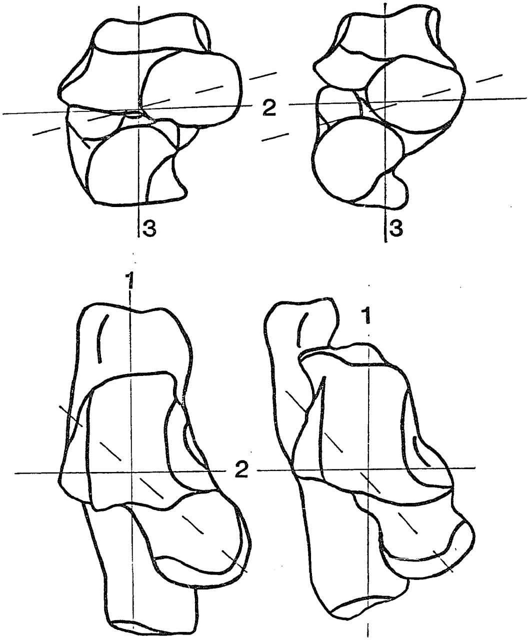

Figure 22. The position of the STJ motion axis in Lemur fulvus (left) and Propithecus diadema (right). Upper pair, proximal view of astragalus and calcaneus; lower pair, dorsal view. Dashed lines indicate the motion axis; solid numbered lines are reference axes as in figure 6..

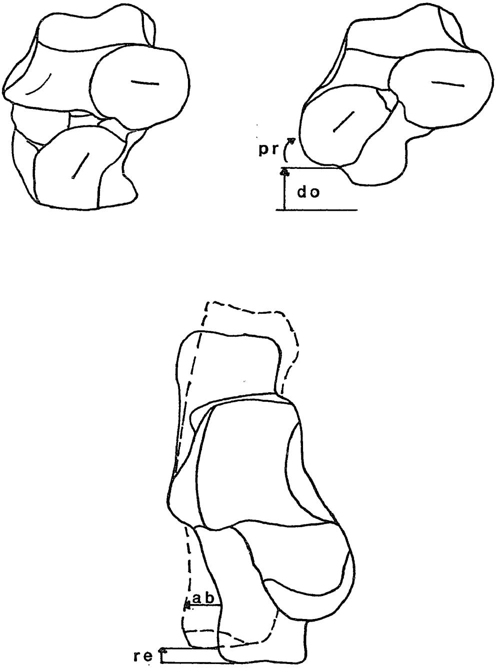

Figure 23. Repositioning of the calcaneus in inversion and eversion in *Lemur fulvus*, relative to a stationary astragalus. Top, left, inversion; right, eversion. Bottom: solid lines are bones in inverted position; dashed line is calcaneus in everted position. pr, pronation; do, dorsiflexion; ab, abduction, re, retraction.

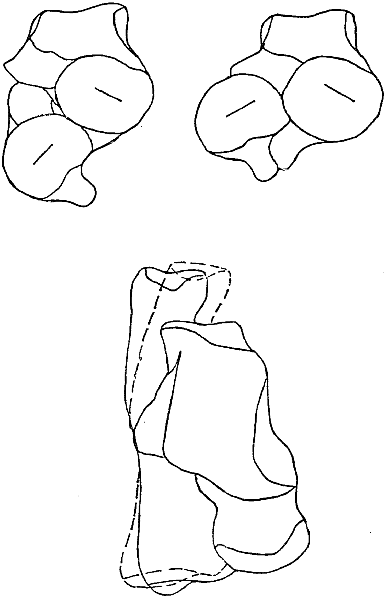

Figure 24. Inversion and eversion at the subtalar joint in *Propithecus diadema*. See fig. 23 for explanation.

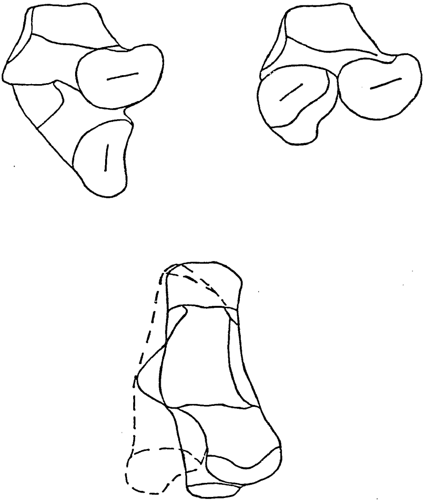

Figure 25. Inversion and eversion at the subtalar joint in *Daubentonia madagascariensis*. See fig. 23 for explanation.

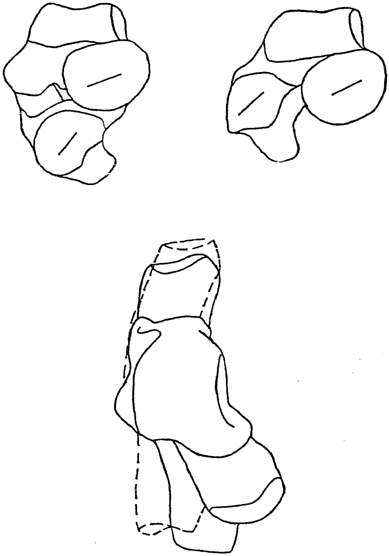

Figure 26. Inversion and eversion at the subtalar joint in *Cheirogaleus major*. See fig. 23 for explanation.

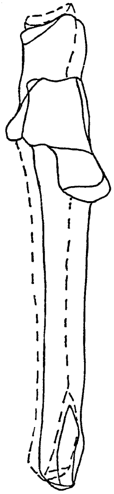

Figure 27. Inversion and eversion at the subtalar joint in *Galago senegalensis*. See fig. 23 for explanation.

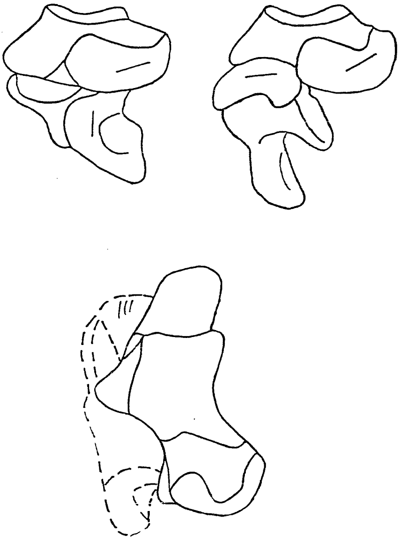

Figure 28. Inversion and eversion at the subtalar joint in *Nycticebus coucang*. See fig. 23 for explanation.

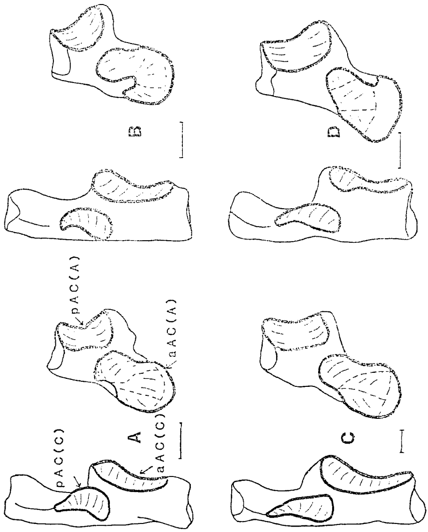

Figure 29. The pAC and aAC in *Lemur fulvus* (A); *Lemur catta* (B); *Indri indri* (C); and *Daubentonia madagascariensis* (D). Scales are 5 mm.

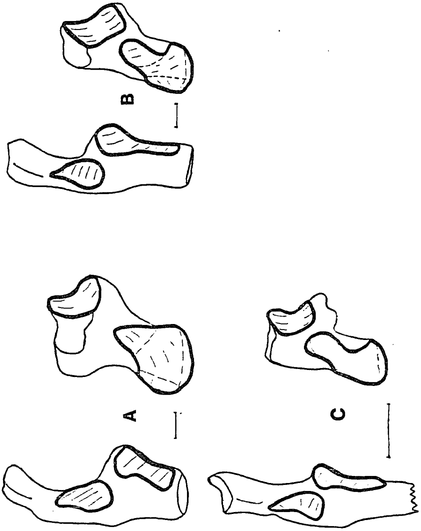

Figure 30. The pAC and aAC in A, *Perodicticus potto*; B, *Cheirogaleus major*; C, *Galago senegalensis*. In *Galago* it is difficult to distinguish subdivisions of the aAC(A). Scales are 2 mm.

CHAPTER 6: THE TRANSVERSE TARSAL JOINT

I. General remarks. The transverse tarsal joint (TTJ) and the subtalar joints (STJ) function as a unit during the movements of inversion and eversion of the forefoot. The TTJ consists of two articulations, the astragalonavicular joint (AN) and the calcaneocuboid joint (CCu). Before describing the form of these joints in the different taxa, it would be worthwhile to review the movements which take place during inversion and eversion of the forefoot in a primate foot. In the following account, the movements of the navicular, cuboid, and calcaneus are described in relation to a stationary astragalus.

Although it is common to stress the role of rotation of the cuboid on the calcaneus as the focus of inversion and eversion (e.g. Szalay and Decker, 1974; Lewis 1980b) and state that the navicular rotates around the astragalar head simply as an adjunct to this movement due to the strong ligamentous attachments of the cuboid and navicular, it is obvious that the primary muscles which produce inversion of the forefoot (tibialis anterior and tibialis posterior) act on the navicular and entocuneiform. Thus, the movement of inversion is affected myologically by changing the relative position of the navicular. The cuboid and calcaneus are reoriented as well, but only by virtue of their ligamentous connections to the navicular. The account of motion given by Kapandji (1970) for humans is applicable to most strepsirhines as well, and is adapted for use here.

In the following account it is assumed that there is little motion between the cuboid and navicular. As discussed below (Chapter 7), there are differences between strepsirhine taxa in the conformation of the naviculocuboid joint, suggesting that there are functional differences regarding relative cuboid-navicular motion. However, given the extensive ligamentous connections between the two bones, motion must be fairly limited in most taxa even if it does occur. Indeed it is impossible to have the cuboid rotate at the CCu joint unless it is tracking the motion of the navicular by virtue of its connections with it. No muscle attaches to the cuboid which can power supination. Muscles attaching to the calcaneus or crossing the calcaneo-cuboid joint may be able to effect supination at this joint, however.

When the forefoot is inverted at the TTJ, the tibialis posterior pulls the navicular medially (adducts it) and rotates it laterally (supinates it). This exposes the superolateral part of the navicular head, but covers the previously exposed medial part of the navicular head. The cuboid also moves medially and conjunctly rotates laterally by virtue of its connection to the navicular, exposing a small part on the dorsolateral surface of the CCu(C). The calcaneus is pulled medially and rotated laterally with the cuboid, but not to the same extent, due to the loss of some of the motion in calcaneocuboid rotation. As it is pulled along with the cuboid, it rotates relative to the astragalus at the pAC. Due to the orientation of the pAC, (discussed in detail above, Chapter 5) the motions of adduction and inversion of the calcaneus are enhanced, and it is pulled anteriorly (protracted) as well. The aAC joint merely acts as a surface on which the calcaneus slides during these other movements. The end result of these motions is a lamina pedis which is adducted, supinated and slightly plantarflexed relative to the astragalus. This is the inverted position of the foot (figs. 31-33).

Eversion must be powered by the peroneal musculature which inserts on the base of MT5 (peroneus brevis) and MT1 (peroneus longus). The actions of these muscles must affect the transverse tarsal joint through a chain of bony connections involving both the metatarsals and cuneiforms. When the forefoot is everted, the cuboid is pulled laterally (abducted) and is medially rotated (pronated), covering the dorsolateral surface of the CCu(C) exposed in inversion. The navicular is also pulled laterally and medially rotated, covering the lateral part of the AN(A) exposed in inversion, but exposing most of the medial side of this joint. The calcaneus is likewise abducted and medially rotated relative to the astragalus, and because of the helical shape of the pAC it is also retracted under the astragalus. These movements result in a lamina pedis which is abducted, pronated and somewhat dorsiflexed relative to the astragalus. This is the everted position of the foot (figs. 31-33).

II. Variations in morphology of the TTJ in strepsirhines. (figs. 34-37).

A. Lemuridae. In lemurids, the AN joint is an unmodified ovoid joint. Thus, two chordal slides are possible. The movements are a flexion-extension of the navicular on the astragalus (or vice-versa) and an abduction-adduction of the navicular on the astragalus (or vice-versa). In addition, arcuate slides in two directions combining these chordal slides are allowed. Axial rotation is also possible; this occurs during inversion-eversion movements. All of these movements are theoretically possible given the form of the AN joint. However, the influence of the calcaneocuboid joint must be considered, given the small range of relative motion allowed between the cuboid and navicular. For example, the amount of flexion and extension can't be too great, since this movement tends to dislocate the CCu joint. This is especially problematic when the forefoot is inverted, because of the greater superimposition of the AN and CCu joints. In eversion, when the astragalus and calcaneus are more laterally positioned, greater degrees of flexion and extension can take place. The range of dorsiflexion is probably greater than that of plantarflexion. Also, as noted above, dorsi- and plantarflexion occur as concomitant displacements of eversion and inversion respectively. Abduction and adduction at the AN joint are extremely limited since they tend to dislocate the CCu joint.

The most important movement of the possible motions at the AN joint is thus the movement of axial rotation, which, as discussed above, is the primary component of inversion and eversion. Only an unmodified ovoid joint allows free axial rotation, thus it is necessary that the AN be this type of joint. However, an unmodified ovoid has three degrees of freedom, and could be relatively unstable, an undesirable quality for a joint in a weight bearing organ like the foot. The tight connections between the navicular and cuboid, however, effectively remove two of the three degrees of freedom, thus stabilizing the joint, while retaining the important adjunct rotation.

The AN joint has a slight dorsolateral orientation. This varies from 0° (parallel to the level of the trochlear crests) to about 15° (Table 16a; figs. 34-35a,b).

The CCu joint of lemurids is an unmodified sellar unit theoretically allowing two chordal slides and an arcuate slide. No independent rotation is allowed. What appears to be axial rotation of the cuboid around the calcaneus is in reality a marked conjunct rotation resulting from the arcuate slide. This arcuate slide results in a calcaneus which is slightly adducted and medially rotated (pronated) (relative to a stationary cuboid) or slightly abducted and laterally rotated (supinated). The first movement is Lewis' (1980b) exorotation, the second is his endorotation. According to Lewis, the first movement is related to inversion of the lamina pedis, the second, eversion. This suggests that the calcaneus would laterally rotate in eversion of the forefoot and would medially rotate during inversion. However, from moving the astragalus and calcaneus at the subtalar joint, it is apparent that the calcaneus laterally rotates during inversion and medially rotates during eversion. The reason for this apparent contradiction is that the lamina pedis does not work as a totally rigid structure; there are relative motions between the parts. The movements at the TTJ and STJ are not totally congruous.

Relative to the astragalus, the calcaneus does laterally rotate in inversion. So does the cuboid. But the cuboid rotates more than the calcaneus. Therefore, the calcaneus appears to have medially rotated relative to the cuboid.

The two chordal slides allowed at the CCu are a dorsoplantar slide and a mediolateral slide. They appear to be relatively unimportant. Dorsal sliding of the cuboid on the calcaneus is soon stopped by the impact of the cuboid pivot against the calcaneus. Plantar sliding of the cuboid on the calcaneus is stopped by the calcaneocuboid ligament. Medial and lateral sliding at the CCu joint are almost completely prevented by the cuboid pivot (Hafferl, 1932).

On the CCu(C), the facet is oval shaped and fairly flat, except for the depression it bears plantarmedially for the pivot. The slope from the dorsal surface to the cuboid depression is gradual. The CCu(Cu) is a flat oval surface as well, except for a marked medioplantar protuberance, which forms the pivot. In lemurids the long axis of the cuboid facet is about 30° dorsad relative to the horizontal (table 16b; fig. 36a,b). The articular surface of the CCu(C) is concentrated more towards the lateral side of the pivot axis (fig. 36a,b). This means that the range of lateral rotation (supination) is greater than that of medial rotation (pronation). The CCu joint is most congruous in a position of semisupination.

Among lemurids, variations in the morphology of the transverse tarsal joint are not very marked. The most distinct taxon is *Lemur catta*, which has dorsoplantarly flattened both the AN and CCu joints

(Table 16c). This would lessen the degree of axial rotation possible before significant astragalonavicular dislocation occurs, and thus the range of inversion and eversion. *Varecia* shows similar modifications. In *Lepilemur* and *Hapalemur* the proximal navicular is more medially extensive, recalling the condition in galagines. The functional significance of this is discussed below (section E).

B. Indriinae. The significant morphological differences from lemurids are as follows: the AN(A) is larger, forming a greater section of a sphere in indriines than in lemurids (fig. 34c). The head of the astragalus has a slightly more marked dorsolateral orientation than in lemurids, being 15° rather than 10°; this difference is statistically significant ($p< .001$) (Table 16a; fig. 34c). The CCu(C) is higher and narrower (Table 16c; fig. 36c). The eminience of the cuboid pivot is not as well developed as in lemurids, giving a much flatter calcaneocuboid articulation.

The larger AN joint would theoretically increase the degree of axial rotation possible, and thus the range of pronation and supination. Movements of dorsiflexion-plantarflexion, abduction-adduction, or medio-lateral sliding are limited for the same reasons as in lemurids. However, a somewhat greater degree of dorsal sliding at the calcaneocuboid joint may be allowed due to the reduction of the cuboid pivot. This may also help increase the degree of rotational movement, since in lemurids one of the main stops to medial rotation (pronation) is the conjunct dorsal sliding of the cuboid which is eventually blocked by the impact of the cuboid pivot against the calcaneus. In addition, the fact that in indriines the calcaneus is only slightly more proximally extensive than the astragalus, whereas in lemurids it is more noticeably so (with the exception of *Varecia*) may also increase the degree of axial rotation possible. In lemurids, lateral rotation (supination) is blocked by the impact of the navicular and the calcaneus. In indriines, since the transverse tarsal joint is not as stepped (essentially forming a serial tarsus) contact of the navicular and the calcaneus is not as much of a problem. In indriines, the consequence of all of this is a foot which is freer in axial rotation at the transverse tarsal joint than is the lemurid foot. It seems that indriines are selectively increasing the range of eversion more than inversion. By reducing the cuboid pivot and increasing the dorsolateral orientation of the AN joint a more everted position of the tarsus can be achieved.

C. *Daubentonia*. In *Daubentonia* the AN joint is essentially lemurid-like, except for a more flattened AN(A) and a dorsomedial orientation of the joint (fig. 35a). The pivot of the CCu joint is reasonably well developed (fig. 37a). The main difference from lemurids (except *Varecia*) is the serial rather than reverse alternating condition of the tarsus.

D. Cheirogaleidae. In *Cheirogaleus* the CCu joint is essentially like that of lemurids (fig. 37b). *Microcebus* and *Mirza* have higher and narrower CCu(C) facets like indriines and galagines (Table 16c). The shape of the AN(A) joint is generally lemurid-like, but differs in two aspects. The AN(A) is somewhat dorsomedially constricted and is dorsomedially oriented (fig. 35b). This latter feature causes an increased medial angulation of the navicular (and presumably the cuneiforms) relative to the astragalus and thus increases the angle of supination possible without changing the range of motion (Hafferl, 1932). *Microcebus* differs in its greater development of the medial side of the proximal navicular, a feature it shares with *Phaner* and galagines. The AN articulation of *Phaner* shares the dorsomedial orientation of *Cheirogaleus*, but is shaped somewhat differently. Like galagos, *Phaner* has some marked flattening of the lateral side of the astragalar head. The significance of this is discussed below.

E. Galaginae. The AN joint is a modified ovoid, not an unmodified unit as in other strepsirhines. The AN(A) is not as smoothly curved as in lemurids or indriines. The medial one third of the facet is highly curved, but the lateral part is flattened and slopes proximally. In all galagos, the medial side of the AN(N) is more proximally extensive than in other strepsirhines forming a deep cup-like articulation for the astragalar head. This feature probably functions to stabilize the TTJ in eversion by preventing any medial dislocation of the astragalar head. As discussed above it is during eversion that the abducted astragalar head stresses the plantar-calcaneonavicular ligament. The medial extent of the navicular in galagines (and *Microcebus*, *Phaner*, and to a lesser degree *Lepilemur* and *Hapalemur*) replaces part of the spring ligament with this bony protuberance, reinforcing the medial side of the foot. The orientation of the AN(A) is dorsomedial as in cheirogaleids and lorisines (fig. 35c).

The calcaneocuboid joint is high and narrow as in indriines and some cheirogaleids but differs in some respects from that of other strepsirhines. On the CCu(C) the depression for the cuboid pivot is deeper and the change in slope into the pivot is more abrupt than in the taxa mentioned above. This is reflected in a somewhat more pronounced pivotal protuberance on the CCu(Cu) (fig. 37c). This larger pivot increases the degree of sellarness of the joint and thus increases the degree of conjunct rotation which accompanies the allowed arcuate slide (MacConaill, 1973). Galagines, then, get more rotation per unit of travel at the CCu joint than do other strepsirhines (except lorisines). In galagines, the degree of sellarness makes the conjunct rotations (pronation and supination) even more predominant over the sliding components (of abduction and adduction) involved in CCu movement than they are in other strepsirhine taxa. A slightly more centrally located pivot axis also helps reduce concomitant abduction-adduction at the CCu joint. This arrangement, while allowing an (almost) pure axial rotation, as does an unmodified ovoid joint, only has one degree of freedom, and is thus very stable. Galagines thus preserve (or perhaps increase) rotational motion while maintaining a very stable joint.

On the dorsolateral surface of the CCu(C) there is a protuberance formed by the attachment of the dorsal calcaneocuboid ligament. This protuberance also serves as a locking mechanism in the everted position. In eversion, it abuts against a protuberance on the dorsolateral side of the cuboid which is formed by the flare of the groove for the peroneus longus tendon, locking the two bones together. (fig. 37c).

Another major difference from all other strepsirhines (except some cheirogaleids) is the extreme lengthening of the calcaneus and the navicular which result in an extreme reverse alternating position of the tarsus, and the wide separation of the elements of the TTJ.

It appears that despite this separation, in galagines inversion and eversion of the forefoot still take place by axial rotations at the TTJ (Hall-Craggs 1966, Lewis 1980b). It is likely however that the degree of axial rotation is more limited in galagines than in other strepsirhines. At least, the assymetry of the AN joint guarantees that little displacement can be achieved before losing congruence of the joint. Although some astragalonavicular rotation does occur, this joint is much less congruent in a supinated position than in a pronated one. In galagines full congruence at the AN joint is only attained in eversion, rather than in all positions as in lemurids or indriines. The more dorsomedial orientation of the astragalar head may compensate for this barrier to supination by throwing the navicular into an automatically more supinated position, decreasing the need for joint motion to create a supinated position of the fore part of the foot. Calcaneocuboid rotation appears to occur as in lemurids. However, there does appear to be less involvement of calcaneal movement during inversion and eversion. A comparison of the calcaneus in the inverted and everted positions in Lemur (fig. 31) and in *Otolemur* (fig. 32) show that the calcaneus rotates less in *Otolemur*. This has two consequences for galagines. It necessitates the development of a naviculocalcaneal joint if reasonable ranges of inversion and eversion are to be maintained (see below) and it decreases the degree of involvement of the subtalar joint in inversion-eversion.

In lemurids, it was noted that due to the reverse alternating condition of the tarsus, the degree of supination possible (lateral rotation) is limited by the eventual impact of the navicular into the calcaneus. In galagines one might expect this to be even more of a problem due to two factors: the increased length of the navicular and calcaneus, further separating the elements of the TTJ, and the lack of relative calcaneal motion during inversion-eversion. This problem was solved by galagines by the development of a diarthroidal calcaneonavicular joint (Hall-Craggs, 1966) which allows the navicular to rotate around the relatively stationary calcaneus.

As in lemurids, indriines, and cheirogaleids, abduction-adduction and flexion-extension at the TTJ are very limited. Abduction-adduction at either part of the joint are obviously limited by the non-transverse alignment of the TTJ. Flexion-extension is limited by the large cuboid pivot, the calcaneo-cuboid ligament, and the ligaments binding the navicular and the calcaneus.

F. Lorisinae. The AN joint is a modified ovoid joint, as in galagines, but the details of shape are very different. In all taxa, the AN(A) is very compressed dorsoplantarly, but is somewhat more extensive medially than in other strepsirhines. It has a strong dorsomedial orientation (fig. 35d). The CCu pivot mechanism is even more exaggerated than in galagines. The pit is very deep and the pivot is likewise very prominent (fig. 37d). As in galagines, this increases the degree of conjunct rotation given per unit of slide, and also makes for a very stable articulation. However, unlike galagos, the pivot axis of lorisines is very off-center (mediad) and therefore pronation and supination of the cuboid are accompanied by concomitant abduction and adduction respectively. Compared to other strepsirhines, the CCu joint is oriented at a very high angle to the long axis of the calcaneus (50-80°) (Table 16b).

These features indicate that lorisines acheive inverted and everted positions of the forefeet differently than do other strepsirhines. In lemurids, indriines, cheirogaleids, and galagines inversion and eversion are mainly the result of axial rotations of the navicular around the astragalar head, the cuboid around the calcaneus, and the calcaneus around the astragalus. In lorisines the dorso-plantar flattening of the AN(A) increases the discrepancy in the curvature of the two axes of the AN joint, and thus prevents any large degree of axial rotation. Inversion of the forefoot is "programmed" by the relationships of the bony elements of the tarsus; joint action is not necessary to attain this position. The relationships of the astragalus and calcaneus (Chapter 5), the dorsomedial orientation of the astragalar head and the increased angle of the calcaneocuboid facet are the significant features of the TTJ and STJ which contribute to the "inverted set" of the lorisine foot (Grand, 1967). It is probable that inversion can be increased somewhat over that given by the bony set by the action of tibialis posterior pulling the navicular medially and backwards (not by axially rotating it). Due to the dorsomedial orientation of the astragalar head this medial swing is accompanied by some concomitant lateral rotation which inverts the forefoot. Assuming that there is little movement between the cuboid and navicular, this movement is limited by the calcaneocuboid articulation which will disarticulate if the navicular is pulled too far medially.

In other strepsirhines, both inverted and everted positions of the foot are reasonably stable. In lorisines, however, the inverted position is clearly the most stable and is the close-packed position.

III. Summary of features of the transverse tarsal joint. The transverse tarsal joint is, along with the STJ, the joint where complex displacements called inversion and eversion of the forefoot take place. These motions are necessary for repositioning the foot in variable orientations. The main motion of both components of the TTJ is pronation and supination of the forefoot, although smaller conjunct and concomitant motions occur.

The variations in TTJ features discussed in this chapter are summarized in Table 17. Among strepsirhines there are few major variations in the form of the elements of the TTJ. However, there are some important differences in four categories: 1) the shape of the AN joint; 2) the orientation of the astragalar head; 3) the size of the cuboid pivot; 4) the condition of the tarsus (serial or alternating).

In the majority of strepsirhines the AN joint is an unmodified ovoid, allowing axial rotation to take place. The two exceptions to this are the galagines and lorisines, which both have unmodified ovoid AN joints, although they are distinctly different from each other. Changing from an unmodified to a modified ovoid reduces the degree to which axial rotation at the AN is possible. Therefore, we might expect the ranges of pronation and supination to be reduced in these two taxa. This does not necesarily mean that either taxon cannot ultimately attain an inverted or everted position equal to that of any other taxon, just that these positions are accomplished through different means. A highly inverted position of the foot is achieved in lorisines by the relationships between the bones, which are pre-set in an inverted position (Grand, 1967). It is difficult to estimate the degree to which lorisines can evert their feet, since movement from inversion into eversion involves considerable dislocation of TTJ and STJ elements. The inverted position is clearly the "favored" (i.e. most stable) foot position in these slow climbers.

Galagines may compensate for their probably reduced AN rotational abilities by repositioning the AN and CCu joints into more dorsomedial positions. This throws the navicular, cuneiforms, and cuboid into an automatically supinated position, without requiring joint motion to achieve this position. The same modification (actually, this is likely the primitive euprimate condition of this trait) occurs in cheirogaleids and lorisines. However, in contrast to lorisines, galagines emphasize stability in the everted rather than inverted position. This is evidenced by the development of the medially extensive navicular cup and the calcaneocuboid locking mechanism. The first modification is shared by *Lepilemur*, *Hapalemur*, *Microcebus*, and *Phaner*, and may be an expected feature in small, long-footed leapers.

The shape of the calcaneocuboid articulation varies from being almost flat (indriines) to being quite deep (lorisines). The main difference between these two types of CCu joint shape concern stability and degree of motion, the deeper joint providing a more stable articulation, and more conjunct rotation per unit of swing. Why galagines and lorisines with their vastly different modes of locomotion both require a more stable CCu joint than do lemurids, indriines, or cheirogaleids is not clear. Why both might want increased ranges of supination-pronation without strong concomitant translations is understandable. In lorisines, this type of CCu joint allows increased ranges of supination and pronation at the CCu joint without too much necessary repositioning of the AN joint, which, as discussed above, can only allow a limited range of rotational motion. In galagines, similar arguments apply. Any concomitant translational movements which occur between the calcaneus and the cuboid would be transferred to the navicular, given the relatively immobile CuN joint in this taxon. This causes the navicular to impact against the calcaneus rather quickly in inversion, or bends the navicular away from the calcaneus in eversion, a motion which would quickly be stopped by the ligaments connecting the navicular and calcaneus.

The reduced pivot of indriines may allow a greater range of eversion by removing one of the main stops to this movement (the abutting of the cuboid pivot against the calcaneus). The increased dorsolateral orientation of the astragalar head in indriines also increases the angle to which the foot can be everted by automatically orienting the navicular and the cuneiforms into a more pronated position. However, this can be compensated for by the very spherical AN articulation which allows considerable rotational movement.

Indriines also increase the range of inversion at the TTJ by having a serial rather than alternating tarsus. With the AN and CCu joints at the same transverse level, more supination is possible before being stopped by the impact of the navicular against the calcaneus. This modification is shared by *Daubentonia*, *Varecia*, and lorisines. It thus seems to be associated with climbers and larger sized strepsirhines [though large size and increased climbing ability are almost certainly related (Cartmill, 1974; Jungers, 1979)]. The CCu joint is relatively higher and narrower in frequent leapers (indriines, galagines, some cheirogaleids) than in other strepsirhines.

In the above discussion, the differences in astragalar head positioning (dorsomedial versus dorsolateral) were related to increasing the naturally supinated (cheirogaleids, galagines, lorisines, *Daubentonia*) or pronated (lemurids, indriines) position of the medial distal tarsals. An alternate, or perhaps complementary explanation is provided by Gebo's (1985) study of grasping in strepsirhine primates. He discovered, based on myological differences and osteological distinctions in the morphology of the cuboideo-ectocuneiform/MT 3,4,5 articulations that prosimians could be divided into two groups: those with a I-V grasp (lorisoids, *Daubentonia*, *Tarsius*) and those with a I-II grasp (indriines and lemurids). The distribution of these traits matches that of astragalar head positioning. The dorsolateral positioning of the astragalar head increases the angle between the first digit (or the first two digits) and the others, contributing to the repositioning of the digits characteristic of I-II graspers. In those prosimians with a dorsomedial position of the astragalar head, the cuboid and cuneiforms are positioned more in parallel so that they tend to lie in the same plane. This suggests that these features may be related. However, anthropoids have a strong dorsolateral orientation of the astragalar head, but a I-V grasp (Gebo, 1985). Obviously the two features can be decoupled.

Table 16. Indices and measurements of the transverse tarsal joint. Conventions as in Table 8. In column A, parentheses around the value indicates that the angle is dorsomedial. No parentheses indicates that the angle is dorsolateral.

	A		B		C	
	Orientation of Astragalar head A12		Orientation of Cuboid facet C9		Height/Width CCu facet [C6/C5]*100	
Lemur fulvus	8.8	3.7	30.64	12.3	70.33	6.3
	0-15	20	25-45	11	59.49-80.95	12
Lemur mongoz	14.3	-			70.13	-
	8-20	3			63.33-76.92	2
Lemur macaco	10.0	-			71.01	-
	-	2			-	1
Lemur rubriventer	13.0	-				
	-	1				
Lemur coronatus	8.67	-	26.00	-	70.17	-
	7-10	3	-	1	-	1
Lemur catta	8.67	5.9	19.34	-	66.99	1.6
	0-15	6	11-28	3	65.71-69.01	4
Varecia variegata	7.91	3.8	31.50	-	54.66	-
	4-15	11	27-36	2	47.37-61.96	2
Hapalemur griseus	9.75	3.2	23.67	-	80.23	4.0
	6-15	8	19-32	3	75.47-86.36	6
Hapalemur simus	10.00	-				
	-	1				
Lepilemur mustelinus	16.35	5.3	10.69	4.7	75.45	8.4
	7-26	17	5-22	13	63.83-89.13	13
Daubentonia madagascariensis	(8.8)	2.6	39.00	-	73.05	-
	5-12	5	-	1	70.42-75.67	2
Avahi laniger	15.00	4.8	28.00	-	86.78	-
	6-20	10	-	1	81.54-91.53	3

continued

Table 16, continued.

	Orientation of Astragalar head		Orientation of Cuboid facet		Height/Width CCu facet	
Propithecus verreauxi	10.86	5.9	27.75	4.7	81.81	7.8
	0-2	7	21-32	4	75.00-90.41	4
Propithecus diadema	18.25	6.8	10.00	-	80.33	-
	10-31	8	-	1	73.79-86.87	2
Indri indri	13.67	9.1	30.00	-	80.41	-
	0-26	9	-	1	-	1
Microcebus murinus	(10.40)	9.1	39.23	11.2	89.36	6.0
	0-27	15	17-52	13	77.78-100.00	15
Mirza coquereli	(10)	-			81.25	-
	-	1			-	1
Cheirogaleus medius	(12.67)	-			76.39	-
	9-19	3			75.00-77.78	2
Cheirogaleus major	(16.6)	7.3	22.00	-	75.53	-
	6-24	5	-	1	64.51-80.55	2
Phaner furcifer	0	-				
	-	1				
Galago senegalensis	(12.17)	7.5			93.75	-
	6-25	6			-	1
Galago moholi	(19.20)	5.2	40.20	9.3	81.57	10.4
	18-23	10	25-48	5	62.5-92.86	6
Galago gallarum	(5.0)	-			76.47	-
	-	1			75.00-76.47	1
Galago elegantulus	(20.63)	7.6	51.00	-	90.91	-
	10-32	16	-	1	-	1
Galago matschei	(20)	-				
	-	1				
Galagoides demidoff	(9.0)	3.5	45.00	-	79.17	-
	5-15	7	-	1	-	1
Galagoides zanzibaricus	(5.0)	-			84.62	-
	-	1			-	1

continued

Table 16, continued.

	Orientation of Astragalar head		Orientation of Cuboid facet		Height/Width CCu facet	
Galagoides	(13.40)	6.8			81.82	-
alleni	4-20	5			-	1
Otolemur	(11.67)	5.9	43.00	-	83.00	8.0
crassicaudatus	5-18	6	-	2	79.36-95.00	4
Otolemur	(16)	-				
garnetti	12-22	3				
Perodicticus	(20.27)	8.4	64.67	9.5	79.75	6.2
potto	10-36	15	54-78	6	75.00-93.18	7
Arctocebus	(11.60)	5.7	48.00	-	78.71	-
calabarensis	6-20	10	-	1	77.42-80.00	2
Nycticebus	(19.82)	7.9	54.00	-	74.09	-
coucang	9-36	11	-	1	71.59-76.59	3
Loris	(18.60)	6.43	62.00	-	75.19	-
tardigradus	12-26	5	52-72	2	70.96-79.41	2
Lemuridae	9.19	3.9	27.75	10.7	71.76	7.1
	0-15	56	11-45	20	47.37-80.95	26
Indriinae	14.44	7.5	25.57	7.7	82.86	6.6
	0-31	36	10-32	7	73.79-91.53	10
Cheirogaleidae	(11.48)	8.5	38.00	11.7	85.98	8.5
	0-27	25	17-52	14	64.51-100.00	20
Galaginae	(15.58)	7.6	42.56	7.5	82.56	8.1
	4-32	56	25-51	9	62.50-95.00	17
Lorisinae	(17.83)	8.1	54.90	19.4	77.44	5.3
	6-36	41	48-78	10	70.96-93.18	14

Table 17. Summary of distribution of TTJ characters.

TAXON	AN	CCU
LEMURIDAE	unmodified ovoid slight dorsolateral orientation	moderately developed pivot
INDRIINAE	unmodified ovoid, but rounder dorsolateral orientation	reduced pivot higher, narrower articulation
DAUBENTONIA	unmodified ovoid slight dorsomedial orientation	moderately developed pivot
CHEIROGALEIDAE	unmodified ovoid dorsomedial orientation	moderately developed pivot
GALAGINAE	modified ovoid dorsomedial orientation develop medial side of joint	large pivot
LORISINAE	modified ovoid dorsomedial orientation	large pivot

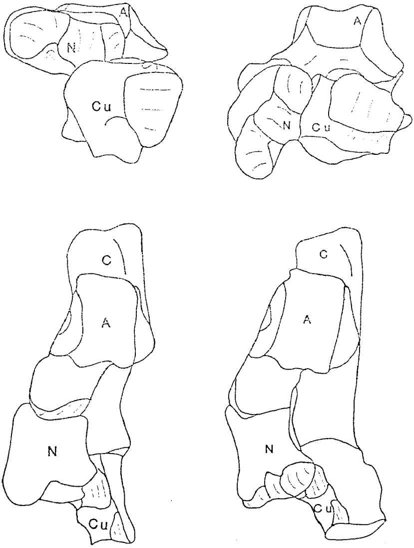

Figure 31. Positions of inversion and eversion in *Lemur fulvus*. The astragalus (A) is stationary; the bones of the *lamina pedis* change position. Top row, distal view; left, inversion, right, eversion. Bottom row, dorsal view; left, inversion, right, eversion.

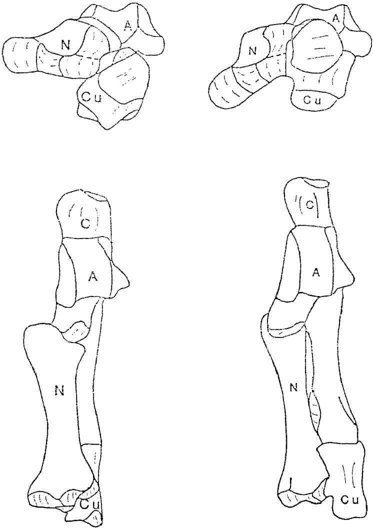

Figure 32. Positions of inversion and eversion in *Otolemur crassicaudatus*. See fig. 31 for explanation.

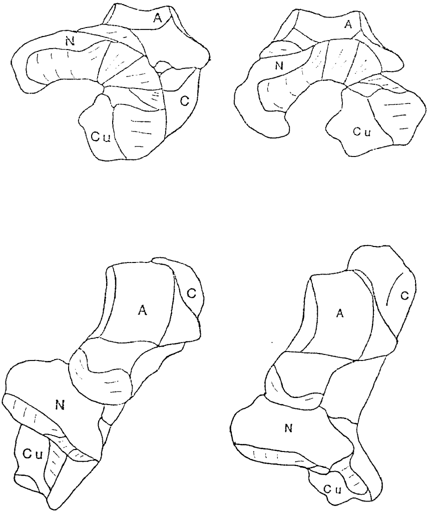

Figure 33. Positions of inversion and eversion in <u>Perodicticus potto</u>. See fig. 31 for explanation.

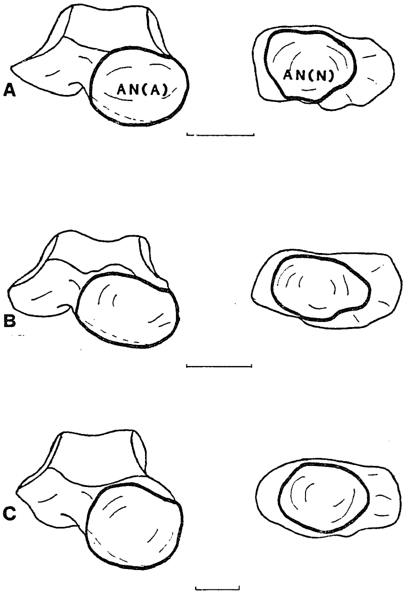

Figure 34. Astragalonavicular joint in *Lemur fulvus* (A); *Lemur catta* (B); and *Indri indri* (C). Scales are 5 mm.

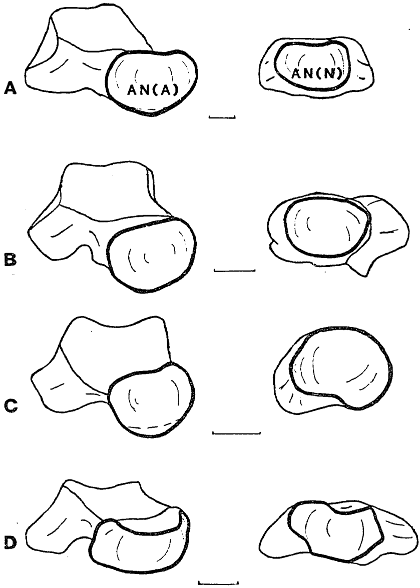

Figure 35. Astragalonavicular joint in *Daubentonia madagascariensis* (A); *Cheirogaleus major* (B); *Galago senegalensis* (C); *Nycticebus coucang* (D). Scales are 2 mm.

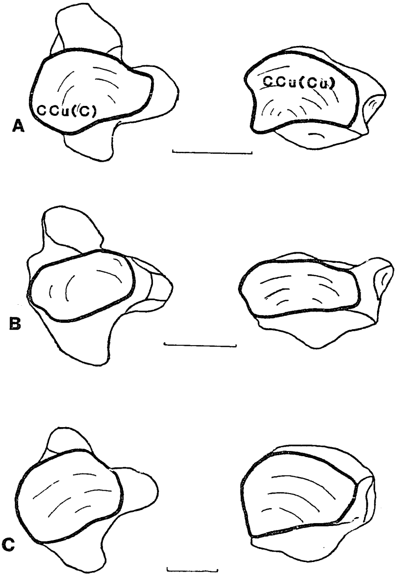

Figure 36. Calcaneocuboid joint of *Lemur fulvus* (A); *Lemur catta* (B); and *Indri indri* (C). Scales are 5 mm.

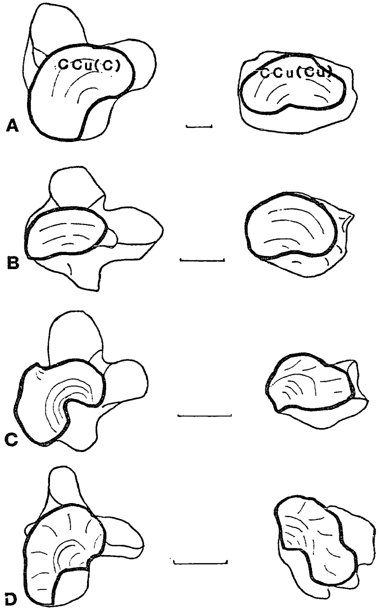

Figure 37. Calcaneociboid joint in *Daubentonia madagascariensis* (A); *Cheirogaleus major* (B); *Galago senegalensis* (C); *Nycticebus coucang* (D). Scales are 2 mm.

CHAPTER 7: THE INTERTARSAL ARTICULATIONS

I. General remarks. Most of the articulations discussed in this chapter are relatively small, and are generally flat, indicating that there are small gliding motions between the bones which are somewhat difficult to analyze in the same ways as the previously discussed joints. However, the relative size, placement, and changes in shape that do occur among strepsirhines in these joints have some functional and phylogenetic importance.

II. Calcaneo-navicular contact. The calcaneus is extensive proximally in most lemuriforms. Thus, the calcaneus and navicular are quite closely juxtaposed, especially when the foot is inverted at the subtalar joint. Certainly there is opportunity for contact between the calcaneus and navicular, but whether or not an actual facet is formed by this contact is apparently variable. Hafferl (1932) claims that such contact exists in *Varecia*, *Lemur*, and *Loris*. Lewis (1980b) observed contact facets in *Lemur catta*, and states that these facets are fairly common in lower primates, a statement disputed by Langdon (1984). My own observations indicate that in *Lemur fulvus* , *Lepilemur mustelinus* and *Daubentonia* there is often a small flat facet on the distal medial edge of the calcaneus (fig. 38). When the cuboid is articulated with the calcaneus, this facet appears to be continuous with the facet of the cuboid-navicular joint. A reciprocal facet exists on the navicular. From manipulations of bones, naviculo-calcaneal contact appears to occur only when the calcaneus is pushed forward in the position of inversion. Such facets were not commonly observed in any specimens of other strepsirhine taxa.

As is well known, the most extensive naviculocalcaneal contact occurs in the Galaginae, but this joint is not homologous to the sort of contact described above. In all species, there is a large, synovial joint about midway in the navicular, and in the distal quarter of the calcaneus. The facet is long proximodistally and narrow dorsoplantarly. It is of the ovoid type; the convex surface is on the calcaneus, and the concave surface is on the navicular. This joint allows the navicular to rotate medially and laterally around the calcaneus during inversion and eversion (Hall-Craggs, 1966). This was discussed above (chapter 5 and 6).

III. The Cuboidnavicular joint. (figs. 39-40).

A. Lemuridae. The contact between the cuboid and navicular occurs at the proximal end of the cuboid and the distal end of the navicular. The facet on the cuboid is confluent with the proximal facet for the ectocuneiform and the facet for the mesocuneiform. The CuN(Cu) facet is fairly flat, but is usually of the ovoid type; the facet on the cuboid is mainly concave in both directions. In some individuals, it may approach the sellar condition exhibited by the indriines. The contact facets overlap nearly 100%, indicating that only small amounts of proximodistal or dorsoventral sliding movements can take place at the joint. The CuN(N) joint is located plantad to the NMe facet and the NEc facet (fig. 41).

B. Indriinae. The shape of the facet may vary from being essentially flat as in lemurids, to the more common condition of being quite sellar shaped. On the cuboid, the dorsoplantar axis is convex, and the proximodistal axis is concave. The orientation of the facet is as in lemurids.

C. *Daubentonia*. *Daubentonia* resembles lemurids in the shape of this joint, but the orientation is different. The CuN(N) facet is plantad only to the NEc facet (fig. 69).

D. Cheirogaleidae. *Cheriogaleus* is essentially lemurid-like in the morphology of this joint. In *Mirza*, *Phaner*, and *Microcebus* the joint tends to be more sellar shaped. In cheirogaleids there is a trend towards shifting the CuN(N) facet laterally, so that it lies plantar-laterally mainly to the NEc facet, in contrast to the majority of other strepsirhines in which the facet is on the plantar face of the bone mainly under the NMe articulation. *Cheirogaleus* is the most lemurid-like in this respect; *Phaner* and especially *Microcebus* more closely approach the galagine condition (see below, and fig. 41).

E. Galaginae. The cuboidnavicular facet on the navicular is shifted laterally. It lies along the lateral edge of the navicular, not on its plantar side (fig. 41f). This is associated with the reorientation of the NEc joint (see section VII). Thus, it is contiguous mainly with the NEc facet, and may not contact the NMe at all. The CuN(Cu) facet is very restricted in size, being a proximodistally long, but dorsoplantarly narrow protuberance which is ensconced in a trochlear shaped depression on the navicular. This fairly effectively locks the two bones together, prohibiting dorsoplantar sliding. Distal sliding is also prevented by the nature of the articulation for the entocuneiform, which juts out medially, blocking any forward motion of the navicular on the cuboid. Proximal sliding may be allowed, but judging from the manipulation of bones, it is not of great magnitude.

F. Lorisinae. Although the actual outline of the facet may vary greatly between individuals, its surface is most often fairly flat. Like lemurids, the facet is planted to both the NEc and the NMe facets.

IV. Notes on movement at the cuboid-navicular joint. The shape of the CuN joint takes two basic forms among living strepsirhines. It is either an ovoid joint with generally very flat surfaces (lemurids, *Cheirogaleus*, lorisines) or a sellar joint (indriids, *Phaner*, *Microcebus*, *Mirza*, galagines). From this distribution it would seem that the more frequent leapers tend to restrict motion at this joint, especially dorsoplantar sliding, thereby increasing the stability of the everted foot. However, it is generally agreed that very little motion can take place at this joint in any case due to the tight ligamentous connections between the two bones. It is probable, therefore that the differences have more to do with demands for joint stability than with any differences in movement. The tongue in groove galagine arrangement of this joint may be specifically designed to counteract forces tending to separate the two bones, as would likely occur during pushoff from an everted, plantigrade foot. This may be necessary due to the more laterally positioned cuboid and navicular in galagines as opposed to other strepsirhines.

There are also significant differences in the orientation of the cuboidnavicular joint. As noted above, in lemurids, indriids, *Cheirogaleus* and lorisines, the CuN(N) facet is located plantar to the NMe(N) and NEc(N) facets. A less exaggerated form of this articulation is present in *Notharctus* and *Smilodectes* and is likely the primitive condition for Strepsirhini. This arrangement reflects the broad "superimposition" of the navicular on the cuboid, and forms a deep arch in the midtarsal region.

However, in *Mirza*, *Microcebus*, *Phaner*, and galagines the cuboid appears to have been rotated medially relative to its position in *Lemur*. Thus, the articulation between the navicular and cuboid is shifted laterally so that its facet lies lateral (but still somewhat plantar) to the NEc(N) and has been shifted away from contact with the NMe(N) articulation. This reorientation explains the reduction or loss of mesocuneiform-cuboid contact in some cheirogaleids and galagines (see below, section VI). By rotating the cuboid, the transverse tarsal arch is lowered and flattened, and the plane of the metatarsals is more parallel to the support. This affords a flatter anterior foot, especially in eversion. This reorientation is no doubt related to being able to position a relatively flat anterior foot against a substrate before a leap.

Daubentonia shares with the above taxa the contiguity of the NCu facet with only the NEc facet, and lack of the mesocuneiform-cuboid contact. However, this is not due to a lateral shift of the cuboid in *Daubentonia*, but rather to a medial extension of the NEc facet which undercuts the NMe facet. _Daubentonia_ may retain the most primitive form of this joint (Chapter 10).

V. The cuboid-ectocuneiform joint.

A. Lemuridae. The ectocuneiform articulates with both the cuboid and the navicular. On the cuboid there are two facets. The proximal one is confluent with the CuN and CuMe facets. It is a fairly flat ovoid joint. The flat distal facet is located at the distodorsal corner of the cuboid. The reciprocal facets on the ecto-cuneiform are also discontinuous; a small ligament connects the two bones in the interspace. The nature of the facets (small size, flatness, discontinuity, nearly complete overlap) guarantees that only small sliding movements can take place between the ectocuneiform and cuboid.

B. Indriinae. The CuEc joint is basically the same as lemurids. Sometimes the distal CuEc facet is not present.

C. _Daubentonia_. _Daubentonia_ is like lemurids, except that there is no cuboid-mesocuneiform facet.

D. Cheirogaleidae. There is usually only a single flat facet which extends nearly to the distal end of the cuboid. It is not clear if the two facets are confluent, or if the distal facet is missing.

E. Galaginae. The CuEc joint has two separate facets which are flat, as in lemurids.

F. Lorisinae. As in cheirogaleids, there is only a single large facet. It is more dorso-plantarly extensive in lorisines than in any other group. The ectocuneiform-navicular facet is elongated dorsoplantarly and narrow medio-laterally.

VI. The cuboid-mesocuneiform joint. The significance of this contact was discussed above (section IV).

A. Lemuridae. There is usually a very small contact between the mesocuneiform and the cuboid, so that the ectocuneiform is wedged in between the two. The contact is very limited, and may sometimes be absent. In *Lepilemur*, however, there is a larger and more clearly developed contact area between the mesocuneiform and the cuboid. In this feature, *Lepilemur* is very indriine-like.

B. Indriinae. The contact between the mesocuneiform and the cuboid is very well developed in all taxa.

C. *Daubentonia*. There is no cuboid-mesocuneiform contact.

D. Cheirogaleidae. There is a fairly large contact in *Cheirogaleus major*, a small facet in *Microcebus*, but it appears to be absent in the only specimen of *Phaner* I examined.

E. Galaginae. There appears to be no mesocuneiform-cuboid contact facet in any galagine genus.

F. Lorisinae. No contact was observed in *Perodicticus* or *Nycticebus*, but contact does occur in *Arctocebus* and *Loris*. The lack of contact in *Perodictiucs* and *Nycticebus* is not due to the same factors as in galagines. In lorises, the cuboid is *not* medially rotated. In fact, due to the permanently inverted position of the cuboid (see Chapter 6), the cuboid is laterally rotated. The change in NMe articulation is in reality the result of changes in the NEn and NMe joints which are bent around to the medial side of the navicular.

This carries the NMe joint away from the cuboid and results in the loss of a mesocuneiform-cuboid articulation. The functional significance of this is discussed below (section VIII).

VII. The navicular-cuneiform joints. (fig. 41). The significance of variations in morphology at these joints is discussed in a separate section (VIII) immediately following these descriptive sections.

A. The navicular-ectocuneiform joint.

1. Lemuridae. The navicular-ectocuneiform facet is a moderately deep ovoid joint, circular in outline; the convex surface is on the proximal end of the ectocuneiform, and the concave surface is on the distal end of the navicular. The lateral edge of this joint is functionally continuous with the proximal CuEc facet forming a notch into which the ectocuneiform is locked.

2. Indriinae. Indriines are very similar to lemurids in the morphology of this joint.

3. *Daubentonia*. The shape of the facets are like those of lemurids, but the joint is more horizontally oriented (fig. 69).

4. Cheirogaleidae. In *Cheirogaleus* the basic shape of the joint is lemurid-like, while in *Microcebus* and *Phaner*, it is more galagine-like (see below).

5. Galaginae. The ectocuneiform-navicular joint is deeper than in lemurids. The more highly arched ectocuneiform surface is almost completely overlapped by the deep semilunar notch which is the NEc(N) surface. Relative to lemurids or indriines, the joint is shifted so

that it lies dorsal to the NMe joint, instead of medial to it.

6. Lorisinae. The facet is an ovoid joint, as in lemurids, but it is much flatter, triangular in outline rather than circular, and is dorsoplantarly elongated and mediolaterally narrow. It is more horizontally oriented than in lemurids or indriines.

B. The Navicular-mesocuneiform joint.

1. Lemuridae. The NMe joint lies medial to the NEc joint. It is a square-shaped, ovoid facet, convex on the navicular, concave on the mesocuneiform.

2. Indriinae. Indriines are like lemurids in the construction of this joint.

3. *Daubentonia*. *Daubentonia* is lemurid-like.

4. Cheirogaleidae. Again, there is a cline of morphologies in the cheirogaleids, from *Cheirogaleus*, which is lemurid-like, to *Phaner*, which is more galagine-like, to *Microcebus murinus*, which is virtually indistinguishable from the galagine condition (see below).

5. Galaginae. The NMe joint is an ovoid joint, like in lemurids, but it is more restricted in size. The surface on the navicular is very restricted dorsoplantarly, but has a higher curvature than in lemurids. It has a generally cylindrical appearance.

6. Lorisinae. In lorisines the small NMe joint takes various shapes. In the potto, the joint is an ovoid, as in lemurids, but the concave surface is on the navicular, and the convex surface is on the mesocuneiform; just the opposite of what is seen in lemurids or *Nycticebus*.

C. The navicular-entocuneiform joint.

1. Lemuridae. It is a modified ovoid joint. The facet on the navicular is narrow dorsoplantarly and long mediolaterally and is convex in both directions. It slopes plantarmedially. The facet on the entocuneiform is rounded and concave.

2. Indriinae. Indriines are lemurid-like in the construction of this joint.

3. *Daubentonia*. The shape of the facets is like that of lemurids, but the joint is more horizontally oriented, and it wraps around the medial edge of the navicular, like in lorisines.

4. Cheirogaleidae. *Cheirogaleus* is lemurid-like; *Phaner* and *Microcebus* have, like galagids, a square-shaped joint.

5. Galaginae. The NEn is deeply cup-shaped. The facet on the navicular is not elongate as in lemurids, but is compressed mediolaterally giving it a more squarish shape, and a higher degree of curvature. There is often a nonarticular gap betwen the NMe(N) and NEc(N) facets.

6. Lorisinae. The NEn is a very flat facet; very elongated mediolaterally and compressed dorsoplantarly. Like *Daubentonia*, the joint is more horizontally oriented, and is bent around the medial edge of the navicular. There is sometimes, as in galagines, a nonarticular gap between the NMe(N) and NEc(N) facets.

VIII. The function of the navicular-cuneiform joints as a unit.

A. Lemuridae. The navicular-cuneiform joints together form a double S shaped modified sellar joint. Effectively, there is only one type of movement possible, an arcuate slide. This movement takes place along an axis which is approximately parallel to the dorsum of the navicular. This joint allows a small amount of dorsiflexion and plantarflexion of the hind part of the foot on the fore part of the foot, but movement is restricted by the articulation of the cuneiforms and navicular with the cuboid. The morphology and movements are essentially the same in indriines, *Daubentonia*, and *Cheirogaleus*.

B. Galaginae. Galagines have the most derived navicular-cuneiform joints of any strepsirhines. The cheirogaleids, with the sole exception of *Cheirogaleus* share these modifications, but exhibit them in a slightly less extreme form. All three navicular-cuneiform articulations are smaller (relative to foot or body size) and are more dorsoplantarly compressed than in lemurids. They all also appear to have higher arcs of curvature than do lemurids. This may give galagines a higher range of flexion and extension at the navicular-cuneiform joints than in lemurids, but it is difficult to estimate the range of movement. In vivo studies of leaping in galagos (Jouffroy and Gasc, 1974) do however, point out the extreme dorsiflexion which occurs in this region of the foot, (approximately 90 degrees judging from their photographs and drawings) and its importance in the leap. Similar modification of the navicular-cuneiform joints occur in *Tarsius*, for similar biomechanical reasons (Gunther and Niemitz, 1980; Niemitz, 1984; Jouffroy *et al*. 1984). This morphology allows the elongated portion of the hindfoot to contribute to the effective length of the leg.

C. Lorisinae. The flatness and almost total overlap of facets at these joints assures that only small sliding movements take place, but Grand (1967) notes about 35 degrees of plantar-dorsiflexion at this joint in *Nycticebus*. This reflects the function of the navicular as a load bearing platform which bridges across the support connecting the medial and lateral moieties of the foot. There are three other modifications of the lorisine navicular-cuneiform joints to consider; the reorientation of the NEn and to some extent the NMe joints to more medial positions, and the more transverse orientation of the NEn and NEc joints. The first feature in combination with the more medial extent of the AN joint swings the MT1En joint distally and into a more adducted position relative to the other metatarsals, contributing to the wide divergence of the first digit. This brings the axis of MT1 to an orientation more perpendicular to the long axis of the foot (fig. 42). The more transverse orientation of this joint reorients the long axis of the MT1En joint to a position more parallel to the long axis of the foot (and thus the support). These two orientations increase the span of the grasp and allow opposition of digit 1 to work more perpendicular to the support than in other strepsirhines. The more transverse orientation of the NEc joint is the result of a rotation of the EcMT3 joint so that it now lies parallel to the CuMT4 and CuMT5 joints. This aligns the lateral three digits in the same dorso-plantar plane and reflects the functional unity of the lateral three digits in lorisines (Wrobel, 1960).

IX. Summary of variations in intertarsal joints. The distribution of intertarsal joint features is listed in Table 18. Calcaneonavicular contacts occur in a few species, but these contacts are not homologous to the apomorphic synovial calcaneonavicular joint of galagines. The cuboidnavicular joint is generally flat, but becomes more sellar shaped in frequent leapers. It is especially modified in galagines, to provide a great deal of stability in the everted position.

Two positions of the CuN(N) facet are found in extant strepsirhines. In lemurs, indriis, Cheirogaleus, and lorisines, the facet is plantar to both the NMe(N) and NEc(N) facets. In the other cheirogaleids and galagines the cuboid is rotated medially, and the navicular-cuboid articulation is shifted laterally so that the facet lies lateral to the NEc(N) and does not contact the NMe(N). Cuboid-mesocuneiform contact is lost. This reorientation of the cuboid and navicular flattens the transverse arch of the foot.

Galagines and some cheirogaleids also greatly modify the navicular-cuneiform joints. The three articulations are smaller, more dorsoplantarly compressed, and are more highly curved than in other strepsirhines. This arrangement allows a great deal of flexion at this joint which is an important component of the leap.

Lorisines modify the navicular-cuneiform joints in a very different way in order to increase the span of the grasp and allow opposition of the first digit to work more effectively.

Table 18. Summary of distribution of features of the intertarsal joints.

JOINT	Lemuridae	Indriinae	Cheirogaleidae
CuN	ovoid, flat plantad to NMe	sellar plantad to N-Me	*Cheirogaleus*-ovoid plantad to N-Me others-sellar plantad to N-Ec
CuMe	present, small (well developed in *Lepilemur*	well developed	*Ch.*-present *Mi.*-small *Ph.*-absent
NEc	moderately deep ovoid	moderately deep ovoid	*Ch.*-lemurid-like others-galagine-like
NMe	modified ovoid, flat, square outline	modified ovoid flat, square outline	*Ch.*-lemurid-like others-galagine-like
NEn	ovoid, NEn(N) narrow dorso- plantarly, long mediolaterally	ovoid, NEn(N) narrow dorso- plantarly, long mediolaterally	*Ch.*-lemurid-like others-galagine-like

Table 18, continued.

JOINT	Galaginae	Lorisinae	*Daubentonia*
CuN	sellar plantad to NEc	flat plantad mainly to NEc	ovoid plantad only to NEc
CuMe	absent	absent in *Perodicticus* and *Nycticebus*	absent
NEc	very deep ovoid highly curved	modified ovoid, very flat. long dorsoplantarly, narrow mediolaterally. more horizontal	lemurid-like
NMe	modified ovoid restricted in size. high curvature.	variable shapes, usually flat	lemurid-like
NEn	very deep ovoid mediolaterally compressed, high curvature	very flat, mediolaterally elongate, horizontal orientation	lemurid-like in shape, but more horizontal orientation

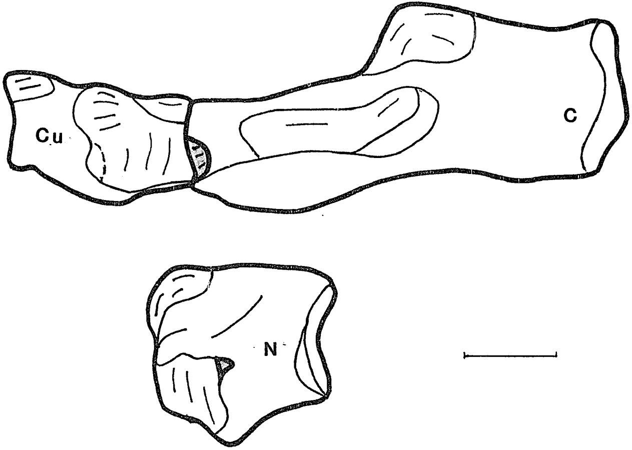

Figure 38. Presence of a calcaneonavicular contact (dark outline) in Lemur fulvus. Scale is 5 mm.

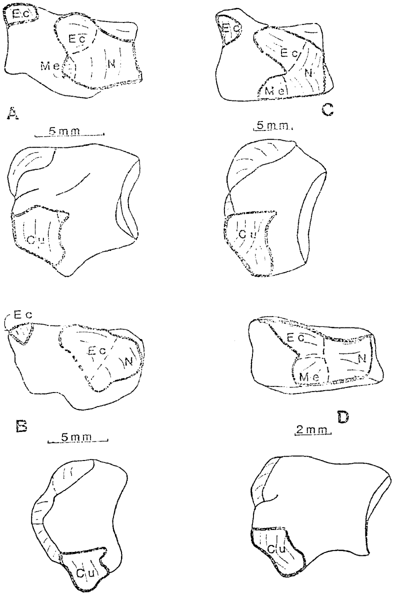

Figure 39. The navicular-cuboid joint in <u>Lemur fulvus</u> (A); <u>Propithecus diadema</u> (C); <u>Daubentonia madagascariensis</u> (B); and <u>Cheirogaleus major</u> (D). The cuboid is the top bone of each pair, the navicular is the bottom bone, rolled away from the articulation. The facets are labeled for the bones with which they articulate.

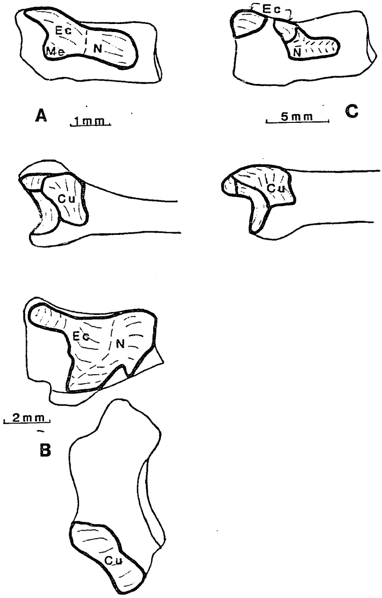

Figure 40. The navicular-cuboid joint in *Microcebus murinus* (A); *Ctolemur crassicaudatus* (C); *Nycticebus coucang* (B). For explanation see fig. 39.

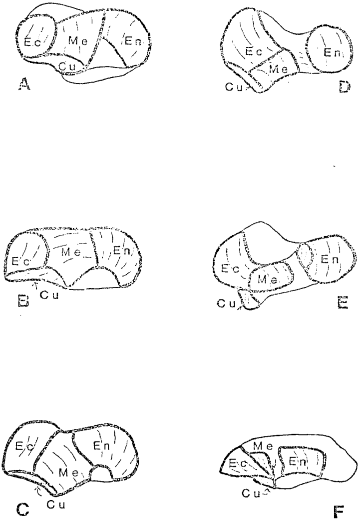

Figure 41. Distal view of the navicular in *Lemur fulvus* (A); *Propithecus diadema* (B); *Cheirogaleus major* (C); *Microcebus murinus* (D); *Galago senegalensis* (E); and *Nycticebus coucang* (F), illustrating navicular-cuneiform facets (labeled by the bone they articulate with) and the position of the NCu(N) facet.

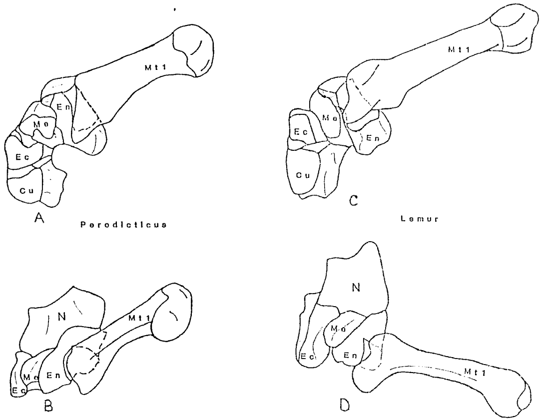

Figure 42. Action of MT1 in a lorisine and a lemurid. A, anterior view of tarsals and MT1 in *Perodicticus potto*. B, dorsal view of *P. potto*. C, anterior view of *Lemur fulvus*. D, dorsal view of *L. fulvus*. MT1 is positioned in maximum extension.

CHAPTER 8: EOCENE FOSSIL STREPSIRHINES

I. The notharctines. Of the five recognized genera of notharctine primates foot bones are known for three: *Cantius*, *Smilodectes*, and *Notharctus* (fig. 43). The notharctines are fairly uniform in terms of foot morphology; the degree of variation is comparable to that seen within extant Lemuridae. The notharctines are the earliest known strepsirhines (justification for grouping Aadapidae and Lemuriformes into a monophyletic Strepsirhini is given in Chapter 10), and among the earliest known euprimates. They thus give us important insights into the probable primitive morphologies for these two groups.

A. *Cantius* (figs. 44-50). The material studied in this thesis is listed in Table 19. Rose and Walker (1985) have recently described a fairly complete skeleton of *Cantius*, and Covert (1983) has briefly discussed additional remains. Foot bones of *Cantius* (AMNH 16852) were first described in 1915 by Matthew, and later discussed by Gregory (1920) and Decker and Szalay (1974). This specimen was listed in the figure legend (Matthew, 1915; fig. 13) as *Pelycodus frugivorous*, but referred to in the text as *P. trigonodus*. Its locality and size make it most likely that it is *Cantius trigonodus* (Gingerich and Simons, 1977; Rose and Walker, 1985). *Copelemur praetutus* is also known from the Upper Graybull horizon, but not definitely from the Big Horn Basin (Gingerich and Simons, 1977), and is probably too small to have postcrania this size. The postcranial remains of AMNH 16852 represent at least two and perhaps three different individuals. There are also numerous "associated" mandibular and maxillary fragments.

One nearly complete and three partial calcanea in the collections of the AMNH from the Alkali site in the Wind River basin (Lost Cabinian level) belong to notharctines. These calcanea are much larger than those of *Cantius trigonodus*. In fact, the complete calcaneus is the longest known notharctine specimen. *C. trigonodus* is slightly smaller than *Lemur fulvus*, the other calcanea are approximately the size of *Varecia*. Both *Cantius venticolis* and *Cantius frugivorous* are recognized at this site, and as both are also larger dentally than *Cantius trigonodus*, it is difficult to definitely assign these bones to one or the other species. *Cantius venticolis*, the larger of the two, is the more likely candidate. However, these Alkali calcanea are much larger and morphologically distinct from probable *C. venticolis* specimens from late Lysite deposits (Gebo, pers. comm.) suggesting that perhaps these bones might best be assigned to another taxon. *Pelycodus jarrovi* is an alternate possiblity for assignment. It is contemporary with the Alkali calcanea in New Mexico and Colorado, but it is not yet known from the Lostcabinian in Wyoming. *P. jarrovi* has, however, been reported from Graybullian age deposits in the Big Horn Basin (Rose and Bown 1984).

It has been suggested that *C. venticolis* is ancestral to *Notharctus* (Osborn, 1902; Gingerich and Haskin, 1981). If these calcanea do represent *C. venticolis*, this species was quite distinct from *Notharctus* postcranially. *Notharctus* and *S. gracilis* resemble *C. trigonodus* much more than this Wind River taxon.

UWA 60308 is a probable *Cantius* astragalus collected by Dr. J. Rensberger from the Wasatch formation (I have no further data as to the exact level). It is just enough larger than the *C. trigonodus* material to suggest that it might belong to a different species, but otherwise it is identical to *C. trigonodus*.

Cantius exhibits all the hallmark euprimate features of the upper ankle joint (see Chapter 4). The body of the astragalus is higher than in *Plesiadapis* (Decker and Szalay, 1974), and is high both medially and laterally. The trochlea is long and relatively narrow (Rose and Walker, 1985) (Table 21). There is a substantial posterior trochlear shelf and a laterally flaring AFi(A). One major distinction between *Cantius* and most extant strepsirhines is the lack of medial twisting of the ATiL(A) and ATiM(A) facets, although the distal tibia is very lemur-like in its anterolaterally facing ATiM(Ti) (Table 21).

The STJ is virtually indistinguishable from that of a living strepsirhine. The pAC(C) is longer and narrower than in lemurids, and is thus more comparable to the condition seen in indriines (Table 21), (but pAC length is compared only to calcaneal length, not to STL; the relatively longer pAC(C) may simply be the result of a shorter calcaneus). The aAC(C) is less regularly continuous than in living strepsirhines, and the aAC(A) is slightly less confluent with the AN and spring ligament facets than in extant forms (Rose and Walker, 1985), with the anterior interosseous ligament invading the lateral part of this articulation slightly more than in other notharctines (at least in *C. trigonodus*).

The AN(A) is fairly rounded and its long axis is essentially parallel to the body of the astragalus. The CCu joint is slightly damaged in AMNH 16852, but appears to have been relatively high, circular, and clearly possesses a depression for a calcaneocuboid pivot. This is more clearly seen in the Alkali calcanea. The cuboid angle averages 28°, the same as in lemurids.

The Alkali calcanea differ from *C. trigonodus* (and those of other notharctines) in the greater relative length of the tuber (Table 21, index C7/C1). This gives these bones a very different aspect (and possibly a more primitive morphology) than other notharctines. Among other strepsirhines, *Adapis* and *Leptadapis*, and some large subfossil forms share this peculiarity. This specimen exhibits the lowest relative length of the distal calcaneus of any notharctine, although the difference is not very great.

There are no known naviculars, cuboids, or cuneiforms for *Cantius* or *Pelycodus*, other than the entocuneiform, so details of intertarsal articulations remain unknown. The entocuneiform-first metatarsal joint indicates that *Cantius* had grasping abilities similar to those of modern lemurs (Matthew, 1915; Rose and Walker, 1985).

B. *Notharctus* and *Smilodectes* (figs. 43, 45-51). These middle Eocene primates are fairly well known from deposits in the Bridger Basin of Wyoming. *Notharctus* has been previously described in detail and analyzed by Gregory (1920) and Decker and Szalay (1974). *Smilodectes* was discussed in Decker and Szalay (1974) and by Covert (1985a). Both *Smilodectes* and *Notharctus* are very similar to *Cantius* in terms of UAJ, STJ, and TTJ morphology, so that most of the discussion above applies equally well to the middle Eocene forms, and will not be repeated here.

There are a few morphological distinctions among Bridgerian notharctines that are potentially indicative of minor locomotor differences. The evaluation of these distinctions, especially as to whether they are indeed species specific morphologies or simply intraspecific variation, is hampered by the the virtual lack of postcranial bones well associated with clearly identifiable dentitions. Only two very reliable associations exist: UWA 35892 for *Smilodectes gracilis* and UWA 37732 for *Notharctus*. (The nearly complete skeleton of *S. gracilis* at the USNM was not examined in this study.) The better known AMNH associations discussed by Gregory (1920) are more problematical than has been previously assumed. One probably good association is AMNH 11478. The teeth of this specimen fall into the size range of *N. tenebrosus* as defined by Gingerich (1979). The reconstructed feet, however, appear to be chimeric. The right foot is probably a good association, but all the bones are unnumbered. The left foot is clearly not all from the same individual. The astragalus and calcaneus are unnumbered, but appear to match the right astragalus and calcaneus fairly well. The navicular, entocuneiform, and second metatarsal are numbered 11484. However, they are too large to be from the same individual as the astragalus and calcaneus labeled 11484. Perhaps they do belong to AMNH 11478 and are mislabeled. The cuboid is numbered 11477, and does seem to be a bit too large for this specimen. It may belong to the astragalus numbered 11477, but the color and texture of this bone do not match either the 11477 astragalus or the 11478 foot bones. Due to these problems, only the right foot of 11478 was considered in the following analysis.

There are other specimens associated with some dental remains, but in which the teeth are broken and/or worn making them difficult to classify. AMNH 13024 is *N. tenebrosus* or *N. pugnax* based on the size of its lower second and third molars. AMNH 11483 and AM 91663 are associated with very small mandibles most comparable to *Smilodectes*. AMNH 13030 is a mixed specimen. The mandible and most of the foot bones are small and probably assignable to *Smilodectes*. The astragalus, however, is quite large and clearly does not belong to the same individual as the rest of the foot bones.

Gingerich's (1979) analysis based on tooth size suggests that there are three species of notharctines in Bridger B level deposits (where virtually all of the postcranial material comes from). The smallest species is *S. gracilis*, *N. tenebrosus* is intermediate, and *N. pugnax* is largest. Unfortunately, foot bones from the Bridger can not be quite as neatly sorted out. Based on astragalar length, the Bridger B notharctines fall into two size classes: a small group (astragalar length 16.8-18.4 mm) and a large group (19.1-20.5 mm) (Table 20). The small group contains associated material of both *S. gracilis* (UWA 35892, AM 91663, AMNH 13030 in part) at the lower end of the range and *N. tenebrosus* (USNM 174444, AMNH 11478) at the upper end, suggesting that both species fall into this group, and that there is no clear dividing line between them. The large group probably corresponds to both *N. tenebrosus* and *N. pugnax*, although the only dentally associated specimens in this group (AMNH 13204, UWA 37732) are labeled *N. tenebrosus*. This name, however, has been widely applied to all Bridger notharctines. There are no features of the foot bones that distinguish these two taxa. Similarly, *N. robustior* from Bridger C deposits is not significantly different from *N. pugnax*, except for its greater size. Covert (1985b) has similarly divided Bridger postcranials.

There are some morphological distinctions between specimens in the small group which may serve to distinguish *S. gracilis* from *N. tenebrosus*. In the smallest members of this group, including dentally associated *Smilodectes* specimens, the AN joint and the CCu joint are more dorsoplantarly flattened than in the larger members (figs. 47 and 50, Table 20). This trend carries over into the large group. However, it should be noted that the index of cuboid height and width for both groups falls into the range exhibited by *L. fulvus* or *L. mongoz*. The cuboid angle is lower in *S. gracilis* than in *Notharctus* (Table 21). Table 20 also shows that calcaneal length does not distribute exactly as astragalar length. This appears to be due to a difference in relative astragalus/calcaneus length between taxa. *S. gracilis* has relatively longer calcanei than *N. tenebrosus*, and *N. tenebrosus* has slightly longer calcanei than *N. pugnax*. This is probably a size related trend; a similar difference is seen in the series *L. fulvus-L. catta- Varecia*. The result of this difference is a reverse alternating tarsus in *Smilodectes*, but an approach toward a serial tarsus in *N. pugnax* and *N. robustior*. There appear to be no associated differences in calcaneal proportions. *S. gracilis* may also be distinguished by relatively longer, narrower headed metatarsals, but no specimens are complete enough to allow a metrical comparison.

Notharctus and *Smilodectes* provide the earliest evidence of distal tarsal structure in euprimates. In both taxa, the AN(N) joint is extremely lemur-like. In *Smilodectes* however, it is more dorso-plantarly flattened, matching the morphology of the AN(A). The CCu(Cu) of *Smilodectes* is similarly flattened. The navicular-cuneiform joints are almost identical to those of lemurids, indriines, or *Cheirogaleus*. The CuN(N) joint is plantad to the NEc(N) and extends a little medially to lie partially under the NMe(N) facet, but it is not as medially extensive as in extant strepsirhines (fig. 69). As a result of this, and the more plantarly elongate keel of the ectocuneiform, the mesocuneiform does not contact the cuboid in *Notharctus* (Decker and Szalay, 1974; but contra Gregory, 1920). This, plus the larger, more vertically positioned mesocuneiform (Gregory, 1920) result in a foot which has a flatter arch across the cuneiform region than in extant strepsirhines. The same features probably apply to *Smilodectes* also, but no specimen is complete enough to verify this. The cuboid of both taxa is relatively long and narrow, and essentially lemuriform in morphology, in terms of its articulations with the navicular, ectocuneiform, and the fourth and fifth metatarsals. In *Smilodectes* the 5th metatarsal appears to overlap the lateral side of the cuboid more than in living lemurs with the exception of *Lepilemur*.

II. Adapines. Of the numerous species of adapine primates only four are represented by any foot bones. I have looked through most of the collections of Eocene bones from the MNHN, BSM, NMB, Montauban,[1] and Montpellier collections without locating material from other species. The bones used in this study are listed in Table 19. *Adapis parisiensis* and *Leptadapis magnus* were previously described and analyzed by Decker and Szalay (1974) and Dagosto (1983). An unassigned middle Eocene adapid probably representing *Protoadapis* or *Europolemur* was described in 1979 by von Koenigswald. An astragalus and three calcanea from Egerkingen, probably representing *Caenopithecus* are described here. Unlike the rather uniform notharctines, the adapines evidence more varied postcranial morphology and presumed locomotor behavior.

A. *Adapis parisiensis* (fig. 52). Two astragali and twenty-one calcanea are known for *Adapis*, all from the Phosphorites du Quercy deposits of France. The size range evidenced by the calcanea (15.9-19.4 mm in length) is fairly large for an animal of this size; it is possible that more than one species is represented by this sample. However, Gingerich (1981b) suggested that this species was more sexually dimorphic than extant strepsirhines; this might explain the variation. There are no obvious breaks in size distribution or any

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[1] Abbreviations are explained in Table 19.

morphological distinctions that would allow sorting. One calcaneus (Basel QE 530) does stand out from both the *Adapis* and *Leptadapis* samples in terms of size (calcaneal length 22.3mm). Two Quercy adapines have been described as being intermediate in size between *A. parisiensis* and *Leptadapis*; *A. stintoni* (Gingerich, 1977) and *Cryptadapis* (Godinot, 1984). It is very likely that this calcaneus belongs to one of these taxa. Morphologically, it presents no differences from *Adapis* or *Leptadapis*.

As evidenced by numerous aspects of its postcranial skeleton, *A. parisiensis* was a slow climbing primate, perhaps not as fully derived as a living lorisine, but approaching it quite closely in many respects (Dagosto, 1983). In the foot the loris-like features which indicate a slow climbing habitus are: a relatively long ATiL(A) (compared to astragalar length), a dorsoplantarly flattened astragalar body, a strongly medially flared ATiM(A) and ATiL(A) (Table 22). *A. parisiensis* also has a large astragalar neck angle, a short astragalar neck, and a lack of elongation of the distal part of the calcaneus, which all indicate a non-leaping mode of locomotion. However, *Adapis* does not exhibit the extremely derived aspects of the lorisine STJ or TTJ which yield the inverted set to the foot.

B. *Leptadapis magnus* (fig. 53). This taxon is similar to *A. parisiensis* in several ways, including the long, low trochlea, marked curvature of the ATiM(A) and ATiL(A), short astragalar neck, and lack of distal calcaneal elongation (Dagosto, 1983). As in *Adapis*, these features indicate that climbing was the preferred mode of locomotion, and leaping was unimportant if practiced at all. *L. magnus* is slightly more primitive than *A. parisiensis* in that it retains a small posterior trochlear shelf. The cuboid of *L. magnus* is quite lemur-like except for its relative shortness.

C. Messel adapid. This specimen is unfortunately crushed badly so that many important details of foot morphology cannot be ascertained with certainty. The overall impression of the foot is much more like a notharctine or a lemurid than an adapine. This comparison extends to other aspects of the postcranium as well (von Koenigswald, 1979). The Messel adapid does not appear to have a posterior trochlear shelf as large as that of North American adapids, nor does it have any of the derived UAJ features exhibited by *A. parisiensis* or *L. magnus*.

D. *Caenopithecus lemuroides* (fig. 54). Three crushed calcanea and one partial astragalus have been recovered from the Egerkingen gamma deposits. Of the two adapid primates known at this site only *Caenopithecus lemuroides* is the proper size to be associated with these bones (the other taxon is *Microadapis sciureus*).

The astragalus is quite similar to that of *Adapis* or *Leptadapis*. The ATiM(A) and ATiL(A) are medially curved and form a moderately deep cup on the astragalar neck. The posterior trochlear shelf is very short and compares more with the condition in *Adapis* than *Leptadapis*. Most of the neck and head of the astragalus is missing; therefore neither the relative length of the neck, nor features of the AN(A) can be ascertained. The neck deviates quite strongly medially.

The calcanea are all distorted to some degree making comparisons and measurements difficult. In general, they appear to be very like the calcanea of *Adapis* and *Leptadapis*. The nature of the CCu joint cannot be ascertained. One the whole, these foot bones support the hypothesis of a close relationship between *Adapis*, *Leptadapis*, and *Caenopithecus* (Szalay and Delson, 1979).

III. Summary of adapid primates. *Cantius* is essentially very lemurid or indriine like in its tarsal joint morphology. The UAJ and STJ have some similarities to indriines; they share a relatively large posterior trochlear shelf and elongated pAC facets. There are however, no other special similarities to indriines, and the overall aspect of these bones is more lemur-like than indriine-like. As noted in the previous chapters, the mechanical and behavioral significance of these two features is not at all clear. *Cantius* lacks the medial twisting of the ATiM present in most strepsirhines. This may be the primitive condition for euprimates, or it may be a reflection of frequent leaping in *Cantius*. Strepsirhines which reduce the degree of ATiM(A) curvature (*Lepilemur*, indriines, galagos) are the specialized leapers. As argued in Chapter 4, most of the other features of the UAJ (high body, even height of crests, long trochlear arc) are adaptations for leaping, as are the increase in length of the load arm of the calcaneus over the primitive primate condition (Chapter 10). The very lemurid-indriine like morphology of the TTJ reflects *Cantius*' ability to invert and evert the lamina pedis in a manner similar to that of extant lemurs (Rose and Walker, 1985). Along with the morphology of the entocuneiform-metatarsal I articulation, this reflects the grasping abilities of the foot and hallux of *Cantius*. Thus, Rose and Walker's (1985:73) description of *Cantius* as an "active arboreal quadruped with a propensity for leaping" is fully justifiable.

The Alkali calcanea differ from *C. trigonodus* in their greater size and longer calcaneal tuber. These features almost certainly mean that leaping was not frequently practiced in this taxon.

Aside from the features of the Alkali calcanea, there are no significant differences in astragalar, calcaneal, or entocuneiform morphology distinguishing *Cantius* from the later notharctines.

There is not much to add to Gregory's (1920) astute assessment of *Notharctus* as an arboreal quadrupedal grasper and leaper most similar to *Lemur*, *Lepilemur*, and to a lesser extent, *Propithecus*. The same description would apply equally well to *Smilodectes* and *Cantius*. The high astragalar body, elongate distal calcaneus, astragalar neck, navicular, and cuboid attest to the leaping abilities of these forms. Like *Cantius*, *Notharctus* and *Smilodectes* lack medial twisting of the ATiL and ATiM joints, perhaps also reflecting their propensity for leaping. The very lemur-like morphology of the TTJ, the naviculo-cuneiform joints, and the entocuneiform-metatarsal I joint are indicative of well developed grasping abilities. In some ways the middle Eocene notharctines are more primitive than modern lemurs especially in the lesser transverse folding of the foot (Gregory, 1920), aspects of the tarsometatarsal joints (Gebo, 1985), and the slightly lesser relative length of the distal calcaneus.

Both *Notharctus* and *Smilodectes* are very similar to each other and to *Cantius* in terms of UAJ, STJ, and TTJ features. As in *Cantius*, there are several particular similarities to indriines; most notably the large posterior trochlear shelf, and the elongate pAC facets. The morphology of the forelimb and limb proportions suggest that vertical clinging was part of the locomotor repertoire of notharctines (Napier and Walker, 1967; Stern and Oxnard, 1973; Szalay and Dagosto, 1980), and perhaps these indriine like features are reflections of such a locomotor mode. However, neither the mechanics nor the biological role of these features are, unfortunately, well understood in living forms; therefore their value for interpreting fossils is limited. On the basis of the tarsometatarsal joint Gebo (1985) has questioned the ability of *Notharctus* or *Smilodectes* to cling to vertical supports. The few other features of indriines which *may* be related to vertical clinging (twisting of the posterior trochlear shelf, plantar angulation of the aAC(C) facet) are lacking in notharctines.

There are minor differences between *Notharctus* and *Smilodectes* in TTJ morphology. Based on comparison with *Cantius*, it would seem that the dorsoplantarly constricted TTJ and low cuboid angle of *S. gracilis* are derived conditions within notharctines. Among living strepsirhines, *Lemur catta*, *Varecia*, *Daubentonia* and lorisines similarly modify the TTJ. *Smilodectes* resembles the first three taxa much more than the very specialized lorisines. This morphology reduces the amount of adjunct supination-pronation occcurring at this joint and may limit the degree to which the foot can be inverted or everted at the TTJ. In *Lemur catta* this is possibly an adaptation to increase foot stability in terrestrial locomotion, but this cannot be the explanation of this feature in the other taxa which come to the ground only rarely. Given that this feature is associated with more than one biological role in living strepsirhines, it is impossible to be sure of its significance in *Smilodectes*. The low cuboid angle and the lateral overlap of the fifth metatarsal over the cuboid are special similarities between *Smilodectes* and *Lepilemur*. These features may be related to clinging to vertical supports, but again, the relationship between these features and particular behaviors is not entirely clear. Other VCL strepsirhines (indriines, bushbabies) do not share these features, and there are no reported differences in foot posture between *Lepilemur* and these primates which would explain the morphological differences. The differences between *Notharctus* and *Smilodectes* are similar in kind to those between *Lemur fulvus* and *Lepilemur*, but differ in degree, being less pronounced in the fossil taxa.   The earliest European adapid for which postcranial evidence is available, the Middle Eocene Messel adapid, is fairly conservative in morphology, most closely resembling the living lemurids or notharctines. Most probably its locomotor behavior would have been similar as well.

There is a great distinction between this Messel primate and the notharctines, and the European adapinans. *Adapis*, *Leptadapis*, and *Caenopithecus*, the only other European adapids represented by postcranial remains, have abandoned the primitive euprimate emphasis on leaping and have evolved locomotor modes which stress quadrupedal locomotion and climbing. I view these primates as derived relative to a euprimate or strepsirhine morphotype (Dagosto, 1983), contra Godinot and Jouffroy (1984), who propose *Adapis parisiensis* as a good model for the ancestral primate or euprimate postcranium.

Table 19. List of adapid foot bones used in this study. AM=Amherst College; AMNH= American Museum of Natural History, New York; NMB= Naturhistorisches Museum, Basel; BSM= Bayerisches Staatssammlung fur Palaontologie, Munich; HLD= Hessisches Landesmuseum, Darmtstadt; UM= Laboratoire de Paleontologie, University of Montpellier; Mont.= Musee d'Histoire Naturelle, Montauban; MNHN = Musee National d'Histoire Naturelle, Paris; USNM= United States National Museum of Natural History, Washington D.C.; UWA= Thomas Burke Memorial Washington State Museum, Seattle; YPM= Yale Peabody Museum. B= B level of Bridger Basin; C= C level of Bridger Basin; EB= early Bartonian, LC= Lost Cabinian; ML= early Middle Lutetian; UGB= Upper Gray Bull. Wasatchian is early Eocene; Bridgerian and early Rhenanian are early Middle Eocene; late Rhenanian is late Middle Eocene; Phosphorites du Quercy deposits are Late Eocene.

SPECIMEN	AGE/HORIZON/LOCALITY	BONES PRESENT
Cantius		
AMNH 16852	Wasatchian (UGB),Big Horn Basin	2 A, 2 C, En
AMNH 117081	Wasatchian, (LC), Wind River	C
AMNH 117082	"	C
AMNH 117083	"	C
AMNH 117084	"	C
UWA 60308	Wasatchian	A
Smilodectes gracilis		
AM 91663	Bridgerian	A
AMNH 11483	Bridgerian (B)	A
AMNH 12582	Bridgerian (B)	A,C
AMNH 11484	Bridgerian (B)	A,C
AMNH 13030	Bridgerian (B)	C,N, Cu
USNM no #	Bridgerian (B)	A
USNM no #	Bridgerian	A
UWA 35892	Bridgerian (B)	nearly complete foot
Notharctus tenebrosus		
AMNH 11478	Bridgerian (B)	A,C,N,Cu
AMNH 12000	Bridgerian (C)	A
USNM 174444	?	nearly complete foot
YPM 26072	Bridgerian	A,C
Notharctus sp.		
AMNH 13030	Bridgerian (B)	C
AMNH 13024	Bridgerian (B)	A, Cu

continued

Table 19, continued.

SPECIMEN	AGE/HORIZON/LOCALITY	BONES PRESENT
Notharctus sp., continued		
AMNH 11721	Bridgerian (B)	A,C
AMNH 12570	Bridgerian (B)	A,C,En, Me
AMNH 11477	Bridgerian (B)	A
USNM no #	Bridgerian (B)	A
USNM 256745	Bridgerian (B)	A
USNM 21968	Bridgerian	A,C,N
UWA 37732	Bridgerian (B)	nearly complete foot
YPM 39810	Bridgerian	A
YPM 39818	?	A,C
YPM 39816	Bridgerian (C)	A
Notharctine sp.		
USNM 21951	Bridgerian (B)	Cu
YPM 39817	Bridgerian	C
YPM 39811	?	C
Adapidae sp.		
HLD ME7430	early Rhenanian (ML), Messel	complete foot
Caenopithecus lemuroides		
NMB EH 719	late Rhenanian, (EB), Egerkingen	C
NMB no #	"	C
NMB no #	"	A
Adapis parisiensis		
NMB QE553	Phosphorites du Quercy*	C
NMB QE558	Phosphorites du Quercy	C
NMB QE564	Phosphorites du Quercy	C
NMB QE741	Phosphorites du Quercy	C
NMB QE742	Phosphorites du Quercy	C
NMB QE750	Phosphorites du Quercy	C
NMB QE753	Phosphorites du Quercy	C

(continued)

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*Phosphorites du Quercy deposits cover a time period from the Late Eocene to the early Oligocene. These particular specimens cannot be dated, but from other deposits it is known that *L. magnus* first appears in the early Priabonian, and *A. parisiensis* in the later part of the Priabonian. Neither survives into the Oligocene (Crochet *et al.*, 1981).

Table 19, continued.

SPECIMEN	AGE/HORIZON/LOCALITY	BONES PRESENT
A. parisiensis, continued.		
NMB QE769	Phosphorites du Quercy	C
NMB QE779	Phosphorites du Quercy	C
NMB QE782	Phosphorites du Quercy	C
NMB QE790	Phosphorites du Quercy	C
NMB QE796	Phosphorites du Quercy	C
NMB QE909	Phosphorites du Quercy	C
NMB QH640	Phosphorites du Quercy	C
NMB QJ664	Phosphorites du Quercy	C
BSM no #	Phosphorites du Quercy	C
Mont. no #	Phosphorites du Quercy	2 A
Mont. no #	Phosphorites du Quercy	5 C
Leptadapis magnus		
NMB QE251	Phosphorites du Quercy	A
NMB QE336	Phosphorites du Quercy	A
NMB QE505	Phosphorites du Quercy	C
NMB QE531	Phosphorites du Quercy	C
NMB QE604	Phosphorites du Quercy	C
NMB QE620	Phosphorites du Quercy	C
NMB QE663	Phosphorites du Quercy	C
NMB QE719	Phosphorites du Quercy	C
NMB QE865	Phosphorites du Quercy	C
NMB QF462	Phosphorites du Quercy	C
NMB QF491	Phosphorites du Quercy	C
NMB QF496	Phosphorites du Quercy	A
NMB QF830	Phosphorites du Quercy	C
BSM no #	Phosphorites du Quercy	A
BSM No #	Phosphorites du Quercy	C
BSM no #	Phosphorites du Quercy	Cu
MNHN Qu11091	Phosphorites du Quercy	A
UM no #	Phosphorites du Quercy	4 C
Adapini sp. (*Adapis stintoni* or *Cryptadapis*)		
NMB QE530	Phosphorites du Quercy	C

Table 20. Astragali and calcanea of notharctine specimens used in this study, and their probable assignments as discussed in the text. AN(A) Height/width index = ht. facet*100/width facet. Other measurements and indices as in Chapters 3-7. *, specimen represents more than one individual. Museum abbreviations are given in Table 19.

SPECIMEN	A1	CU 6/5	AN H/W	C1	A1/C1	DENTAL ASSOCIATION	ASSIGNMENT
Cantius							
AMNH 16852*	16.3		77.94	21.8	74.77	none	*C.trigonodus*
AMNH 117081				28.2		none	?*C.venticolis* or ?*P. jarrovi*
AMNH 117082		77.92				none	"
AMNH 117083		76.92				none	"
UWA 60308	18.2		76.32			none	*Cantius* sp.
"small group" of Bridger notharctines							
AM 91663	16.8	65.33	72.60	23.7	70.88	*S. gracilis*	*S. gracilis*
USNM no #	16.9					none	*S. gracilis*
AMNH 11483	17.3					none	*S. gracilis*
UWA 35892	17.3	65.33	71.42	25.4	68.11	*S. gracilis*	*S. gracilis*
AMNH 12582	17.5	70.00				none	*S. gracilis*
AMNH 11484	17.7	71.64	74.28			none	*S. gracilis*
USNM no #	17.9					none	*S. gracilis*
AMNH 11478	18.0		81.08	25.0	72.00	*N. tenebrosus*	*N. tenebrosus*
YPM 26072	18.1			25.7	71.54	none	*N. tenebrosus*
AMNH 12000	18.1		79.73			*N. robustior*	*N. tenebrosus*
USNM 174444	18.4			25.7	71.59	none	*N. tenebrosus*
"large group" of Bridger notharctines							
USNM no #	19.1					none	*Notharctus* sp.
AMNH 13030*	19.2		74.68			*S. gracilis*	*Notharctus* sp.
YPM 39810	19.4					none	*Notharctus* sp.
USNM 256745	19.5					*N. tenebrosus*	*Notharctus* sp.
YPM 39818	19.5			25.9	75.29	none	*Notharctus* sp.
AMNH 13024	19.7		83.78			*N. tenebrosus*	*Notharctus* sp.
AMNH 11721	20.0	75.64	87.50	25.8	77.52	none	*Notharctus* sp.
UWA 37732	20.3			26.9	75.46	*N. tenebrosus*	*Notharctus* sp.
AMNH 12570	20.5	77.63	79.52			none	*Notharctus* sp.
AMNH 11477	20.5		80.25			none	*Notharctus* sp.
USNM 21968	21.2		81.93	26.2	80.91	none	*Notharctus* sp.
YPM 39816	22.8					none	*Notharctus* sp.

Table 21. Measurements and indices of notharctine primates. Conventions as in Table 8. Measurements are described in Table 5.

	Cantius sp.		*Notharctus* sp.		*Smilodectes gracilis*	
A1	17.3	-	19.64	1.27	17.34	.40
	16.3-19.3	2	18.0-22.80	16	16.8-17.9	7
A2	9.5	-	11.48	.98	10.15	.41
	9.0-10.0	2	10.1-13.8	11	9.8-10.5	6
A3	9.70	-	10.38	.62	10.37	.70
	8.4-11.0	2	9.1-11.5	16	9.7-11.8	7
A4	5.10	-	6.15	.60	5.42	.45
	-	2	5.8-7.8	16	4.8-5.8	5
A8	8.55	-	9.51	.60	8.12	.09
	8.4-8.7	2	8.3-11.3	13	8.0-8.3	6
A9	8.00	-	8.5	.94	7.63	.29
	7.3-8.7	2	7.3-9.1	5	7.2-7.8	4
A10	3.65	-	3.9	.23	3.72	.26
	3.6-3.7	2	3.5-4.1	5	3.5-4.1	4
A13	14	-	22.40	10.45	22.2	6.5
	10-18	2	12-40	5	14-31	5
A11	28	-	29.75	6.89	29.5	1.0
	22-34	2	15-40	12	28-30	4
A12	(7)	-	(6.33)	3.77	(8.75)	3.86
	-	1	(0-12)	12	(5-14)	4
A15a	6.0	-	5.6	.69	5.10	.64
	-	1	5.3-6.7	8	5.2-6.0	5
A15b	193	-	178.37	.607	172.0	13.51
	-	1	165-185	8	155-185	5
A15c	20.21	-	17.17	2.16	15.27	2.1
	-	1	14.66-20.36	8	3.61-18.85	5
C1	25.00	-	25.92	.62	24.55	-
	21.8-28.2	2	25.0-26.9	6	23.7-25.4	2

continued

Table 21, continued.

	Cantius sp.		*Notharctus* sp.		*Smilodectes gracilis*	
C2	11.27	1.25	11.28	.62	10.12	.95
	9.5-12.4	4	10.2-12.1	7	8.9-11.1	5
C3	8.2	-	8.61	.99	7.4	.16
	7.6-8.9	3	7.2-9.9	7	7.2-7.6	5
C4	3.9	-	4.27	.33	3.66	.15
	3.4-4.2	2	3.7-4.6	7	3.4-3.8	5
C8	14.00	-	14.67	-	15.67	-
	10-18	2	10-22	3	15-16	3
C5	7.33	-	7.8	-	7.18	.39
	6.5-7.8	3	-	2	6.7-7.5	4
C6	6.85	-	6.2	-	4.88	.05
	4.5-6.0	3	5.9-6.5	2	4.8-4.9	4
C9	27.67	-	32.67	-	16.5	2.38
	23-35	3	2.7-3.8	3	15-20	4
C10a	3.43	-	3.88	.42	3.80	-
	2.8-3.8	3	3.5-4.7	6	-	1
C10b	160.7	-	153.83	8.38	150	-
	160-162	3	140-165	6	-	1
A3/A1	55.82	-	52.92	2.53	59.79	3.48
	51.53-60.11	2	48.78-56.35	16	55.43-65.92	7
tibial malleolar rotation	30	-			35	-
	-	1			-	1
ATiL(Ti) AP/ML	142.65	-			125.71	-
	-	1			-	1
C3/C1	31.79	-	34.14	3.06	30.80	-
	28.72-34.86	2	29.84-38.22	7	29.53-32.07	2
C7/C1	28.90*		29.43	2.4	31.34	-
	35.82@		26.33-31.60	6	30.80-31.88	2

continued

*Alkali calcanea (N=1); @other *Cantius* calcanea (N=1)

Table 21, continued.

	Cantius sp.		*Notharctus* sp.		*Smilodectes gracilis*	
C6/C5	74.69 69.23-77.92	- 3	76.64 75.64-77.63	- 2	68.08 65.33-71.64	3.2 4
relative load arm length [C1-(C7+C4)]/C1*100	38.34 37.23-39.45	- 2	40.75 38.91-42.01	1.3 6	39.69 38.82-40.55	- 2

Table 22. Measurements and indices of adapine primates. Conventions as in Table 8. Measurements are described in Table 5.

	Adapis parisiensis		*Leptadapis magnus*		*Caenopithecus lemuroides*	
A1	11.50	-	24.78	1.31		
	11.3-11.7	2	22.8-26.3	5		
A2	7.75	-	16.10	1.89	9.4	-
	7.1-8.4	2	14.0-18.8	5	-	1
A3	7.45	-	15.56	1.85	10.2	-
	7.4-7.5	2	14.0-18.7	5	-	1
A4	4.65	-	10.10	1.22	5.9	-
	4.4-4.9	2	8.2-11.5	5	-	1
A8	5.45	-	12.34	1.32		
	5.3-5.6	2	10.6-13.9	5		
A9	6.4	-	11.40	1.66	5.9	-
	-	1	9.5-12.6	3	-	1
A10	2.90	-	6.0	-	4.2	-
	-	1	-	2	-	1
A13	21	-	27	-		
	-	1	24-30	2		
A11	40.50	-	36.00	7.14		
	35-46	2	26-41	5		
A12	(6.5)	-	(10.8)	6.83		
	(5-8)	2	(0-18)	5		
A15a			7.0	-		
			-	1		
A15b			160	-		
			-	1		
A15c			19.54	-		
			-	1		
C1	17.84	1.1	33.84	1.8	21.0	-
	15.9-19.4	19	31.7-38.2	14	-	1

Table 22, continued.

	Adapis parisiensis	*Leptadapis magnus*	*Caenopithecus lemuroides*
C2	6.71 .46 5.7-7.5 21	12.2 .85 10.9-13.7 15	8.3 - - 1
C3	5.58 .68 4.5-7.1 21	10.75 1.1 9.3-12.3 15	7.0 - - 1
C4	3.34 .49 2.2-3.9 21	5.56 .69 4.4-6.5 15	3.9 - - 1
C8	8.89 3.06 5.0-13.0 9	16 1.0 15-17 3	
C5	5.23 .36 4.8-5.7 11	9.07 1.28 7.4-10.6 10	
C6	3.15 .52 2.4-3.9 11	6.52 .77 5.7-7.8 9	
C9	43.71 9.1 29-60 21	34.08 6.99 25-49 12	
C10a	2.88 .62 2.2-4.2 20	5.62 .67 4.7-6.7 10	6.0 - - 1
C10b	140.25 13.2 119-160 20	143.5 13.32 125-165 10	160 - - 1
A3/A1	64.79 - 64.10-65.49 2	62.73 5.64 57.61-71.10 5	
tibial malleolar rotation	32.00 - 27-37 2		
ATiL(Ti) AP/ML	135.09 - 130.19-140.00 2		
C4/C1	31.64 4.2 19.47-37.97 19	32.42 3.7 26.27-36.99 14	33.33 - - 1
C7/C1	37.17 3.3 30.72-43.50 18	35.46 2.9 29.84-41.84 14	32.38 - - 1

Table 22, continued.

	Adapis parisiensis		*Leptadapis magnus*		*Caenopithecus lemuroides*	
C6/C5	60.07	8.2	73.38	7.7		
	49.02-73.58	11	58.10-83.73	9		
relative load arm length [C1-(C7+C4)]/C1*100	32.16	3.02	31.31	3.5	36.00	-
	28.14-40.74	18	27.84-38.15	13	-	1

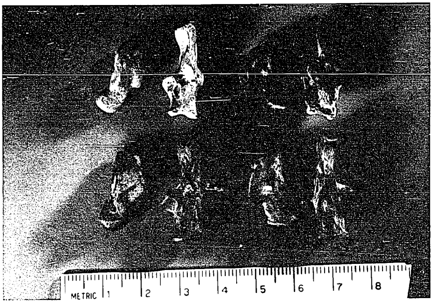

Figure 43. Foot bones of notharctine primates. Top row left to right, Smilodectes gracilis (AM 91663); Cantius trigonodus (AMNH 16852). Bottom row left to right Notharctus (astragalus is AMNH 11477, calcaneus is AMNH 11721), and Notharctus USNM 21968. For locality data on specimens see Table 19.

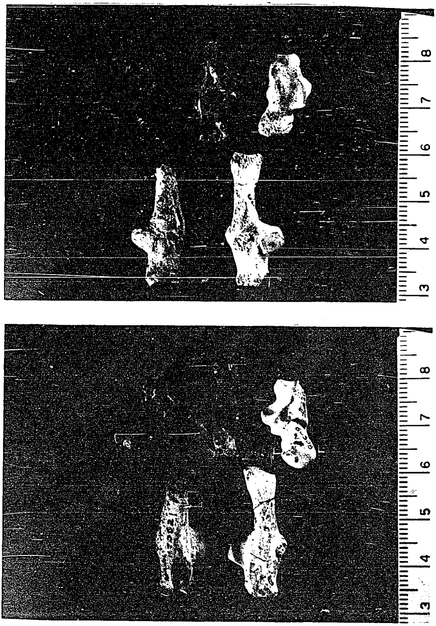

Figure 44. Foot bones of *Cantius*. Top, dorsal view, bottom, ventral view. Top row from left to right *Cantius trigonodus* (AMNH 16852), *Cantius trigonodus* (AMNH 16852), *Cantius* sp. (UWA 60308). Bottom row from left to right ?*Cantius venticolis* (AMNH 117082), ?*Cantius venticolis* (AMNH 117081). For locality data on specimens see Table 19.

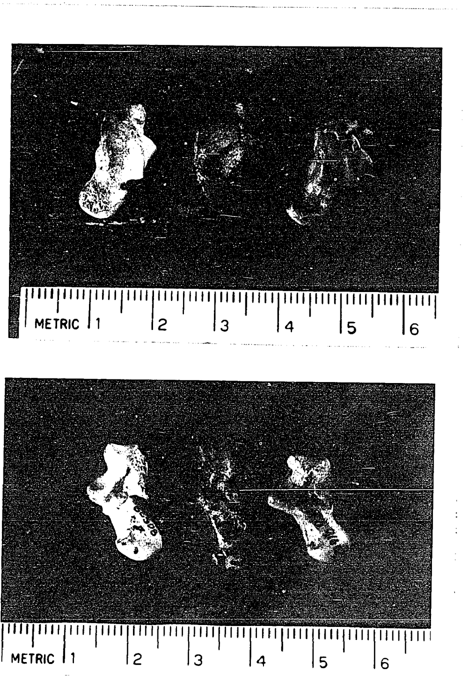

Figure 45. Dorsal (top) and ventral (bottom) views of notharctine astragali. Left to right *Cantius* (UWA 60308), *Notharctus* (AMNH 11477), and *Smilodectes* (AM 91663).

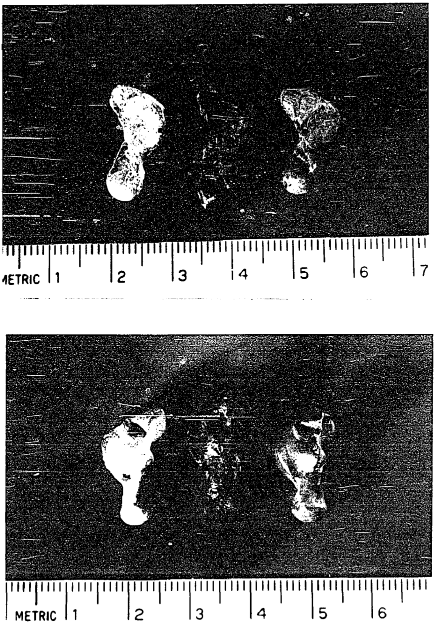

Figure 46. Medial (top) and lateral (bottom) views of notharctine astragali. Left to right *Cantius* (UWA 60308), *Notharctus* (AMNH 11477), and *Smilodectes* (AM 91663).

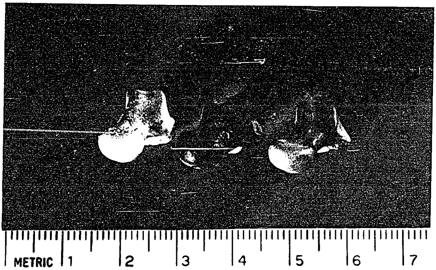

Figure 47. Distal view of astragalus of notharctines. From left to right Cantius (UWA 60308), Notharctus (AMNH 11477), and Smilodectes (AM 91663).

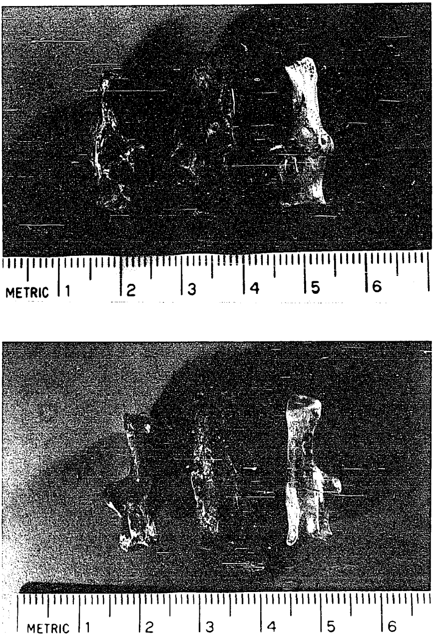

Figure 48. Dorsal (top) and ventral (bottom) views of notharctine calcanea. From left to right *Cantius* (AMNH 16852), *Notharctus* (AMNH 11721), and *Smilodectes gracilis* (AM 91663).

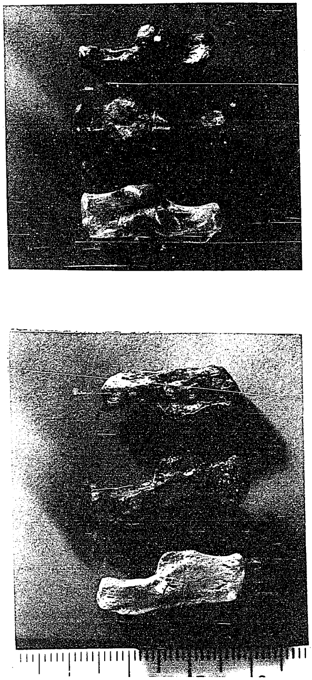

Figure 49. Medial (top) and lateral (bottom) views of notharctine calcanea. From left to right *Cantius* (AMNH 16852), *Notharctus* (AMNH 11721), and *Smilodectes gracilis* (AM 91663).

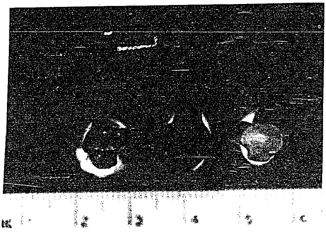

Figure 50. Distal view of calcaneus of notharctines. From left to right *Cantius* (AMNH 16852), *Notharctus* (AMNH 11721), and *Smilodectes gracilis* (AM 91663).

Figure 51. Calcaneus (top) and astragalus (bottom) of *Smilodectes gracilis* based on UWA 35892. From left to right dorsal, ventral, lateral, medial, and distal views. Scale represents 1 mm.

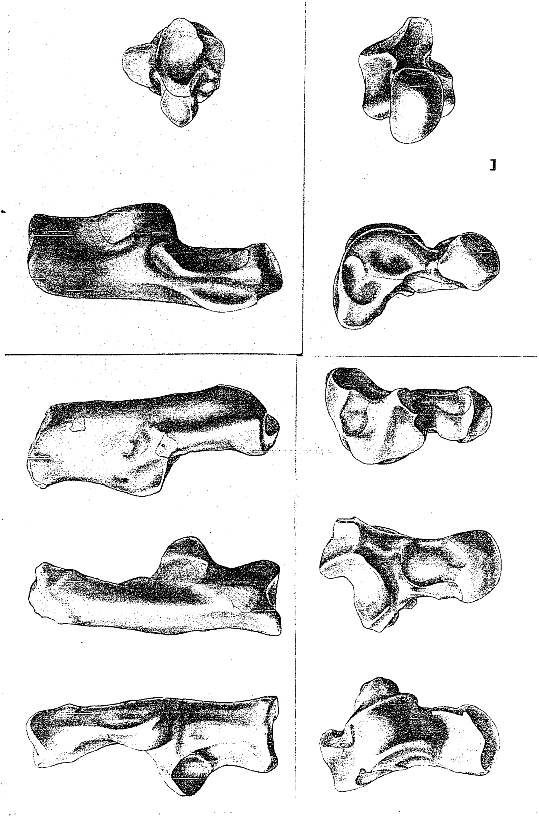

Figure 51

Figure 52. Calcaneus (top) and astragalus (bottom) of *Adapis parisiensis* based on unnumbered specimens in the Musee d'Histoire Naturelle, Montauban. From left to right dorsal, ventral, lateral, medial and distal views. Scale represents 1 mm.

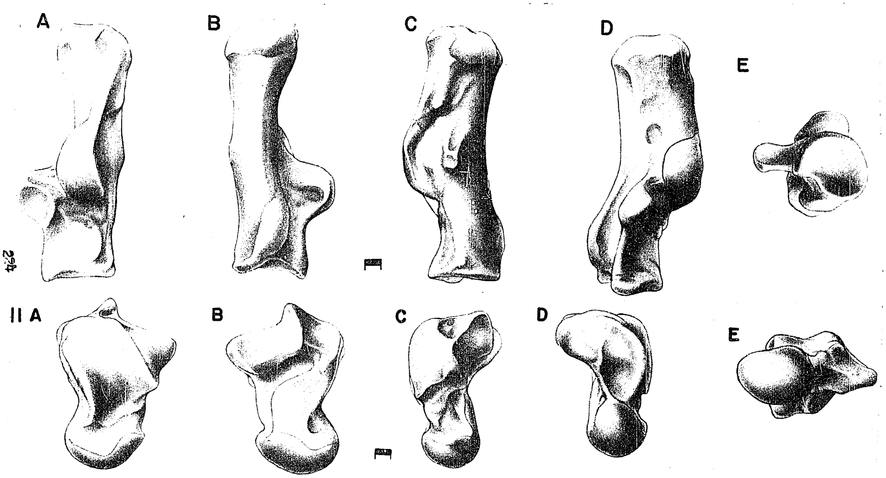

Figure 52

Figure 53. Calcaneus (top) and astragalus (bottom) of *L. magnus*, based on NMB QF 491 and NMB QF 496, respectively. From left to right dorsal, ventral, lateral, medial, and distal views. Scale represents 5 mm.

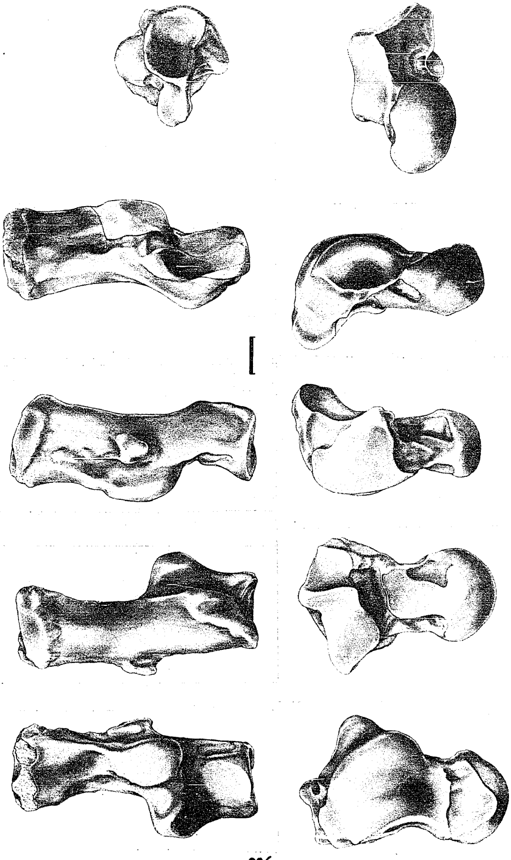

Figure 53

Figure 54. Calcaneus (top) and astragalus (bottom) of *Caenopithecus lemuroides* based on NMB EH 719 and unnumbered specimens. From left to right dorsal, ventral, lateral, medial, and distal views. Scale represents 1 mm.

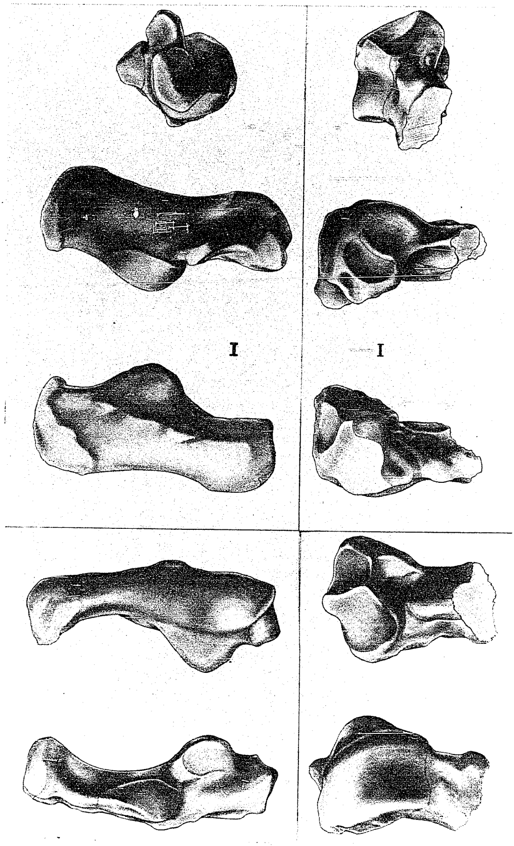

Figure 54

CHAPTER 9. THE SUBFOSSIL LEMURS

I. Introduction. As evidenced by their limb bones, many of the subfossil lemurs of Madagascar had locomotor adaptations unlike those of any extant forms (Lamberton, 1939; Walker, 1967). The foot bones of these species likewise reflect their unusual locomotor repertoires.

The critical problem in the analysis of subfossil primate foot bones is one of association. Not a single foot bone [except for the recently excavated Paleopropithecus material (MacPhee, pers. comm.) which was not examined in this study] is undoubtedly associated with cranial or dental remains. The assignments which have been made by previous workers, and which will be examined in this study, are all based on several kinds of inference. The criteria for assignment are: the presence of cranial or dental remains of taxa at the same site as the foot bones; relative size; and morphological resemblance to groups of extant lemurs. For the most part I agree with the original attributions made by Lamberton (1939) and accepted by Walker (1967), however, I will also point out where room for doubt exists, and discuss likely alternate possibilities for assignment.

This analysis is based on a large sample of Academie Malgache specimens from Tsiravé, and smaller samples from Ampasambazimba and Bevoha (Table 23). Some of these bones appear to be the ones originally described by Lamberton (1939). At all these sites several genera of subfossil and extant lemurs are known, making assignment on the basis of site alone impossible. At Tsiravé there appear to be three calcaneal morphs and three astragalar morphs. The smallest calcanea and astragali have been assigned by Lamberton to *Varecia insignis*. I support this assignment, as apart from some proportional differences, these bones are quite lemurine in appearance.

The largest calcanea and astragali have been assigned to *Archaeolemur majori*, the largest (cranially and dentally) strepsirhine represented at Tsiravé. The calcanea are quite similar to probable *Archaeolemur edwardsi* calcanea from Ampasambazimba. However, *Hadropithecus stenognathus* is also present at both sites. *Hadropithecus* is both closely related and similar in size to *Archaeolemur* (Tattersall, 1973), and the postcranial remains of this genus indicate locomotor behavior of a generally similar type (Walker, 1967). Thus, I think it is really impossible to discern if these bones should be assigned to *Archaeolemur*, *Hadropithecus*, or if both genera are represented. The same reasoning applies to the large Tsiravé astragali, which morphologically differ somewhat from the "*A. edwardsi*" astragalus from Ampasambazimba (see below).

The medium size group (2 calcanea, 1 astragalus) is the most problematical. These bones have been assigned to *Daubentonia robusta* by Lamberton (1939), but are apparently not associated with the nearly complete skeleton of *D. robusta* described by him in 1934. As I argue below, the astragalus is much more indriine-like than *Daubentonia*-like, and the calcanea are very difficult to place. Although I cannot rule out that these are the foot bones of *D. robusta*, I do think that the other non-archaeolemurine indriid known at Tsiravé (*Mesopropithecus globiceps*) is an equally likely association. *Propithecus verreauxoides* (=*P. verreauxi*) is also known at Tsiravé, but none of the subfossil bones belong to it.

In the Ampasambazimba collection, there are foot bones of two morphs. A single very large astragalus has been assigned to *Megaladapis grandidieri* (Lamberton, 1939) and is quite similar to *Megaladapis edwardsi* described by Lorenz (1905). The only other taxon to which this bone could possibly belong is *Archaeoindris fontoynonti*. Two smaller, but morphologically identical astragali are known from Beavoha and have been assigned to *Megaladapis madagascariensis*. The other taxon at Ampasambazimba is an archaeolemurine, most likely *A. edwardsi*.

II. *V. insignis* (figs. 55-57). Absolute measures and indices of *V. insignis* and *V. variegata* are given in Table 24. In *V. insignis* the ATiM(A) is deeper than in extant lemurids including *V. variegata*. The ATiL(A) is often slightly taller laterally than medially; the opposite is true in the majority of strepsirhines. The archaeolemurine from Ampasambazimba also exhibits this feature. The trochlea is a much larger proportion of astragalar length (62%) in *V. insignis* than in *V. variegata* (54%) or in the majority of other extant strepsirhines (except lorisines). This is a common feature of large animals, and is most likely the result of negative scaling of astragalar length with body size (Chapter 4). This scaling appears to effect neck length more than trochlea length. The posterior astragalar foramen is prominent dorsally, but does not appear to be patent.

Some individuals of *V. insignis* show more invasion of the pAC(A) space by the anterior interosseous ligaments, like in *L. catta*. The AN joint is quite similar to that of *V. variegata*. The astragalus of *V. insignis* differs from *V. variegata* in the relative shortness of the neck (index A5/A1); the greater obliquity of the astragalar neck (A11); and the greater relative width of the bone (A2/A1) (Lamberton, 1939).

Neither the pAC(C) or the aAC(A) are shaped differently than in other lemurids. However, the degree of arc of the pAC(C) is significantly lower than in other lemurids, suggesting less subtalar motion. This is a feature shared with *Archaeolemur*. The pAC(C) facet does make up a greater proportion of calcaneal length in *V. insignis* (C3/C1), but this is almost certainly due to a relatively shorter calcaneus in this species. A short calcaneus is also reflected in a relatively short load arm. The CCu facet is relatively higher and narrower in *V. insignis* than in *V. variegata*. In this feature *V. insignis* is more like other lemurids than is *V. variegata*.

The calcanea have expanded proximolateral tubercles similar to, but smaller than, those in archaeolemurines or "*D. robusta*". This is probably not only the peroneal tubercle, but an expanded attachment area for the calcaneofibular and astragalocalcaneal ligaments (Lamberton, 1939; Decker and Szalay, 1974). The medial side of the tuber calcanei is slightly expanded perhaps indicating a relatively larger abd. digiti minimi. Lamberton (1939) notes that V. insignis has, like archaeolemurines, a broader, flatter heel than extant lemurids.

The two naviculars which Lamberton (1939) assigned to V. insignis differ from extant Varecia only in their relative shortness, and, again like Archaeolemur, a dorsoplantarly flattened, mediolaterally elongate NEn(N) facet. The cuboid of V. insignis is likewise extremely lemurid-like, but does present some unusual features. These are: a deeper groove for peroneus longus, which proximolaterally is expanded into a pronounced tubercle extending laterally from the bone. Leptadapis shares this feature (Dagosto, 1983). The cuboid facet is long and low, as in extant Varecia. The most lateral part of the joint is deepened and closed off laterally by the peroneus longus tubercle. The deep convex lateral part of the CCu(Cu) articulates with a concomitantly expanded protuberance on the lateral half of the CCu(C).

According to Walker (1967, 1974) V. insignis differs from V. variegata in having stouter, more equal length limbs, which would reduce the efficiency of leaping in this species. The calcaneal, astragalar, navicular, and cuboidal proportions also attest to poorer leaping abilities. Based on V. insignis's equal length limbs, flattened broad cuboid, and larger styloid process of the fifth metatarsal, Walker (1967, 1974) supposed that V. insignis might have been somewhat more terrestrial than its congeners. The greater invasion of the anterior interosseous ligament into the aAC(A) facet, a feature shared with *L. catta*, the extended lateral tubercle of the peroneus longus groove, and the deeper lateral part of the C-Cu joint, which would stabilize the C-Cu joint in eversion, and the long, narrow NEn(N) which possibly indicates a smaller hallux, are other probable indications of more extensive use of the ground. However, as Walker (1974) has noted, it is unlikely that *V. insignis* was committed to a terrestrial existence.

III. *Daubentonia robusta* (see Table 25, figs. 58-60). Lamberton (1939) assigned two calcanea, one astragalus and one navicular to a large subfossil species of *Daubentonia*. The foot bones are of an indri-sized animal. Both the astragalus and calcanea are very difficult to assign. They are not lemurid, but share features with both the extant indriines and *Daubentonia*, and at the same time differ from both taxa.

The astragalus of extant *Daubentonia* is distinguished from that of other strepsirhines by its more strongly wedged ATiL(A), and the virtual lack of depth to the tibial trochlea. The subfossil shares neither of these features, although Lamberton (1939) claimed that the trochlea was noticeably wedged. Like *Daubentonia*, but unlike extant indriines, the astragalar head is relatively dorsoplantarly flattened, but this morphology occurs often in other groups (*L. catta*, *Varecia*, lorisines, *Smilodectes*), and also in other indriids (archaeolemurines). The posterior trochlear shelf is fairly long, a feature shared with both *Daubentonia* and indriines. But the shelf is not dorsoplantarly twisted in the subfossil as it is in all extant indriines. In this feature the subfossil resembles Daubentonia (or other strepsirhines), but archaeolemurines also lack twisting of the shelf. The medial and lateral tubercles are quite long, which is more Daubentonia-like than indriine-like. The AFi(A) is fairly vertical, like indriines, and a distinction from Daubentonia or lemurids. The ATiM(A) is more curved than in either indriines or Daubentonia. The neck of the astragalus is fairly short and the tubercle for the dorsal talonavicular ligament is robust; these are similarities to indriines, and differences from Daubentonia. The astragalar head has a slight dorsolateral tilt, like indriines but unlike Daubentonia.

Overall, this bone is much more indriine-like than Daubentonia-like. It is also quite similar to the astragalus assigned to A. majori by Lamberton (1939). More importantly, it shares no particular feature with Daubentonia clearly linking it with this animal. This is unexpected given the essential identity of other D. robusta postcranial bones (including the calcaneus and navicular) to those of Daubentonia (Lamberton, 1934; Walker, 1967). Two nonarchaeolemurine indriids are represented at Tsiravé; Propithecus verreauxi and Mesopropithecus globiceps. This astragalus does not belong to P. verreauxi, but I believe that M. globiceps is a strong alternate possibility for assignment. The distinctions of the astragalus from Indri or Propithecus, to whom M. globiceps is very closely related (Tattersall, 1971), reflect a different locomotor mode with leaping less emphasized. Other postcranial bones of Mesopropithecus have been described as Megaladapis-like (Walker, 1967), certainly supporting a hypothesis of a locomotor mode very different from that of extant indriines.

Some authors have argued for a close relationship between *Daubentonia* and indriids (Tattersall and Schwartz, 1974; but see Chapter 10). The similarities of the "*D. robusta*" astragalus to indriines are perhaps not surprising in the light of this hypothesis. If this is indeed the astragalus of *D. robusta*, extant *Daubentonia* would have to be interpreted as being more derived postcranially than its subfossil relative, losing most of its resemblances to extant indriines.

Until well associated material is found, I do not think it is possible to be completely sure of the assignment of this astragalus. The most that can be said is that it belonged to a large, nonleaping, nonlemurid strepsirhine, most likely a climber rather than a leaper.

Similar difficulties in allocation are faced with the calcanea. As in both indriines and *Daubentonia*, the pAC facets are long and narrow and are aligned close to the long axis of the bone. Unlike indriines, the heel is long, and the load arm relatively short. Another difference from indriines is that the aAC(C) faces dorsally, not laterally. Again, this is a similarity to *Daubentonia*, but is also a primitive feature shared by all non-indriine strepsirhines. The CCu facet is deeper in *Daubentonia* and in the subfossil than in indriines, but is not different from the morphology of the archaeolemurines. The fossil calcanea differ from both indriines and *Daubentonia* in developing a rather large proximolateral protuberance, similar to that seen in *V. insignis* or archaeolemurines.

Like the astragalus, the calcanea are very difficult to place. The overall appearance is most similar to *Daubentonia*, but the differences between the subfossil and extant indriines would be expected in *Mesopropithecus*. These calcanea differ more from archaeolemurine calcanea than the astragalus does.

The navicular of *D. robusta* is almost certainly correctly assigned. The navicular of *Daubentonia madagascariensis* is distinguished from that of lemurids or indriines by several features: the failure of the NCu(N) facet to extend under the NMe(N) facet; the more horizontal position of the NEc(N) facet; and the dorsolateral angle of the NEn(N) facet. These features are all closely matched by the subfossil navicular, which is also relatively short, like the corresponding bone of *Daubentonia* (or indriines). The naviculars of archaeolemurines are reasonably similar to those of *Daubentonia* in that the NCu(N) facet is not medially extensive and the NEc(N) is horizontal. However, the archaeolemurine naviculars are much larger than this one, and differ in other minor morphological details; I do not think that this navicular is from an archaeolemurine or *Mesopropithecus*.

IV. Archaeolemurines (see Table 25, figs. 61-63). Lamberton assigned foot bones to both *Archaeolemur majori* and *A. edwardsi*. *Hadropithecus* occurs at both sites where *Archaeolemur* bones are found, and as argued above, I see no way in which these bones can definitely be assigned to either of these genera. Lamberton (1939) also recognized this problem. In this discussion I simply refer to these bones as archaeolemurine.

Both Archaeolemur and Hadropithecus are undoubtedly closely related to the indriines (Tattersall, 1973). However, there are virtually no features of the foot bones which reflect this relationship. The Tsiravé astragali differ from those of indriines in the following ways: the posterior trochlear shelf is shorter and not plantarly twisted, the AFi(A) is not as vertical, the ATiM(A) is deeper and more medially curved, the astragalar head is less spherical and is not as strongly dorsolaterally oriented. These are all ways in which archaeolemurines are more primitive (or possibly more derived) than extant indriines, and of course are also reflections of their very different locomotor modes. The general aspect of this bone is more lemurid-like than indriine-like. The above description applies equally well to the Ampasambazimba astragalus. It differs from the Tsiravé bone in being larger, and having a shorter, more widely deviated neck. In the Tsiravé astragali the invasion of the aAC(A) space by the interosseous ligaments is extreme; the aAC(A) is almost completely separate from the AN(A). This is not the case in the Ampasambazimba astragalus.

It is equally difficult to find any indriine characters on the calcanea. The proportions are very different than in extant indriines; the heel is long, and the load arm is very short. The pAC(C) facets are relatively short and wide and are not aligned close to the long axis of the bone. [An index of facet length to calcaneal length (C3/C1) is high, but only due to the relative shortness of the calcaneus]. The aAC(C) faces dorsally, not medially. The cuboid facet is longer, lower, and deeper than in indriines. These again are ways in which these calcanea are more primitive than extant indriines. The angle of arc of the pAC(C) is very low in the Tsirave specimens, suggesting less mobility at the subtalar joint.

The most distinctive feature of the archaeolemurine calcaneus is the massive development of a proximolateral tubercle. The homology of this tubercle is unclear. It may partly represent an enlarged peroneal tubercle, but its position is slightly more proximal than in other strepsirhines. Unlike the peroneal tubercle, in archaeolemurines this process is usually marked by a deep pit, probably for the calcaneofibular ligament (Lamberton, 1939; Decker and Szalay, 1974). Less extensive development of a similar process is seen in _V. insignis_ and "_D. robusta_"; however, in these taxa the tubercle is more dorsally placed. In archaeolemurines the tubercle is on the plantar surface of the bone and forms a broad, distal plantar surface for the heel. The medial side of the tuber calcanei is expanded as well, yielding a broader insertion for the Achilles tendon. The combination of these two expansions gives the tuber a broad, flat appearance (Lamberton, 1939).

The Ampasambazimba calcanei differ from those from Tsiravé in the following ways: the pAC(C) facet angle is much lower in the Tsiravé specimens; the cuboid facet higher, with a prominent dorsal beak.

This latter feature probably stabilizes the CCu joint. The calcanea differ less than the astragali.

The naviculars assigned to archaeolemurines by Lamberton (1939) differ from those of either indriines or lemurids in that the CuN(N) facet is not as medially extensive, and does not run fully under the NMe(N) facet. This is a feature which archaeolemurines share with *Daubentonia* and notharctines. The NEn(N) facet appears to be relatively smaller than in indriines or lemurids.

Walker (1967, 1974) has analyzed the postcranium of *Archaeolemur* and *Hadropithecus* and found numerous ways in which both converged upon ground dwelling cercopithecid monkeys. Langdon (1984) found that cercopithecines differ from other catarrhines in having a more tightly fitting, restrictive UAJ as evidenced by a deeper trochlea, sharp trochlear borders, and tight support for the anterior tibia. Inversion-eversion capabilities are reduced as is astragalar head diameter. The CCu joint is shallower, and the hallux is reduced. He notes that these features are equally useful for high speed above branch or ground running. In any case, archaeolemurines exhibit few of these traits. UAJ morphology is not distinct from lemurids or indriines and AN structure only slightly so. The CCu joint is actually deeper than in lemurids (except for *V. insignis*), indriines or cercopithecines indicating, as in lorisines or galagines, that rotation is preserved, but stability increased.

Stronger potential indicators of a terrestrial habitus for archaeolemurines concern the flatness and shortness of the STJ articulations which almost certainly reduce STJ motion and thus stabilize this joint (the STJ is also stabilized in leapers). The large proximolateral tubercle may indicate increased size of the peroneal (evertor) musculature, stabilizing retinaculum, and/or the calcaneofibular ligaments. The small size of the NEn(N) joint and the EnMT1(En) joint reflect the reduced size of the hallux (Lamberton, 1939; Walker, 1967, 1974; Decker and Szalay, 1974). The powers of opposition and adduction are reduced.

V. Megaladapis. (Table 26; figs. 64-66). The astragali which have been attributed to Megaladapis have many unusual characteristics. The massive bone is very broad and short; the shortness is mainly due to a relatively short neck. (The smaller M. madagascariensis has a much longer neck than M. grandidieri.) The posterior astragalar foramen is prominent dorsally, but does not appear to be patent. The posterior trochlear shelf is absent, probably because of the extraordinarily deep groove for the tendon of fl. fibularis (Decker and Szalay, 1974). The ATiL(A) is long relative to astragalar length, but no doubt will prove to be short relative to body size, as in lorisines. The shape of the ATiL(A) is very similar to other strepsirhines, except that the central groove is displaced slightly laterally. The angle of the UAJ is much lower (120-145°) than in other strepsirhines suggesting that UAJ motion was more limited in Megaladapis. The ATiM(A) is strongly curved medially and extends distally nearly to the AN(A) facet as in lorisines. Unlike all other strepsirhines, the ATiM(A) is very constricted dorsoplantarly, matching the fairly short tibial malleolus (Lamberton, 1939). The area for insertion of the deltoid ligament is correspondingly expanded. The AFi(A) is also very short, but is strongly flared laterally, to even a greater extent than in lorisines.

The pAC(A) is very flat, short, broad, and highly offset. Depending on the morphology of the pAC(C), this probably indicates great freedom of movement (but not stability) of the STJ. In *M. madagascariensis*, the medial part of this facet is larger than the lateral and flares posteriorly. The aAC(A) is largely restricted to the lateral side of the neck; a peculiarity shared only with lorisines. This is due to the dorsomedial orientation of the astragalar head which lifts the medial surface away from the aAC(C) and the plantarcalcaneonavicular ligament.

The AN(A) is dorsoplantarly restricted and dorsomedially oriented, like lorisines, but unlike all other lemuroids. The neck itself is strongly medially oriented, dorsomedially bent, and plantarly bent, as in lorisines. Lamberton (1939) thought that these features would yield a flat, poorly prehensile foot in *Megaladapis*, but as in lorisoids, this orientation of the neck and AN(A) forces the digits into a naturally supinated position, which is simply an alternate solution for attaining a supinated fore part of the foot.

The greatest similarity of the astragalus of *Megaladapis* is with the extant Lorisinae. They do differ in several features including the short ATiM(A) and AFi(A) facets, and the position of the groove for fl. fibularis (posterior in *Megaladapis*; posterolateral in lorisines). The overall similarity to lorisines, however, strongly implies that *Megaladapis* was a specialized climber. It possibly had an inverted set to the foot, like lorisines, but more information is needed to verify this.

Lamberton (1939) thought *Megaladapis* may have been terrestrial based on the AN joint evidence cited above, but the remainder of astragalar morphology, as well as analyses of the rest of the postcranium (Lorenz, 1905; Zapfe, 1963; Walker, 1967; 1974; Jungers, 1976) argue against this interpretation. These authors stress the arboreality of *Megaladapis*, and especially its climbing abilities. Jungers (1976) has marshalled strong support for the hypothesis that *Megaladapis* was primarily a vertical clinger and climber. Astragalar morphology does not preclude this reconstruction.

VI. Summary. The foot bones of *Varecia insignis* differ from those of its extant congener in their greater size and robusticity; shorter neck; lower arc of the pAC(C); expanded proximolateral calcaneal tubercle; smaller NEn(N) facet; and pronounced lateral tubercle of the cuboid. Many of these features are shared with *Archaeolemur*, and along with other aspects of postcranial morphology suggest that *V. insignis* may have exploited the ground more than other lemuroids.

Archaeolemurines appear to have been even more committed to terrestrial locomotion as evidenced in very flat and short articular surfaces of the subtalar joint; very large proximolateral calcaneal tubercle; and a reduced hallux.

I have analyzed only the astragalus of *Megaladapis*. It shares many features with the extant Lorisinae, suggesting that climbing was the major component of its locomotion. Upper ankle joint motion appears to have been limited, but would have been accompanied by strong concomitant abduction and adduction, judging by the curvature and flare of the ATiM(A) and ATiL(A) surfaces. The most unique feature of *Megaladapis* is the dorsoplantar constriction of the ATiM(A), corresponding to a short tibial malleolus. This suggests that the upper ankle joint was less stable in weight bearing positions than in other strepsirhines. The subtalar joint probably allowed a large range of motion, but would also have been relatively unstable. These two features are strong evidence against the hypothesis of committed terrestrial locomotion in *Megaladapis*. This animal was probably highly arboreal, and an adept climber.

The astragalus Lamberton assigned to *Daubentonia robusta* may in fact belong to *Mesopropithecus*. Although indriine-like in some respects, it differs from extant indriines in ways which suggest that this animal was not a frequent leaper. Other limb bones of *Mesopropithecus* also indicate that it was a climber (Walker, 1967), or perhaps even sloth-like (Godfrey, 1986).

The calcaneus and navicular attributed to *D. robusta* are probably correctly assigned. The calcaneus differs from extant *Daubentonia* in its proportions (longer heel, shorter load arm); which may well be expected allometric effects. It, like other large subfossil lemurs (*V. insignis*, archaeolemurines) has an expanded proximolateral tubercle on the calcaneus. The navicular is identical to that of extant *Daubenonia*.

Table 23. Foot bones of subfossil lemurs used in this study. All are unnumbered specimens from the Academie Malgache.

TAXON/LOCALITY	ASTRAGALI	CALCANEA	NAVICULARS	CUBOIDS
Varecia insignis most from Tsiravé	7	8	2	1
Archaeolemurine Tsiravé	2	8	1	
Archaeolemurine Ampasambazimba	2	2	1	
"*Daubentonia robusta*" Tsiravé	1	2	1	
Megaladapis madagascariensis Bevoha	2			
Megaladapis grandidieri Ampasambazimba	1			

Table 24. Measurements and indices of *Varecia insignis* compared with *Varecia variegata*. Conventions as in Table 8. Measurements are described in Table 5.

	Varecia variegata		*Varecia insignis*	
A1	20.43	.95	22.39	.97
	19.4-22.3	12	20.9-23.5	7
A2	13.79	.98	15.86	.67
	11.5-15.4	12	15.2-16.7	7
A3	11.02	.90	13.83	.55
	9.2-12.7	12	12.9-14.5	7
A4	7.24	.49	8.19	.71
	6.4-8.0	12	7.4-9.2	7
A8	9.34	.46	11.06	.40
	8.6-9.9	9	10.6-11.7	7
A9	9.47	.55	11.4	.57
	8.1-10.1	12	10.9-12.5	6
A10	5.0		5.84	.48
	4.8-5.2	2	5.3-6.6	5
A13	14.5		19.43	2.5
	14-15	2	15-23	7
A11	35.82	7.2	50.71	6.3
	24-47	11	41-62	7
A12	7.91	3.8	11.57	4.1
	4-15	11	7-19	7
A15a	6.07	.34	6.26	.45
	5.5-6.6	11	5.8-6.8	6
A15b	180.18	9.1	164.17	9.9
	169-193	11	156-180	6
A15c	19.11	.83	18.03	2.19
	18.2-20.7	11	15.88-21.47	6
C1	29.12	.93	31.74	.49
	27.4-30.8	12	30.9-32.2	8

continued

Table 24, continued.

	Varecia variegata		*Varecia insignis*	
C2	11.37	.63	13.69	.43
	10.7-12.7	12	13.1-14.4	8
C3	9.24	.87	11.31	.54
	7.8-10.3	12	10.4-12.2	8
C4	4.81	.36	5.74	.11
	4.2-5.4	12	5.6-5.9	8
C8	17.5	-	16.75	3.4
	17-18	2	10-20	8
C6	5.47	-	8.20	.25
	4.5-6.2	3	7.9-8.7	7
C5	9.03	-	10.87	.16
	8.4-9.5	3	10.6-11.0	7
C9	31.5	-	40.13	8.1
	27-36	2	25-50	8
C10a	4.92	.42	4.81	.47
	4.2-5.6	11	4.0-5.2	8
C10b	141.63	10.9	123.75	11.6
	130-163	11	100-135	8
A2/A1	66.48	4.8	70.88	2.48
	59.28-72.91	11	65.53-72.23	7
A3/A1	53.65	3.9	61.85	3.1
	47.02-59.18	11	58.3-65.91	7
A5/A1	48.31	2.0	43.64	1.7
	45.91-52.28	11	43.64-45.02	7
C3/C1	31.72	2.6	42.00	3.6
	27.27-35.56	12	33.54-44.86	8
C6/C5	54.66	-	76.09	3.0
	47.37-61.96	2	72.47-81.31	7
rel length load arm [C1-(C4+C7)]/C1*100	41.26	2.8	33.76	1.8
	35.47-46.23	12	31.06-35.83	7

Table 25. Measurements and indices of subfossil lemurs. Conventions as in Table 8. Measurements are described in Table 5.

	"*D. robusta*" Tsiravé	"*A. majori*" Tsiravé	"*A.edwardsi*" Ampasambazimba
A1	26.50	29.60	28.9
	1	2	1
A2	15.50	19.4	20.8
	1	19.0-19.8 2	1
A3	16.70	17.36	18.3
	1	17.1-17.6 2	1
A4	9.40	11.3	12.3
	1	11.2-11.4 2	1
A8	12.70	13.6	14.8
	1	13.3-13.9 2	1
A9	13.40	13.5	14.5
	1	13.1-13.9 2	1
A10	6.10	7.65	8.7
	1	7.5-7.8 2	1
A13	20.00	16.5	5.0
	1	16-17 2	1
A11	40.00	36.5	46.0
	1	33-40 2	1
A12	15.00	11.00	10
	1	4-18 2	1
A15a	7.70	6.67	8.3
	1	1	1
A15b	163.00	160.00	173.00
	1	1	1
A15c	21.81	18.62	25.16
	1	1	1

continued

Table 25, continued.

	"*D. robusta*" Tsirave'		"*A. majori*" Tsirave'		"*A. edwardsi*" Ampasambazimba	
C1	38.80		38.55	2.2	38.5	
	38.60-38.90	2	36.5-41.6	4	1	
C2	15.85		17.69	.87	19.0	
	15.80-15.90	2	16.5-19.0	8	1	
C3	11.60		13.77	.65	14.0	
	2		13.0-14.7	8	1	
C4	6.10		8.06	.82	9.7	
	6.00-6.20	2	7.0-9.6	8	1	
C8	10.00		18.00	2.8	19.0	
	2		14-22	6	1	
C6	8.70		9.97	.28	11.5	
	8.60-8.80	2	9.5-10.4	7	1	
C5	11.90		13.17	.50	12.5	
	11.80-12.00	2	12.5-13.6	7	1	
C9	34.00		32.5	5.0	29.0	
	32.0-36.0	2	25-40	6	28-30	2
C10a			6.17	.54	5.17	
			5.33-6.67	6	1	
C10b			112.5	5.4	156	
			105-120	6	1	
A3/A1	63.02		58.64		63.32	
	1		57.77-59.52	2	1	
C3/C1	29.89		35.87	2.5	36.36	
	29.74-30.05	2	33.65-39.41	4	1	
C6/C5	73.11		75.09	1.5	92.00	
	72.88-73.33	2	72.29-76.69	7	1	
rel.length	39.30		34.09	3.6	34.54	
load arm	38.86-39.74	2	30.14-37.74	4	1	
[C1-(C4+C7)]/C1*100						

Table 26. Measurements and indices of *Megaladapis*. Conventions as in Table 8. Measuremetns are described in Table 5.

	Megaladapis madagascariensis		*Megaladapis grandidieri*
A1	34.95		41.2
	32.2-37.7	2	1
A2	26.40		30.2
	1		1
A3	26.15		27.2
	25.0-27.3	2	1
A4	12.6		15.2
	11.4-13.8	2	1
A8	18.6		24.6
	1		1
A9	16.6		18.2
	1		1
A10	10.6		13.9
	1		1
A13	57.5		
	55-60	2	
A11	30		33
	26-34	2	1
A12	13.5		16
	10-17	2	1
A15a	8.3		15.83
	1		1
A15b	145		110
	1		1
A15c	21.09		30.4
	1		1
A3/A1	75.27		66.02
	72.41-78.13	2	1

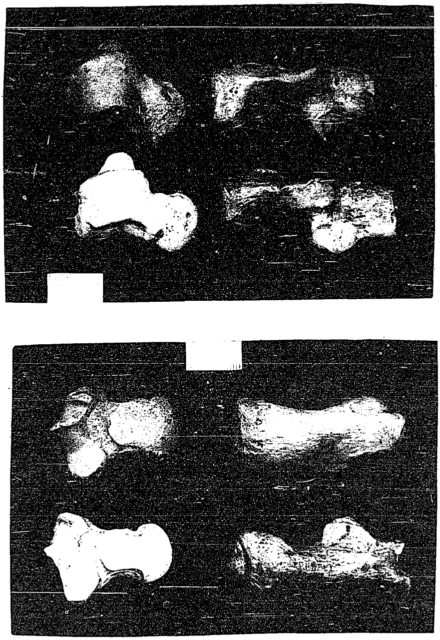

Figure 55. Dorsal (top) and ventral (bottom) views of astragalus and calcaneus of *Varecia insignis* (Tsirave). Unnumbered specimens from the Academie Malgache.

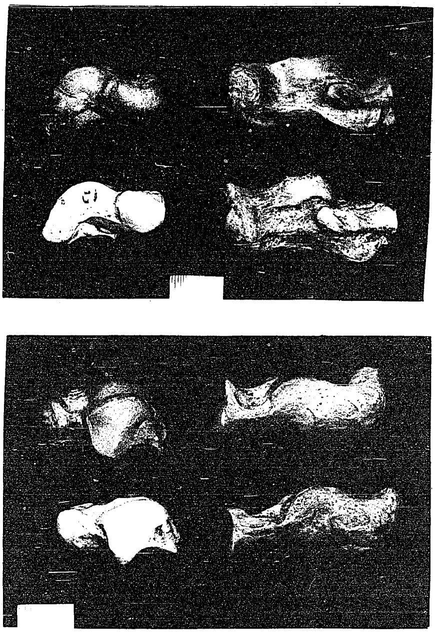

Figure 56. Medial (top) and lateral (bottom) views of astragalus and calcaneus of *Varecia insignis* (Tsirave). Unnumbered specimens from the Academie Malgache.

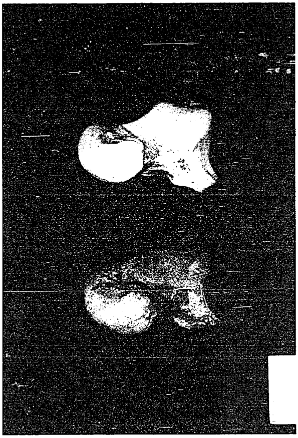

Figure 57. Distal view of astragalus of *Varecia insignis* (Tsirave). Unnumbered specimens from the Academie Malgache.

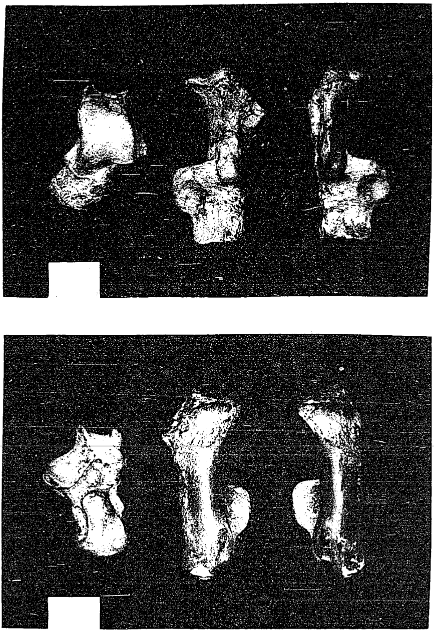

Figure 58. Dorsal (top) and ventral (bottom) views of "*Daubentonia robusta*" (Tsirave). Unnumbered specimens from the Academie Malgache. The astragalus is probably *Mesopropithecus* (see text).

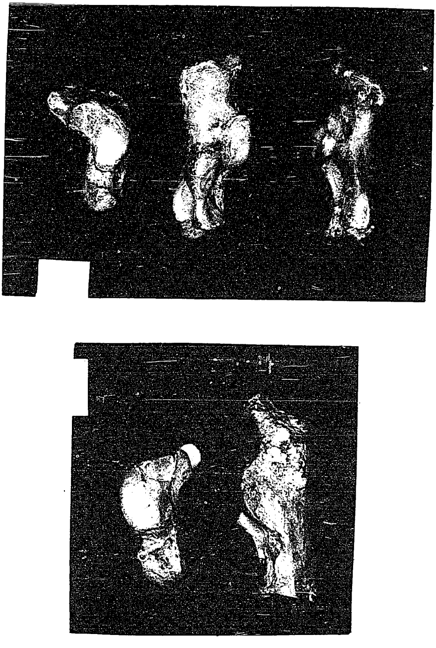

Figure 59. Medial (top) and lateral (bottom) views of "*Daubentonia robusta* (Tsirave). Unnumbered specimens from the Academie Malgache. The astragalus is probably *Mesopropithecus* (see text).

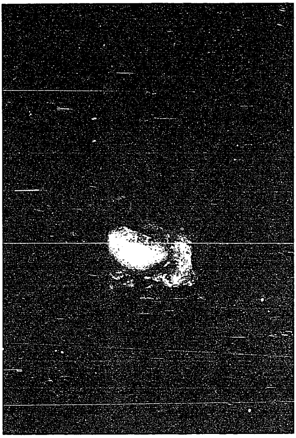

Figure 60. Distal view of astragalus of "Daubenonia robusta" (Tsirave). Unnumbered specimens from the Academie Malgache. The astragalus is probably *Mesopropithecus* (see text).

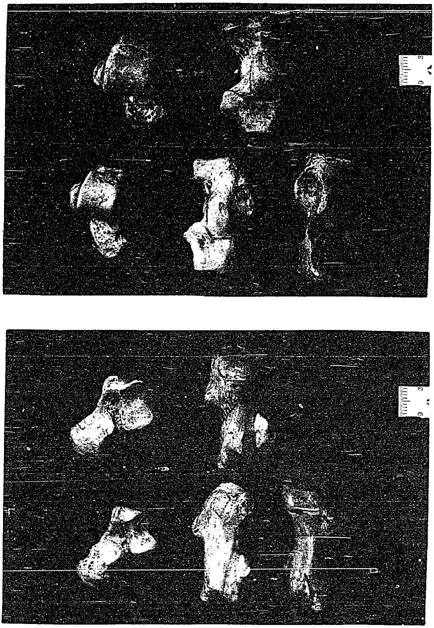

Figure 61. Dorsal (top) and ventral (bottom) views of astragalus and calcaneus of archaeolemurines. Top row "*A. edwardsi*" (Ampasambazimba), bottom row "*A. majori*" (Tsirave). Unnumbered specimens from the Academie Malgache.

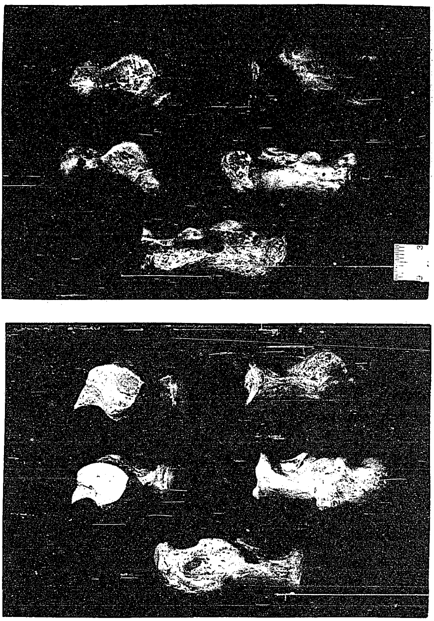

Figure 62. Medial (top) and lateral (bottom) views of astragalus and calcaneus of archaeolemurines. Top row "*A. edwardsi*" (Ampasambazimba), bottom two rows "*A. majori*" (Tsirave). Unnumbered specimens from the Academie Malgache.

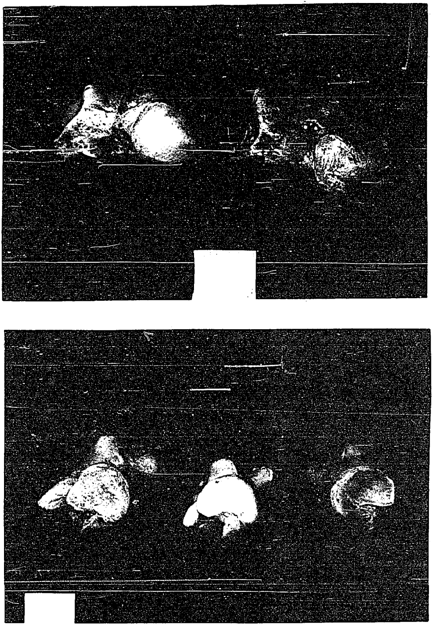

Figure 63. Distal views of astragalus (top) and calcaneus (bottom) of archaeolemurinea. Astragali, left is "*A. majori*", right is " *A. edwardsi*". Calcanea, left is "*A. edwardsi*", right two are "*A. majori*". Unnumbered specimens from the Academie Malgache.

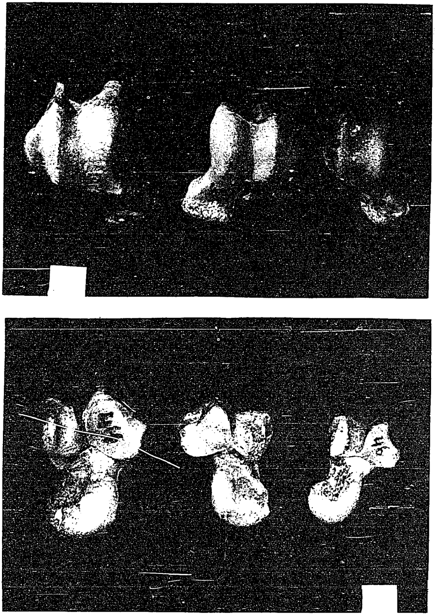

Figure 64. Dorsal (top) and ventral (bottom) views of astragalus of *Megaladapis*. From left to right *M. grandidieri* (Ampasambazimba), and two *M. madagascariensis* (Bevoha). Unnumbered specimens from the Academie Malgache.

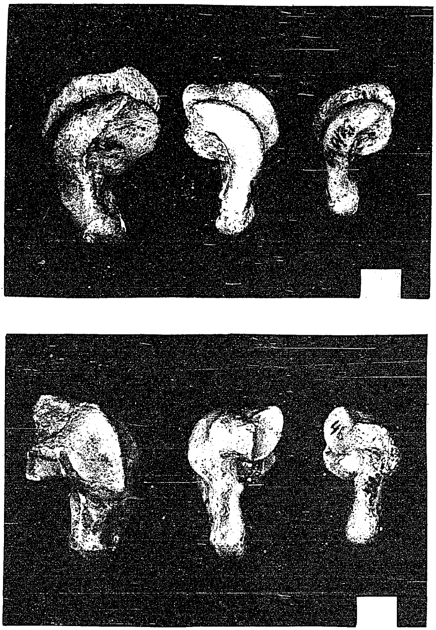

Figure 65. Medial (top) and lateral (bottom) views of astragalus of *Megaladapis*. From left to right *M. grandidieri* (Ampasambazimba), and two *M. madagascariensis* (Bevoha). Unnumbered specimens from the Academie Malgache.

Figure 66. Distal view of astragalus of Megaladapis. From left to right M. grandidieri (Ampasambazimba), and two M. madagascariensis (Bevoha). Unnumbered specimens from the Academie Malgache.

Chapter 10. A phylogenetic analysis of patterns of tarsal articular form and a discussion of the adaptational significance of transformations of tarsal form in lower primates.

I. Introduction. This study has focused on documenting the variety of shapes and orientations of the tarsal joint surfaces of strepsirhine primates. Where possible, the mechanical and behavioral consequences of these various morphologies is discussed. In this chapter I will attempt to summarize this information in a phylogenetic and adaptive framework, uniting groups of primates on the basis of what I believe are shared derived character states of tarsal articular form, and discussing the probable adaptational meaning of sets of nodal characters (morphotypes) and of the various transformations which have occurred from these morphotype conditions.

The hypothesis of relationships presented here is based on principles of phylogeny reconstruction explained in Chapter one. The proposed relationships between morphological features and aspects of positional behavior are based on the analysis of features in Chapters 4-7. If causal (i.e. functional) relationships between features and behavior are not argued explicitly here, the arguments will be found in the relevant parts of these chapters.

The main subject of this discussion will be the interrelationships between the extant and subfossil Malagasy strepsirhines. However, one important issue which must first be addressed is the question of strepsirhine monophyly. Is there any feature uniquely shared by the extant lemuriforms and the adapiforms which supports the hypothesis that they are sister groups? This is certainly an important issue, and is one that may have to be resolved using evidence from the postcranium, as dental and cranial evidence are as yet inconclusive (Cartmill and Kay, 1978, but see Rosenberger *et al.*, 1985). In order to answer this question, it is imperative to know what morphology was likely to have been present in the ancestor of all primates, and especially in the ancestor of all euprimates. It is only against this background that the morphology of lemuriforms and adapiforms can be compared, and uniquely shared derived features recognized. Thus, a morphotype for the group Primates, and especially for the group Euprimates must be constructed. Although plesiadapiforms, *Tarsius*, omomyids, and anthropoids have not been described in detail in this project, their morphologies are obviously relevant to the construction of primate and euprimate morphotypes, and will be discussed in this section where appropriate. These issues have been addressed in several previous papers (Decker and Szalay, 1974; Szalay and Decker, 1974; Szalay, 1977; Szalay *et al.*, 1975; Szalay and Drawhorn, 1980; Dagosto, 1983) and the relevant information is summarized here. Figure 67 presents the hypothesis of relationships; nodal synapomorphies are given in the legend. Additional summaries of morphotype features for major taxa are given in Tables 28 and 29.

II A. The ancestral primate (Node B, fig. 10.1). As discussed in detail by Szalay and Decker (1974), there are several features of the UAJ, the STJ, and the TTJ which distinguish primates from the majority of extant mammals, and more importantly, from the probable eutherian morphotype. In the UAJ primates lose calcaneofibular contact, deepen the body of the astragalus laterally, and increase the relative length and narrowness of the tibial trochlea. Loss of calcaneofibular contact is also characteristic of many other mammalian groups, and relates to freeing the UAJ to allow pronation and supination at the STJ (Schaeffer, 1947; Szalay and Decker, 1974; Szalay, 1984). The relative narrowness in plesiadapiforms may simply be an artifact of increased length of the ATiL(A). This, along with the increased height of the body (reflecting a higher radius of curvature at the UAJ) yields a slightly increased degree of curvature. Plesiadapiforms, then, have slightly increased ranges of plantarflexion-dorsiflexion than an animal like Protungulatum. Since the joint surface is increased more anteriorly than posteriorly (Szalay and Decker, 1974), it is likely that increasing the range of dorsiflexion was more important than plantarflexion.

The pAC(A) and pAC(C) facets are longer and aligned more parallel to the long axes of the calcaneus and astragalus in primates than in the primitive eutherian. Assuming that the STJ motion axis is similarly placed (at least in terms of its posterolateral orientation) as it seems to be in Protungulatum, Procerberus, and various other extant and fossil mammals (Schaeffer, 1947; Barnett, 1970; Szalay and Decker, 1974), the more anteroposterior orientation of the facets means that they are arranged helically relative to the joint motion axis, rather than being perpendicular to it. This changes motion at the STJ from being purely rotational to partly helical, increasing the degree to which the moving bone abducts/adducts and protracts/retracts during subtalar motion.

Movements at the pAC in primates are enhanced due to the greater length of the facets (especially posteriorly, increasing the range of inversion), and their greater curvature.

The aAC(C) also reflects changes in relative astragalocalcaneal motion by slightly elongating and continuing onto the body of the calcaneus. The aAC(A) is rounder, more helically shaped, and more medially extensive, becoming confluent with the facet made by the spring ligament, and more proximally extensive, becoming confluent with the AN facet. Similar modifications occur convergently in other mammals where inversion of the foot is important (Jenkins and McClearn, 1984), and reflect the superposition of the astragalus and calcaneus and the protraction of the calcaneus in inverted positions at the STJ.

The transition from the primitive eutherian to the primitive primate is associated with many changes in the TTJ. The AN joint of primitive eutherians is dorsolaterally oriented and mediolaterally elongate. The lateral side of the facet is slightly larger than the medial. In plesiadapiforms the medial side is larger than in other Paleogene eutherians. Szalay and Decker (1974) argue that this indicates that stresses were greater on the medial half of this joint, which one can correlate with the more medial position of the navicular relative to the astragalar head in an inverted position of the foot. The more dorsomedial position of the astragalar head tends to orient the medial digits into a more naturally supinated positon relative to the hind part of the tarsus.

The CCu joint of early primates differs from the eutherian morphotype in being aligned more perpendicularly to the long axis of the calcaneus, and in being more circular in outline. These features allow slightly more pronation-supination around the long axis of the foot than the more mediolaterally elongate, flatter, more obliquely aligned CCu joint of primitive eutherians.

II B. Overview of the Primate Morphotype. The morphological changes associated with the eutherian to primate transition in the tarsus are functionally related to 1) a slightly increased range of motion, especially dorsiflexion, at the UAJ; 2) increased ranges of inversion and protraction of the lamina pedis at the subtalar joint; 3) increased range of pronation-supination movements at the TTJ (mainly by increasing the degree of axial rotation at the CCu joint).

Considering all of these factors as a whole, the mechanical significance of the nonprimate-to-primate transition is concerned with increasing the ability of the foot to achieve variable orientations; mainly by increasing the ability to invert the lamina pedis. The biological role of this morphological complex is to allow the animal to deal with the complex spatial orientation and varying diameters of supports in the arboreal environment (Szalay and Decker, 1974). Features of the elbow joint of plesiadapiforms indicate similar increased rotational abilities of the forelimb (Szalay et al. 1975; Szalay and Dagosto, 1980).

This suite of features, though clearly related to allowing the animal to deal with the physical structure of the arboreal environment, does not allow one to reconstruct any more specific habitus for the early primates. Jenkins and McClearn (1984) have shown that similar modifications of the foot occur in arboreal animals such as squirrels and kinkajous who combine plantarflexion and inversion abilities to either hang upside down from branches or descend large trunks headfirst. This suggests that early primates may have had similar abilities. The relatively short, stocky limbs and aspects of the hip joint, knee joint, and elbow joint indicate that Plesiadapis (and thus by extension other plesiadapids) were likely to have been cautious climbers and show no features which are associated with leaping in living primates (Simpson, 1935; Gingerich, 1976; Szalay and Decker, 1974; Szalay, Tattersall and Decker, 1975; Dagosto, 1983). In the foot, this quadrupedal claw-climbing habitus is reflected in the low astragalar body, relatively long trochlea, short astragalar neck, and short distal calcaneus.

Although all the characters enumerated above are valid distinctions between the eutherian morphotype and the primate morphotype, they are also characteristic of a larger group of mammals including tree shrews and dermopterans (Node A, fig. 67) (Szalay and Drawhorn, 1980). Thus it was probably the first archontan rather than the first primate which ventured to become a committed arborealist. As noted by Szalay and Drawhorn (1980), the archontan-primate transition is not accompanied by any major morphological change in the foot. The only feature which is cited to unite plesiadapiforms and euprimates as a sister group within the Archonta is the greater size of the groove for fl. fibularis, an important digital flexor. Assuming that an increase in the size of the groove indicates a relatively larger muscle and/or a need to stabilize the tendon of this muscle (Szalay and Decker, 1974), then primates seem to be enhancing the grasping ability of their digits. This may be some indication that relatively smaller supports could be utilized by plesiadapiforms than by other archontans.

III A. The Euprimate Morphotype (Node D). Unlike the archontan-primate transition, the primate-euprimate transition is marked by a dramatic reorganization of the foot skeleton. To some extent we see the continuation of trends developed in the archontans and early primates, but there are major changes in the UAJ, TTJ, and in other osteological features such as foot proportions, development of a large and opposable hallux, and the replacement of claws by nails. These features, as well as those noted below, are shared by adapiforms, lemuriforms, omomyids, and anthropoids (although they may be modified in some members of each group), and thus clearly indicate euprimate monophyly, as do some cranial features (Szalay, 1977; Szalay and Delson, 1979).

The UAJ of euprimates differs from that of archaic primates (and archaic and modern eutherians) in several ways. The body of the astragalus is very high. The medial and lateral crests are approximately equal in height; in lemurids and indriines the medial crest is slightly higher than the lateral. This is a great departure from the primitive low bodied astragalus of *Protungulatum* or of many other mammals where the lateral crest exceeds the medial in height (e.g. *Plesiadapis*). The increased height of the body probably reflects an increase in the radius of curvature of the UAJ relative to body size. Although these parameters cannot be directly compared in plesiadapiforms and euprimates, a similar difference exists between leaping (lemurs, galagines) and nonleaping (lorisine) strepsirhines (Chapter 4).

The equal heights of the crests serve to reduce concomitant pronation and supination movements which accompany dorsiflexion and plantarflexion at the UAJ in mammals with high lateral crests (Jenkins and McClearn, 1984). (The astragalus does however, pronate and supinate a little during UAJ motion.) This may seem contradictory to the primate trend of increasing the ability of the foot to invert and evert, but in euprimates, this ability is concentrated in the TTJ and STJ.

Euprimates increase the range of plantarflexion possible by lengthening the degree of faceting for the UAJ on the posterior part of the astragalus. This surface is also lengthened by the addition of the posterior trochlear shelf, a feature which is unique to euprimates (although it is modified in many euprimate taxa). The depth of the trochlea in euprimates (except for *Daubentonia* and *Avahi*) is increased over that in archaic primates adding an increased degree of stability to the UAJ.

These features of the UAJ are reflections of the importance of leaping in the earliest euprimates. Increasing the range of UAJ motion, especially for plantarflexion, restricting conjunct pronation-supination motions at the UAJ, and increasing its stability are all features mechanically advantageous for leaping. The increase in relative length of the tarsal bones present in most euprimates is also a reflection of changes in foot lever mechanics for leaping (Hall-Craggs, 1965). The relationship between these features and leaping can be appreciated by comparing a specialized leaper (e.g. a galago or *Lepilemur*) with a nonleaper (e.g. a loris). Galagos show the most development of these features, lorises the least. It is also noteworthy that in other mammals where quick, stable motion at the UAJ is desirable (other leapers like rabbits, cursors like artiodactyls) similar adaptations occur at the UAJ and STJ (see for example, Schaeffer, 1947; Szalay, 1985; Bleefeld, in prep.).

Another set of UAJ features which may be part of the euprimate morphotype is related to the production of conjunct abduction-adduction at the UAJ. In almost all extant lemuriforms the ATiM(Ti) is medially rotated to face 30-40 degrees from the sagittal plane, the distal part of the malleolus is highly convex to articulate with a concave ATiM(A) which ends in a marked cup on the astragalar neck. The ATiL(A) is curved medially as it progresses distally. These curvatures dictate that as the astragalus moves from a plantarflexed to a dorsiflexed position it also abducts relative to the tibia (Hafferl, 1932; Lewis, 1980a; Dagosto, 1985). These features are most exaggerated in climbers like lorisines, and least expressed in leapers like galagines and Lepilemur, suggesting a possible mechanical relationship to climbing. Lewis (1980a) however, has related these features to grasping.

In other euprimates these features are not as well expressed as in lemuriforms. They seem to be lemuriform-like in Adapis and Leptadapis, but are not as well developed in notharctines. In these latter taxa, medial malleolar rotation is advanced, but medial cupping and twisting of the ATiL and ATiM are very slight. This can be explained as an indication of more specialized leaping in these forms (Gregory, 1920; Covert, 1985b), or that the first euprimate or strepsirhine was more conservative in these features than are extant Lemuriformes.

Omomyids, tarsiers, and anthropoids exhibit less exaggerated malleolar rotation than adapids, deviating only 10-15 degrees from a parasagittal plane in the former two taxa (Dagosto, 1985). Only the anterior part of the ATiM(Ti) is convex and anterolaterally oriented, the posterior part is very flat and faces laterally. Associated with these features, the ATiM(A) is less concave and less cupped. The ATiL(A) does not curve medially. The inferior tibiofibular joint is relatively rigid. Functionally, these features reduce the amount of conjunct or concomitant abduction-adduction which accompany dorsi- and plantarflexion. This restricts motion at the UAJ to a more sagittal plane, and is a morphofunctional complex associated with small-bodied leaping primates (Dagosto, 1985). These are probably haplorhine synapomorphies (Dagosto, 1985).

It is very difficult to determine if the malleolar rotation-medial astragalar twisting of Lemuriformes was present in the euprimate ancestor. It seems likely that it was since all euprimates that deviate from these conditions (notharctines, tarsiiformes, anthropoids) show evidence in the form of partial malleolar rotations and moderate astragalar twisting of having once had this pattern, but abandoning it for functional reasons. On the other hand, the earliest known euprimates (*Cantius*, *Teilhardina*) do not show any great development of this complex. Perhaps the best solution for the present is to assume that at least a moderate degree of development of this complex was present in the euprimate ancestor, modified rapidly in omomyids and notharctines, and is present in a somewhat exaggerated form in living strepsirhines.

Another UAJ feature which is equally hard to interpret phylogenetically is the posterior trochlear shelf. It is present and rather large in notharctines, moderate in lemuriforms (except indriines, where it is very large, and galagines and lorisines where it is absent), small but present in omomyids (except *Necrolemur* where it is very large (Godinot and Dagosto, 1983)), absent in *Tarsius* and anthropoids. Again, it is most likely that at least some development of this structure was primitively present, since virtually all euprimates show some evidence of it. If however, a relatively large shelf was present in the first euprimate, it was rapidly reduced in the first tarsiiform; the shelf is much smaller in *Teilhardina* than in *Cantius*.

The STJ exhibits relatively few changes from the primitive primate or archontan condition. The pAC facets may be slightly more elongated, related to the development of the posterior trochlear shelf (Decker and Szalay, 1974). The confluence of the pAC(A) and AN and spring ligament facets is more definite and regular than in plesiadapiforms. The aAC(C) is much longer than in *Plesiadapis*. This may simply be the result of a relatively longer astragalar neck and distal calcaneus. Elongation of the tarsal elements is usually ascribed to changes in foot lever mechanics advantageous for leaping. However, the relatively long astragalar necks of *Potos*, *Felis wiedii*, and *Ptilocercus*, mammals which show increased ranges of subtalar motion (Szalay and Drawhorn, 1980; Jenkins and McClearn, 1984) suggest that some lengthening of the astragalar neck may be the result of the elaboration of subtalar motion in euprimates.

The TTJ of euprimates is more advanced than in the archaic primates. The AN joint is more spherical, and thus tends toward an unmodified ovoid. The medial and lateral sides of this joint are equivalent in size, unlike plesiadapiforms where the medial side is larger. The CCu joint is a sellar joint rather than an ovoid. The joint takes the form of a pivot articulation; there is a protuberance of moderate size on the cuboid and a corresponding depression on the calcaneus. These modifications increase the degree to which the lamina pedis inverts and everts by increasing the degree to which adjunct supination and pronation are allowed at the TTJ. In other mammals (Jenkins and McClearn, 1984), and probably in plesiadapiforms, motion at the TTJ is a combination of pronation-supination and mediolateral translation. In euprimates the pronation-supination component is enhanced and the translational component is reduced. Jenkins and McClearn (1984) found that in *Potos* and *Sciurus* inversion (supination) is associated with a lateral translation of the navicular relative to the astragalus. This study, and my unpublished X-ray study of anesthesized macaques, shows that in euprimates, on the other hand, supination is associated with a medial translation of the navicular (actually, there is very little translation at all). This is a marked difference in the details of TTJ motion between euprimates and other mammals, and is reflected in the morphological differences in the AN and CCu joints. It probably also reflects a shift in the motion axis of the TTJ away from the CCu articulation towards the AN joint. This in turn may be related to the enlargement and functional independence of the hallux.

III B. An overview of the euprimate morphotype. The transition from a primitive primate tarsus to a euprimate one involves numerous morphological change in the UAJ, the TTJ, and other aspects of foot structure. The UAJ loses most of its ability to pronate and supinate during dorsiflexion and plantarflexion, but its range of motion is increased. Stability of this joint is increased by deepening the trochlear groove. These features, along with the lengthening of the tarsal region, especially of the astragalar neck, distal calcaneus, navicular, cuboid, and cuneiforms, reflects the importance of leaping in the earliest euprimates.

The STJ of euprimates shows very little change from the primate condition, except for the greater lengthening of the aAC and the more regular confluence of facets on the head of the astragalus. These features reflect the continued importance of elaborate subtalar motion in euprimates.

The TTJ is distinguished by the change of the AN joint to an unmodified ovoid, and the development of the CCu "pivot" (actually a sellar joint). This latter allows rotation, but also provides a degree of stability which is lacking in the primitive ovoid form of this joint. Together, these changes indicate an increased degree of axial rotational motion at the TTJ at the expense of translational movements. The loss of concomitant pronation-supination abilities at the UAJ as a result of modifying this joint for leaping meant that euprimates had to increase this ability at other joints. The morphological changes in the STJ and the TTJ are related to increasing the range of pronation and supination of the fore part of the foot at these joints.

Other clearly euprimate hallmarks are the enlargement of the hallux, and the specialization of the entocuneiform-MT1 joint into a sellar shaped joint. Claws are replaced by nails. These features reflect the importance of grasping in the earliest euprimates.

There are other features which are probably also part of the euprimate morphotype, but are more difficult to interpret. The morphological features of the ATiM and ATiL joints, which reflect the conjunct abduction of the foot which accompanies dorsiflexion and is probably related to climbing and grasping, are most strongly expressed in the extant lemuriforms, and very mildly developed in the notharctine adapids, omomyids, *Tarsius*, and anthropoids. However, in most cases, these latter groups show some evidence of reorganization of the tarsus along these lines, and thus these features are considered here to be euprimate synapomorphies.

The suite of postcranial characters which I envision to have been present in the ancestral euprimate suggest an animal which, in terms of its locomotor behavior, is likely to have been best adapted to an arboreal milieu, could certainly climb well, grasp thin supports with an opposable hallux, and had hindlimbs which were well adapted for leaping. These are the same general descriptors of locomotion that, with some qualifications, I would apply to the lemurids, cheirogaleids, and the majority of platyrrhines and cercopithecoids. This locomotor mode has been termed "grasp-leaping" by Szalay and Dagosto (1980) to emphasize the importance of grasping and leaping in the emergence of euprimates. Martin (1972) reconstructed a similar ancestral locomotor mode for "primates" (=euprimates), but called it hindlimb dominated locomotion.

This notion is in conflict with other proposed ideas of the ancestral euprimate locomotor mode. Napier and Walker (1967) advanced the hypothesis that vertical clinging and leaping may have been the type of locomotor behavior used by the earliest primates. This idea has previously been criticized on several grounds (Szalay, 1972; Cartmill, 1972; Stern and Oxnard, 1973). This study of the foot yields no evidence that the primitive euprimate was specialized for vertical clinging postures, although features related to this are extremely difficult to identify. Nor was the ancestral euprimate as specialized for leaping as are indriines, bushbabies, tarsiers, or *Lepilemur*.

I do not share the opinion of Godinot and Jouffroy (1984) that *Adapis* is morphologically close to the primitive euprimate condition, or that the ancestral euprimate was an arboreal, quadrupedal walker-runner, and not a leaper. Although the hand of *Adapis* may preserve some primitive euprimate features, an analysis of the rest of the postcranium shows that it was a specialized slow moving, quadrupedal, non-leaping primate (Dagosto, 1983). For reasons outlined above, mostly having to do with the morphology of the UAJ and the proportions of foot bones, both the primitive euprimate and the primitive strepsirhine were both likely to have been accomplished leapers, unlike *Adapis*. The relative uniqueness of *Adapis*-like morphology among living and fossil euprimates, the fact that it occurs only in a few isolated groups, and that it first appears well after the origin of euprimates are additional arguments which support the contention that *Adapis* is derived, not primitive in its postcranial morphology (Dagosto, 1983). It is, however, probable that the ancestral *primate* was the non-leaping, quadrupedal branch runner and walker envisioned by Godinot and Jouffroy (1984) (see above, Szalay *et al.* 1975; Dagosto, 1983).

The grouping of strepsirhines and haplorhines into a monophyletic taxon Euprimates is one of the best supported nodes on this cladogram. Curiously, this category has never been formally proposed or widely used.

IV. The Strepsirhine Morphotype (node E). On the basis of cranial and dental features Cartmill and Kay (1978) were unable to cite any features shared uniquely between adapids and extant lemurs. There are, however, a few features of the foot which do support the hypothesis of strepsirhine monophyly. In both groups of adapids and living lemuriforms the AFi(A) facet slopes gently laterally for its entire extent fig. 68). A cline exists in strepsirhines; the flaring is most well developed in the slow climbing lorisines (and *Adapis*), and least developed in the specialized leapers like galagines, *Lepilemur* and indriids. It is moderately developed in notharctines. In *Tarsius*, omomyids, and anthropoids (Gebo, pers. comm.) the AFi(A) is very flat laterally but about halfway plantad it makes an abrupt flare, resulting in a small pointed process. From its proximal to its distal end, the facet is flat, whereas in strepsirhines, as noted in Chapter 4, the AFi(A) is convex proximally and becomes concave distally resulting in sinuous AFi movement. In haplorhines, motion is more purely sagittal. This is no doubt related to the more complex tibioastragalar UAJ motion in strepsirhines, which may indicate that climbing was more important in ancestral strepsirhines, or because of larger body size (see below) climbing demanded different morphological solutions.

The condition seen in adapiforms and lemuriforms is unique among mammals; the haplorhine condition is similar to that exhibited by plesiadapiforms, and by other mammals (although the plantar process is normally absent). Therefore, I believe the strepsirhine condition to be the derived morphology.

A second strepsirhine autapomorphy concerns the way the navicular and cuboid articulate. In notharctines and lemuriforms the navicular and cuboid have a broad area of articulation. As a result, the CuN(N) facet is related to the NEc and NMe facets (fig. 69). These features are less developed in *Notharctus* and *Smilodectes*, where the CuN(N) facet just approaches the lateral edge of the NMe facet, but the beginnings of the pattern are present. This region is unknown in adapines.

In contrast, in *Tarsius*, anthropoids, omomyids (this region is known only in *Hemiacodon* and *Arapahovius*, both omomyines[1]) and in all other mammals examined, the CuN(N) is related only to the NEc(N) facet and never extends under the NMe(N) facet (fig. 69). This results in a greater folding of the midtarsal region in strepsirhines, in which the mesocuneiform is approximated to the cuboid (fig. 70).

Strepsirhines have navicular-cuneiform facets which are more separate and have greater curvatures than haplorhines (except *Tarsius*), which tend to have very flat, amorphous navicular-cuneiform facets.

A very important determinant of locomotor and thus morphological

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[1] Szalay (pers. comm.) believes that *Arapahovius* may be an anaptomorphine.

differences between primitive strepsirhines and haplorhines is likely to have been body size. Although today the average haplorhine is larger than the average strepsirhine, at the time these groups diverged from each other the opposite was true. The great majority of early and middle Eocene adapids are estimated to have weighed more than 1000 gms. (Gingerich et al., 1982). In contrast, almost all known Eocene haplorhines are estimated to have weighed less than 500 gms. (Gingerich, 1981). [Martin (1972, 1979) visualizes a rather smaller (Cheirogaleus-Microcebus sized) lemuriform and strepsirhine ancestor than I would, but still an animal larger than most omomyids.] Based on this dichotomy in body size alone, one would expect that adapids emphasized climbing in their locomotion while omomyids were more likely to have been frequent leapers (Jungers, 1979; Fleagle, 1977a,b; Cartmill and Milton, 1977). The morphological differences between strepsirhines and haplorhines may reflect this distinction. The flaring AFi joint of strepsirhines allows complex UAJ motion. The broader articulation of the navicular and cuboid serves to increase the transverse arch of the foot, and the morphology of the navicular-cuneiform joints probably allows minor readjustments of the distal tarsus to increase conformation of the grasping foot on the support (Hafferl, 1932). Three interpretations of this evidence are possible: 1) The actual mechanics of grasping differs in strepsirhines and haplorhines; 2) there are major differences in support size or orientation choice; or 3) increases in body size alone require morphological readjustments for grasping. Without more detailed behavioral studies addressed to points 1 and 2, it is impossible to choose among these alternatives.

There are two other features, ectaxony and the presence of a toilet claw on the second digit, which are potential strepsirhine synapomorphies. These features are present in all lemuriforms (no toilet claw in *Daubentonia*), and in the Messel adapid (?ectaxony). *Notharctus* may also have exhibited ectaxony (Gregory, 1920). *Tarsius* shows both derived features, but anthropoids have neither. The state of these characters is unknown in all other adapids and omomyids. Given this distribution and the gaps in our knowledge, three hypotheses are possible: 1) the two features are primitive for all euprimates, but were lost in the ancestor of anthropoids. 2) These are strepsirhine or lemuriform synapomorphies, and were convergently evolved in *Tarsius*. 3) These are strepsirhine or lemuriform synapomorphies and *Tarsius* is a strepsirhine or lemuriform, not a haplorhine. Based on features of the nasal region, placenta, ear region, and skull (Luckett and Szalay, 1978), hypothesis 1 seems most likely at this point.

V. Adapiformes. I am unable to identify any character of the foot uniquely shared between the notharctine and adapine adapids. Thus, these two groups and lemuriforms are left as an unresolved trichotomy of Strepsirhini. Eocene strepsirhines are discussed together here in view of their conventional grouping.

Schwartz and Tattersall (1979, 1985) have also questioned the notion that the Adapinae and Notharctinae form a sister group. They prefer to link different adapid taxa to specific lemuriform taxa: *Adapis* and *Leptadapis* are linked to indriines and *Lepilemur*; *Anchomomys*, *Periconodon* and *Huerzeleris* to lorisoids; the notharctines to lemurids (1979), or as a sister group to the whole assemblage of lemuriforms and adapines (1985). At present the postcranial evidence is inadequate to fully test all of these hypotheses. *Adapis* and *Leptadapis* are extremely unindriine-like in postcranial morphology (Dagosto, 1983). This in itself does not falsify Schwartz and Tattersall's hypothesis, but certainly provides no support for it. No postcrania are known for *Anchomomyos*, *Periconodon*, or *Huerzeleris*.

The known notharctines (Node F) are united by the development of a very large posterior trochlear shelf, which otherwise occurs only in indriines, and the reduction in medial rotation of the ATiM(A) and ATiL(A) facets. These features are reflections of the importance of leaping in the locomotor behavior of notharctines over the probably more quadrupedal, climbing primate ancestor. Among notharctines, *S. gracilis* appears to be the most advanced.

Adapis, *Leptadapis*, and *Caenopithecus* (Node G) are linked by several derived features of the astragalus and calcaneus including increased medial rotation of the ATiM(A) and ATiL(A) facets, increased relative length of the ATiL(A), short astragalar neck, and short distal calcaneus. These features also occur in lorisines, and are related to the adoption of quadrupedal climbing and walking as the preferred mode of locomotion. This group is more distinct from my concept of the strepsirhine ancestor than is the notharctine group.

In its analyzable features, the Messel adapid shares none of the derived pedal features of either the Notharctinae or Adapini, thus it cannot be securely linked to either one.

VI. Lemuriform morphotype (Node H). The extant (and subfossil) lemuriform primates share a few features of the foot which support the hypothesis of their union into a monophyletic group, which is traditionally based on the presence of a tooth comb in these animals. Most of these features are not strongly marked distinctions from adapids, but represent further development of trends first evidenced in early strepsirhines. Thus, the medial extent of the CuN(N) facet is increased, so the facet lies under both the NEc(N) and the NMe(N) facets (except in Daubentonia and archaeolemurines). The plantar keel of the ectocuneiform is reduced and the mesocuneiform develops contact with the cuboid (except in Daubentonia and galagines). The medial curvature of the ATiM(A) and ATiL(A) facets is stronger than in notharctines (but not adapinans).

Within Lemuriformes two main groups can be defined based on foot morphology. First the "lemurid-indriid" group will be discussed, then the lorisoids. The enigmatic Daubentonia is discussed separately. Until now, my phylogenetic interpretation of the postcranial evidence has closely paralleled traditional phylogenies and classifications. In the following discussion, however, I find it helpful to recognize a group uniting the lemurids and indriids. This grouping has been implicitly recognized in recent analyses of strepsirhine phylogeny (Eaglen, 1980; Schwartz and Tattersall, 1985; Szalay and Delson, 1979;

Tattersall, 1982), but has never been named. I propose here that the superfamily Lemuroidea be restricted to contain the families Lemuridae and Indriidae, thus recognizing a basic dichotomy of the toothcombed strepsirhines into lemuroid and lorisoid groups. The lemuroid/ lorisoid dichotomy is supported by cranial, dental, and postcranial evidence, but not by immunodiffusion work (Dene et al., 1976a,b; Sarich and Cronin, 1976). Not completely coincidentally, it also divides toothcombed strepsirhines, with a few exceptions, into large (>1000 gms)/small (<1000gms), folivorous-frugivorous/ insectivorous-gummivorous, diurnal/nocturnal, and glandular scent markers/urine-washing scent markers moieties. Similar distinctions, at least in terms of size and diet, apply to the adapid/omomyid dichotomy.

This classificatory scheme (Table 3) has the advantage of requiring no new names or categories, but the possible disadvantage of requiring a reduction in rank of some groups within the Lemuroidea that others (e.g. Szalay and Delson, 1979; Tattersall, 1982; Schwartz and Tattersall, 1985) recognize at higher levels.

VII. Lemuroids. (Node I). This group contains the living and fossil indriids and lemurids. A sister-group relationship here is supported by some craniodental features (Tattersall, 1982; Schwartz and Tattersall, 1985), and by the meager molecular evidence (Dene et al., 1976; Sarich and Cronin, 1976). In addition, two (possibly related) foot features link these groups. Gebo (1985) has identified a complex of traits at the tarsometatarsal joint which are shared by all lemurids and indriines, but no other mammals. He hypothesizes that these traits enable larger animals to utilize vertical supports.

All lemurids and indriids (with the exception of some subfossil forms) share a moderate to strong dorsolateral orientation of the AN joint (refer to figures 34 and 35). This is the condition also observed in most mammals, in some omomyids, and in anthropoids. However, a moderate dorsomedial orientation of the AN joint is characteristic of plesiadapiforms, all adapids, *Tarsius*, and some omomyids. Thus, a dorsomedial orientation, not a dorsolateral one, is probably the primitive condition in primates and strepsirhines. The dorsolateral orientation of the AN joint throws the navicular (and cuneiforms) at an angle relative to the cuboid and helps oppose the first digit to the others (Conroy, 1976). In primates with dorsomedially oriented AN joints (*Daubentonia*, lorisoids, adapids) the metatarsals tend to be more in straight alignment (Gebo, 1985), but in a supinated position relative to the tarsals.

The primitive lemuroid thus differs from the primitve strepsirhine in aspects of the foot which have to do with grasping, and in particular for grasping vertical supports. This is correlated with an increase in body size in this group (Gebo, 1985).

VIII. Within the lemuroid group the extant indriines (*Avahi*, *Propithecus*, *Indri*, Node K) are distinguished by several derived features of the foot. All indriines have a large, posteriorly expanded, twisted posterior trochlear shelf. The extension of the shelf itself is probably related to the extent of the pAC facets (Decker and Szalay, 1974), which are more parallel to the long axes of the astragalus and calcaneus than in any other strepsirhines. As discussed in Chapters 4 and 5, the elongation of the pAC facets should increase the ranges of inversion and eversion at the STJ in indriines; but paradoxically the flattening out of the proximal parts of these facets would reduce the degree of inversion. Indriines are perhaps reducing motion at the STJ in order to stabilize the foot for leaping.

Possibly as a way of compensating for loss of STJ mobility, indriines are characterized by a more spherical AN, a high, flat CCu joint, and a serial tarsus, all of which contribute to freer rotation at the TTJ.

Indriines are also distinguished by a plantarly bent aAC(C) facet; which might be related to the dorsolateral tilt of the astragalar head. The CuN joint is more sellar shaped than in lemurids, and the CuMe contact is greatly expanded. Gebo (1985) has described modifications of the tarsometatarsal joints and intrinsic foot musculature which increase grasping power in large vertically clinging indriines.

Vertical clinging behavior in indriines is possibly evidenced by the twisted posterior trochlear shelf (Chapter 5), the plantarly bent aAC(C) and the features noted by Gebo (1985) listed above, although the mechanical connection between any of these traits and vertical clinging has not been established. The features of the tarsometatarsal joint are also present in lemurids, but are not present in galagines. Body size differences between these two groups of vertically clinging primates explains this lack of correlation.

The indriine foot shows a few specializations reflecting their frequent leaping such as the less curved ATiM and ATiL joints and the less flaring AFi joint. These traits are shared with *Lepilemur* and galagines. The flattening of the STJ may act to stabilize this joint, but this is not seen in other leapers. The NCu joint is also slightly more stabilized than in lemurids, but the distinction is not great. The leaping adaptations of indriines are only subtly different from lemurids, and tend to be concentrated at the UAJ. They do not show the extreme modifications of foot lengthening seen in galagines and *Tarsius* (Table 27), or the modifications of the TTJ and navicular-cuneiform articulations which characterize these groups. This is almost certainly a result of the large body size of indriines (Walker, 1970) sugesting that the indriine ancestor adopted frequent leaping only after it was relatively large.

The leaps of indriines are probably "thigh powered" rather than "foot powered". Most of the other characteristically indriine features--the relatively short tarsus (Jouffroy and Lessertisseur, 1979), the serial tarsus, the spherical AN joint, the high, flat CCu joint, and the large CuMe articulation are adaptations to increase mobility and/or folding of the foot in the distal tarsal region. These features are likely to be more mechanically advantageous for climbing or grasping than leaping. I suspect that climbing and hanging behaviors have been underemphasized in describing indriine locomotion in favor of the more spectacular leaps made by these animals. Both climbing and forelimb and hindlimb suspension during feeding have been described by Petter (1962), Petter *et al.* (1977), and Jolly (1966). Indriines thus have a foot which is an interesting compromise for leaping, climbing, and vertical clinging. The adaptations for leaping are largely confined to the upper ankle joint; climbing and clinging are reflected in the transverse tarsal joint, and distal tarsal and metatarsal structure.

Like Eaglen (1980) and Schwartz and Tattersall (1985) I am unable to resolve a trichotomy between *Indri*, *Propithecus*, and *Avahi*. *Indri* and *Propithecus* are most like each other (but probably only patristically). *Avahi* is easily distinguishable by its smaller size, and fairly flat ATiL(A).

IX. Subfossil indriids. (Node L). Foot bones are known for only *Archaeolemur*, possibly *Hadropithecus*, and possibly *Mesopropithecus*, thus only the phyletic position of these taxa will be discussed. These animals are undoubtedly closely related to the extant indriines as evidenced by craniodental features (Tattersall, 1973), but do not share any of the special pedal features which distinguish indriines from lemurids. As noted above (Chapter 9) the astragalus and calcaneus of archaeolemurines differ from indriines in ways which make them more lemurid-like, and thus probably more primitive than the extant indriines. The few meager features which might be cited to reflect the relationship between indriines and archaeolemurines are a slightly less flaring AFi(A) and a more marked tubercle for the dorsal talonavicular ligament (this latter feature is also found in *L. catta*, and *V. insignis*). In some ways these animals are very distinct from any others of the lemuroid group especially in lacking any appreciable tilt to the astragalar head and in the lack of extensive contact between the CuN(N) facet and the NMe facet. Considering the extensive undoubted cranial and dental shared-derived similarities with indriines, these pedal features are best interpreted as secondary reversions to a state which is more like the primitive strepsirhine condition than evidence that these animals are primitive strepsirhines. Similarly, if the Tsirave bones are indeed *Mesopropithecus*, and not *D. robusta*, this animal also is quite distinct postcranially from its close relative *Propithecus*, in ways which make it appear more primitive (i.e. more lemurid-like).

In sum, the subfossil indriids share almost no pedal features with indriines. This makes it virtually impossible to reconstruct a pedal morphotype for the indriids other than a lemurid-like animal. Was this animal indriine-like, or archaeolemurine-like (primitive)? If the latter, the primitve indriid foot is not easily distinguishable from that of a lemurid. If the former, all of the subfossil groups have undergone major changes in pedal morphology--a perfectly reasonable hypothesis in view of their distinctive locomotor adaptations. The taxon Indriidae is thus defined solely by cranial and dental features for the time being.

X. Lemuridae. (Node M). The lemurids are, in terms of pedal morphology, the more primitive members of the Lemuroidea. I cannot cite any character which would distinguish a lemurid from my concept of the morphotype lemuroid. Eaglen (1980) and Schwartz and Tattersall

(1985) have, however, described several cranial and dental features uniting the lemurids.

The species of the genus Lemur are all indistinguishable from each other with the exception of Lemur catta. This species has rather more robust, relatively shorter tarsals, greater invasion of the anterior interosseous ligaments into the aAC(A) and AN(A) joint space, and dorsoplantarly flattened AN and CCu joints. These features are all mechanically advantageous in stabilizing the foot against axial rotations and probably reflect the greater use of the terrestrial substrate in this lemur (Sussman, 1974; Ward and Sussman, 1979).

The probable autapomorphies of Varecia variegata include a relatively less elongate astragalar neck, distal calcaneus, cuboid, and navicular, and moderate dorsoplantar flattening of the components of the TTJ. Except for the last feature, which is associated with several different locomotor modes, these distinctions from other lemurids are no doubt related to the increased body size of Varecia, and probably reduced efficiency of leaping. A continuation of these trends is manifest in Varecia's even larger congener, V. insignis.

The foot of Hapalemur is distinguished from the above taxa solely by the enlargement of the proximal navicular to more fully encompass the astragalar head. This feature is also found (convergently, I believe) in Lepilemur, Tarsius and some lorisoids, and is probably an adaptation to stabilize the foot in leaping. This is the only feature of Hapalemur which suggests more frequent leaping than in other lemurids.

Both Eaglen (1980) and Schwartz and Tattersall (1985) propose a branching sequence within lemurids which recognizes *Hapalemur* as the earliest offshoot, then *Varecia*, then the species of *Lemur*. I can offer no evidence which either supports or contradicts this arrangement.

XI. The status of *Lepilemur* (Node N) requires special attention. *Lepilemur* is usually considered to be a highly derived lemurid, but there is evidence that suggests a potential derivation from the indriid rather than lemurid line. In 1873 Mivart (p. 490) noted that "*Lepilemur* seems to be that genus of the Lemurinae which most approximates the Indrisinae." He based his conclusion on the fact that these taxa share fusion of the os intermedium with the scaphoid (also found in *Hapalemur*), and some resemblances in the vertebral column. *Lepilemur* and indriines share derived features of the elbow joint (Szalay and Dagosto, 1980). *Lepilemur* also shares some derived pedal features with indriines. These features are: reduction of curvature of ATiM(A) and ATiL(A) facets, lesser rotation of the tibial malleolus, a high astragalar body, a long UAJ arc, a large CuMe articulation, a more sellar shaped CuN joint surface, a strong dorsolateral orientation of the astragalar head, and a stong plantad bend to the aAC(C) facet. It does not, however, share the large, plantarly bent posterior trochlear shelf, the foot proportions, the serial tarsus, or the spherical astragalar head of indriines. One might argue that these postcranial resemblances are convergences due to the very similar locomotor modes of indriines and *Lepilemur*.

However, a close relation betweeen indriines and Lepilemur is also supported by craniodental evidence (Schwartz and Tattersall, 1985) and the available molecular work (Dene *et al.*, 1976a,b).

If Lepilemur is indeed an early offshoot of the indriid line, the ancestral indriid was likely to have been a vertical clinger and leaper. This differs from the interpretation given above (section IX) when only indriines and subfossil indriids were considered. If this is so, then the subfossil indriids [which are clearly more closely related to indriines than is Lepilemur (Tattersall, 1973)] have undergone radical reorganizations of their postcranial skeleton.

Megaladapis (Node O) is often linked to Lepilemur on grounds of shared derived dental features such as the loss of the upper incisors. These two taxa are about as distinct as can be postcranially. No feature of the foot can be cited to support (or contradict) this linkage. However if they are related, then linking Lepilemur (and thus Megaladapis) to the indriid line has the interesting consequence of having all the very large subfossil forms as derivatives of the indriid line.

XII. Lorisoidea. (Node P). The cheirogaleids and lorisids are united into this superfamily because they all share a derived carotid arterial pattern and associated features of the skull (Saban, 1963; Szalay and Katz, 1973; Cartmill, 1975). There are no strongly convincing postcranial synapomorphies uniting all members of the group. [One might cite a slight increase in the dorsomedial orientation of the astragalar head and unusual limb length/body size proportions

(Jungers, 1985)]. As noted frequently in Chapters (4-7), cheirogaleids are heterogeneous in foot morphology. *Cheirogaleus* is very primitive, exhibiting few differences from lemurids. The other taxa are very derived and share many unique structural specializations of the foot with galagines.

Decipihering the sequence of relationships within this group presents great problems. It is virtually impossible to devise any scheme of relationships without proposing multiple parallelisms, losses, and/or reversals. This is true when using dental, cranial, behavioral, or postcranial characters, separately or in concert.

Most authors recognize a group (either at the family or subfamily level) containing the genera *Cheirogaleus*, *Microcebus*, *Mirza*, *Phaner*, and *Allocebus*. The remaining lorisoids are put in the family Lorisidae. However, with the exception of Schwartz and Tattersall (1985), and Eaglen (1980), no one has listed traits to define a monophyletic Cheirogaleidae which cannot just as easily be interpreted as traits primitive for all lorisoids. Even in these schemes, numerous parallelisms and reversals are required.

Similarly, there are very few postcranial traits which are useful in sorting out these taxa. The phylogeny of lorisoids by Szalay and Delson (1979) and Schwartz and Tattersall (1985), and supported by immunodiffusion studies (Sarich and Cronin, 1976), or those proposed by Cartmill (1975) and Eaglen (1980) (fig. 71 a-c) are all problematical in that they require a significant increase in elongation of the tarsals to occur three times: in Galaginae, the *Mirza*-*Microcebus* group, and the *Allocebus-Phaner* group. While this is not totally unlikely (it must also have occurred other times, i.e. in *Tarsius* and some omomyids), an arrangement of taxa as in fig. 71d avoids this problem, and explains other features shared by the *Mirza-Microcebus* group, the *Allocebus-Phaner* group, and galagines, but not *Cheirogaleus* (and *Cheirogaleus* has the conservative state of these features). These features include a highly derived complex of traits on the distal end of the navicular, distinctive AN joint morphology, (see legend of figure 71), and the presence of the distinctive lorisoid hypocone. It is very unlikely that the postcranial features were present in the common lorisoid ancestor and then lost in *Cheirogaleus*, since the navicular of *Cheirogaleus* is indistinguishable from that of lemurids or indriines. It is possible that the morphology of the *Microcebus* and *Phaner* groups evolved in parallel to the galagines since *Tarsius* (if it is not derived from this group) has independently evolved similar (but not identical) modifications. The virtual identity of the cheirogaleid distal navicular to that of the galagines does, however, seem to be strong evidence against this interpretation.

Thus, the most parsimonious explanation for the distribution of postcranial features in lorisoids is hypothesis 71d. However, it implies a paraphyletic Cheirogaleidae. No matter what phylogeny is correct, it is obvious that considerable parallelism has occurred in dental and/or postcranial traits in this superfamily. I have retained a family Cheirogaleidae in my classification in view of their traditional placement and my uncertainty of lorisoid phylogeny.

The lengthening of the tarsals and the morphology of the distal navicular in lorisoids (except *Cheirogaleus*) indicates that their common ancestor emphasized leaping in its locomotor behavior. The fact that some lorisoids (*Microcebus*, *G. demidovii*) no longer leap extensively does not falsify this hypothesis. There is no other valid mechanical explanation for these traits.

I have not had the opportunity to examine the Miocene lorisid postcranial material first hand. Casts and photographs of this material (Walker, 1970; Szalay and Delson, 1979) show that the CCu articulation is deeper than in cheirogaleines, but perhaps not quite as deep as in extant lorisids. Except for *Komba minor*, the degree of distal calcaneal lengthening is however, not any greater than in *Cheirogaleus* (or lemurids). There is little evidence to link any of these Miocene calcanea to galagines or lorisines. I concur with Szalay (1976) that these bones are overwhelmingly cheirogaleid-like (i.e. primitive lorisoid-like). The dental and cranial material is apparently equally difficult to place (Simpson, 1967).

XIII. Lorisidae. (Node R). The galagos and lorises are considered to be a monophyletic group largely on the strength of shared specializations in the conformation of the auditory tube and the petromastoid region (Szalay, 1975; Szalay and Delson, 1979). Schwartz and Tattersall (1985) have linked these groups on the basis of shared derived dental features, and the molecular work supports this arrangement (Dene *et al.*, 1976a,b; Sarich and Cronin, 1976).

Although these two groups are clearly closely related, they have widely divergent positional behaviors. Thus, there are very few postcranial features which unite them. The only two features I can cite are the increased depth of the CCu joint and the loss of the posterior trochlear shelf.

The deeper CCu joint functions to increase the degree of axial rotation possible without incurring large translational movements (Chapter 5). This mechanical advantage can be interpreted as useful for both leapers and slow climbers. Likewise, the loss of the posterior trochlear shelf occurs in both other leapers (omomyids, Tarsius), and slow climbers (Adapis). It is thus quite difficult to determine if these morphotype features indicate a lorisid ancestor more like a galagine or a lorisine.

Considering the morphology of cheirogaleids and Miocene lorisoids, it seems obvious that the ancestral lorisid was more likely to have been an agile leaper than a slow climber. Galagines have exaggerated this ancestral adaptation, while lorisines have abandoned it altogether for a completely different mode of locomotion. Their distinctive autapomorphies reflect these differences.

XIV. Galaginae. (Node S). Galagines are distinguished from all other strepsirhines by the possession of a synovial CN joint, a highly sellar CuN articulation, a high pAC(C) angle, and a very centrally located CCu pivot. These are derived features compared to a lorisoid morphotype. There are many other features of the galagine foot which are derived compared to a strepsirhine morphotype, but which are also exhibited by some cheirogaleids. These are: less rotation of the medial malleolus and less curvature of the ATiL, ATiM, and AFi joints, a high radius of curvature at the UAJ causing the formation of a high astragalar body; relatively long pAC(C) facets; a laterally flattened AN joint with a proximally extensive cup on the navicular; the suite of features at the navicular-cuneiform joints; the lateral shift of the CuN joint which leads to reduction or loss of CuMe contact; lengthened distal calcaneus and navicular. These are probably all primitive non-*Cheirogaleus* lorisoid features, but galagines usually exhibit a more exaggerated form of these features than do *Microcebus* or *Phaner*.

These features of galagines are all adaptations to frequent leaping. The elongated calcaneus and navicular serve to increase the distance between the flexed and extended positions of the leg. It is this variable that partly determines take-off velocity and thus the maximum distance of a leap. However, the increased length of the foot can only be added to that of the leg if flexion within the foot is allowed; the morphology of the navicular-cuneiform articulation increases flexion in the midfoot. The features of the UAJ provide stability for this joint by decreasing conjunct and concomitant rotations. The transverse arch of galagines is flattened by the repositioning of the NCu joint and the sellar shaped form of this joint bolsters the midtarsal region against shearing forces which would probably occur in leaping. The AN is most congruent (and thus stable) in the everted position. The galagine foot is thus well adapted for resisting stresses in an everted, plantigrade position.

However, galagines still maintain the ability to invert the foot at the TTJ. The CCu joint is deep and its centrally placed pivot assures almost pure rotational movements without the conjunct abduction and adduction which accompany CCu motion in other strepsirhines. It is undesirable, however, for the long footed galagines to have much subtalar motion (Hall-Craggs, 1966) due to the concomitant flexion and extension which occur at this joint. The great overlap of the components of the STJ assures that little motion will take place. This necessitates the development of the CN joint to allow the navicular to rotate around the stationary calcaneus.

Among galagines the most distinct taxa are *Otolemur* and *Galago elegantulus*. *Otolemur* is distinctive in having a less elongate distal calcaneus and navicular, a slightly lower ATiL length/STL index, a higher degree of tibial malleolar rotation, a higher ATiL(Ti) AP/ML index, a lower astragalar body, a lower pAC(C) arc, and a higher pAC offset angle. These are features which suggest a less extreme morphological adaptation for leaping in *Otolemur* than in other galagines. *Otolemur* does leap less often than other galagos (Crompton, 1984), probably partly as a result of its large body size. *Otolemur garnetii* is more like other galagos than *O. crassicaudatus*; this corresponds well to the fact that *O. garnetti* is smaller and leaps more often than *O. crassicaudatus* (Harcourt and Nash, in press).

G. elegantulus differs from other galagines (except *Otolemur*) in the same ways, but this is not explicable in terms of larger body size or less frequent leaping, since it weighs only 300 grams and leaps fairly often (Charles-Dominique, 1974). It may well be the most primitive living galago, since it is the only one to maintain any remnant of the posterior trochlear shelf.

XV. Lorisinae (Node T). Lorisines have departed greatly from the primitve lorisoid emphasis on leaping locomotion. They are the only living prosimians which have never been observed to leap. The postcranial characters which define the members of the Lorisinae are reflections of their slow climbing mode of locomotion.

At the UAJ conjunct and concomitant motions which facilitate the variable foot orientations useful for climbing are greater curvature at the ATiM and ATiL joints, and a more laterally flaring AFi joint. The radius of curvature at this joint is low, and there is probably less UAJ motion than in other strepsirhines. As demonstrated by Grand (1967) the lorisine foot is set in an inverted position. The more marked plantar medial angle of the STJ, the strong dorsomedial orientation of the AN joint and the CCU joint, and the lateral rotation of the cuboid contribue to this orientation of the tarsus, which is very stable in inversion, but unstable in eversion. The AN joint is a modified ovoid which does not allow free rotation, but the CCu joint is very deep, providing both stability and mobility. CuN motion may be possible in lorisines; the facet is relatively much larger in lorisines than in other strepsirhines.

The navicular-cuneiform joints are small and flat, allowing very little motion. The more medial position of the NEn and NMe joints and the transverse orientation of the NEn and NEc joints increase the breadth of the grasp in lorisines. The greatest phenetic similarity of the distal navicular facets of lorisines is with lemuroid primates. However, the very small NMe(N) articulation, the fact that there is sometimes a small non-articular gap between the NMe(N) and NEn(N) facets, and the lack of cuboid-mesocuneiform contact in some lorisines are small clues that distal navicular morphology of lorisines may be derived from that of galagines (or non-Cheirogaleus-cheirogaleids). If this polarity is correct, (and it must be if lorisines are the sister group of galagines), lorisines exhibit a reversal of several distal navicular features [e.g. more dorsal orientation of the NEc(N), more lateral orientation of the CuN(N)].

The relatively short tarsus (Jouffroy and Lessertisseur, 1979) results from shortening of all the tarsal bones; the tarsus is serially arranged.

There are no features of the tarsus which allow clear discrimination among the four genera of lorisine primates.

XVI. Daubentonia. (Node U). The phylogenetic placement of Daubentonia has always been a complex problem given the unusual morphology of this species. Some authors have argued for a great phylogenetic (and taxonomic) separation (e.g. Groves, 1974; Oxnard 1981), while some have cited cranial and dental features supporting derivation of Daubentonia from within the Indriidae (Tattersall and Schwartz 1974; Schwartz and Tattersall, 1985). Eaglen (1980), with some reservations, placed Daubentonia at the base of the lemuroid (my sense) radiation.

The pedal evidence is equally difficult to interpret. *Daubentonia* shares a few special similarities with indriines such as relatively long and narrow pAC facets[1] aligned along the long axis of the bones, a high astragalar body, a high arc length of the UAJ, a serial tarsus, and a fairly short navicular. These traits lend some weak support to the Tattersall and Schwartz (1974) hypothesis. However, if *Daubentonia* is an indriid, it is more likely to be related to subfossil forms like archaeolemurines (Gregory, 1915) or *Paleopropithecus*, which also revert to a more primitive morphology of the CuN articulation (and increase incisor size), than to the extant indriines (contra Tattersall and Schwartz, 1974).

On the other hand, there are numerous ways in which *Daubentonia* is distinctly different from all other lemuroids. *Daubentonia* does not share the distinctive morphology of the tarsometatarsal complex described by Gebo (1985) which is present in all other members of this group (evidence is not available from subfossil lemurs). In *Daubentonia* the CuN(N) facet is not as medially extensive as in other Lemuriformes; it fails to extend under the NMe(N) facet. Like *N. tenebrosus* and *S. gracilis*, but unlike the more derived lemuriformes, *Daubentonia* has an elongate ectocuneiform keel which prevents cuboid-mesocuneiform contact (Decker and Szalay, 1974). The astragalar head is not dorsolaterally oriented as in other lemuroids.

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[1] *Daubentonia*'s facets are long only in relation to a short calcaneus *not* to STL. Relatively long facets are found in adapids and archaeolemurines for the same reason.

Daubentonia thus seems to lack some very basic attributes of the lemuroid and even lemuriform groups. One could always posit a reversion to a more primitive state due to special selective pressures, given the presence of claws in *Daubentonia*. This would probably lessen the need for the specialized grasping features described by Gebo (1985) or the increased folding of the foot afforded by the lemuriform type CuN(N) joint. However, one could just as easily argue that *Daubentonia* developed claws precisely because it (or its ancestor) lacked these other adaptations for dealing with vertical supports.

The pedal evidence thus suggests that *Daubentonia* diverged quite early in the history of strepsirhines, before the divergence of the lemuroids and lorisoids. Any other hypothesis requires several reversals in details of foot structure. The tarsus of *Daubentonia* is in fact very close to my concept of the morphotype strepsirhine tarsus, with the exception of its apomorphic features listed in fig. 67. Other features which support a very primitive position for *Daubentonia* are its large maxillary plate making contact with the frontal, the lack of a frontopalatine suture, lack of ethmoid exposure, large number of turbinals, depth of deep matrix on the claws; these are all interpreted as being more primitive than in any other extant strepsirhine by Groves (1974). Some molecular evidence supports an early divergence (Sarich and Cronin, 1976), while other evidence links *Daubentonia* with lemuroids, but before the split into lemurids and indriids (Dene *et al.*, 1976a,b).

XVII. Summary.

1. The transition from a nonprimate eutherian mammal to the first primate (or archontan) involved morphological changes of the tarsus directed towards allowing the foot to achieve greater ranges of variable spatial orientations. This allowed the animal to deal with the complexities of the structure of an arboreal substrate.

2. The ancestral euprimate developed specializations of the tarsus which indicate that both leaping and grasping were crucial components of locomotion. The influence of leaping is reflected primarily in the morphology of the upper ankle joint (added stability, increased arc of plantarflexion-dorsiflexion, decreased conjunct pronatory-supinatory motions) and in the lengthening of the distal calcaneus. The influence of grasping is reflected in the morphology of the entocuneiform-MTI joint, and possibly in the increased axial rotation at the TTJ. The locomotor behavior (but not all aspects of morphology) of the ancestral euprimate was probably most similar to that of living lemurines.

3. The common ancestor of all strepsirhine primates differed from the euprimate ancestor in the construction of the AFi joint and in the greater degree of arching of the foot in the midddle tarsal region. Both of these features almost certainly reflect the influence of increased body size which also distinguishes early strepsirhines from haplorhines. Both features probably indicate an increase in importance of climbing in the ancestral strepsirhine. The last set of features may indicate that the mechanics of grasping differed in the

two suborders.

4. No feature of the foot can be cited to unite "adapids" into a sister group. The two groups of adapiform primates, notharctines and adapines, differ greatly in foot morphology. The former group has specializations which indicate more frequent leaping; the latter (only members of the Adapini are known) specializations for quadrupedal slow climbing.

5. The tooth combed strepsirhines (Lemuriformes) do not differ greatly in foot structure from the strepsirhine ancestor, but all are more derived than known adapids in increasing the degree of midtarsal folding and distal calcaneal elongation.

6. The lemuriform primates can be divided into lemuroids (lemurids and indriids) and lorisoids (cheirogaleids and lorisids). The lemuroids are united by modifications of the tarsometatarsal and astragalonavicular joints which reflect large body size and increased use of vertical supports. The lemurids are very conservative in all other features, but the indriines are quite derived. Extant indriines show some modifications of the upper ankle joint and subtalar joint which indicate more frequent leaping than in lemurids, but many other specializations are mechanically related to climbing. Very few features of the foot can clearly be related to vertical clinging.

Archaeolemur has a very derived foot which shows few similarities to indriines (or any other strepsirhine). *Lepilemur*, on the other hand, while not being overtly very similar to indriines, does share quite a number of derived pedal features with this group, which are probably synapomorphies.

7. No derived postcranial features are shared by all lorisoids. Except for Cheirogaleus, the most primitive member of this group, and lorisines (the most derived) all lorisoids share increased relative length of the distal calcaneus, navicular, and cuboid, a complex of features allowing increased flexion at the navicular-cuneiform joints, and a laterally oriented navicular-cuboid joint, all of which are mechanically advantageous for leaping. Lorisines, of course do not share these traits, but do have a few features of the foot confirming the relationship with galagines suggested by cranial evidence.

8. Galagines preserve the basic foot morphology which probably first evolved in the non-Cheirogaleus cheirogaleids and have exaggerated the ancestral leaping specializations, in keeping with their generally more frequent use of leaping in their locomotion.

9. Lorisines depart substantially from other strepsirhines in their very short tarsus and inverted set of the foot. They have become committed to a mode of locomotion in which climbing is predominant.

10. Daubentonia lacks derived features of foot structure present in lemuroids and lemuriformes, suggesting that it diverged early in the history of strepsirhines. The evidence linking it with indriids is very weak.

Table 27. Relative length of the distal calcaneus (load arm) in strepsirhine primates. [C1-(C7+C4)]/C1*100.

TAXON	MEAN	SD
	RANGE	N
Lemur fulvus	44.06	3.74
	38.58-55.60	20
Lemur mongoz	47.83	1.11
	47.03-49.79	5
Lemur macaco	44.64	-
	42.24-46.06	3
Lemur rubriventer	46.88	-
	-	1
Lemur coronatus	49.30	-
	47.39-52.97	3
Lemur catta	44.72	2.13
	41.99-49.20	10
Varecia variegata	41.26	2.80
	35.47-46.23	12
Hapalemur griseus	46.89	1.64
	43.01-48.62	11
Hapalemur simus	46.96	-
	-	1
Lepilemur mustelinus	48.38	1.69
	45.99-50.76	12
Daubentonia madagascariensis	44.39	2.07
	42.49-46.44	5
Avahi laniger	40.99	4.40
	34.57-49.76	10
Propithecus verreauxi	43.68	2.29
	41.13-46.84	6
Propithecus diadema	45.78	2.26
	42.45-50.46	11

continued

Table 27, continued.

TAXON	MEAN	SD
	RANGE	N
Indri indri	44.30	3.52
	37.84-49.45	11
Microcebus murinus	63.99	2.88
	56.25-67.35	14
Mirza coquereli	53.89	-
	53.18-54.60	2
Cheirogaleus medius	49.99	2.30
	46.46-52.34	5
Cheirogaleus major	47.85	1.86
	46.10-50.00	5
Phaner furcifer	59.18	-
	-	1
Progalago songhorensis	48.90	-
	-	1
Komba robustus	46.72	-
	-	1
Komba minor	53.10	-
	-	1
Galago senegalensis	72.36	2.01
	70.55-76.21	6
Galago moholi	72.46	.79
	71.14-73.21	9
Galago gallarum	75.00	-
	-	1
Galago elegantulus	65.41	2.09
	63.00-71.93	16
Galago matschei	72.12	-
	-	1
Galagoides demidoff	77.20	1.31
	75.12-78.57	8

continued

Table 27, continued.

TAXON	MEAN	SD
	RANGE	N
Galagoides	72.87	-
zanzibaricus	-	1
Galagoides	70.66	2.22
alleni	68.53-74.39	5
Otolemur	64.15	1.00
crassicaudatus	62.71-65.40	6
Otolemur	65.80	2.10
garnetti	63.50-67.53	3
Perodicticus	38.94	4.59
potto	32.26-46.31	15
Arctocebus	43.42	16.5
calabarensis	41.18-45.74	11
Nycticebus	38.87	4.49
coucang	31.75-46.81	12
Loris	47.70	5.44
tardigradus	39.79-55.24	6
Adapis	32.30	3.00
parisiensis	28.14-40.74	19
Leptadapis	31.31	3.50
magnus	27.84-38.15	13
Caenopithecus	36.00	-
lemuroides	-	1
Cantius	39.45	-
trigonodus	-	1
Cantius	37.23	-
?*venticolis*	-	1
Smilodectes	39.69	-
gracilis	38.82-40.55	2
Notharctus	40.75	1.30
sp.	38.91-42.01	6

Table 28. A summary of features of morphotypes of major taxa discussed in this study.

FEATURE	EUTHERIA	PRIMATES	EUPRIMATES
Calcaneofibular contact	yes	no	no
body of astragalus	shallow, lateral crest higher	deep laterally, lateral crest higher	deep both medially and laterally, crests equal in height
length of ATiL(A)	short	long	long
ATiM(A) ATiL(A)	not curved	not curved	moderately curved
ATiM(Ti)	flat, faces laterally	flat, faces laterally	curved, faces 30-40 from sagittal plane
AFi(A)	not sloping	not sloping	not sloping
fl. fibularis groove	shallow	deep	deep
posterior trochelar shelf	absent	absent	present
pAC(A) pAC(C)	short, aligned oblique to long axes of bones	long, aligned parallel to long axes of bones	long, aligned parallel to long axes of bones
aAC(A) aAC(C)	short	long	long
aAC(A)	separate from AN(A) + spring ligament facets	confluent with AN(A) + spring ligament facets	confluent with AN(A) + spring ligament facets

continued

Table 28, continued

FEATURE	EUTHERIA	PRIMATES	EUPRIMATES
AN	dorsolateral orientation, lateral side greater than medial side	dorsomedial orientation, medial side greater than lateral side	dorsomedial orientation, lateral side = medial side
CCu	oblique to long axis of calcaneus, oblate outline	perpendicular to long axis of calcaneus, circular outline	perpendicular to long axis of calcaneus, pivot type articulation
CuN	CuN(N) lateral to NEc(N)	?CuN(N) lateral to NEc(N)	CuN(N) lateral to NEc(N)
EnMT1	ovoid, non-opposable	?	sellar joint, opposable
length of tarsals	short	short	long
relative length of load arm of calcaneus	35.00	35.00	40.00
functional axis of foot	mesaxony	?mesaxony	?ectaxony
claws	claws	claws	nails
toilet claw on digit 2	no	?	?yes

continued

Table 28, continued

FEATURE	STREPSIRHINI	LEMURIFORMES
Calcaneofibular contact	no	no
body of astragalus	deep both medially and laterally, crests equal in height	deep both medially and laterally, crests equal in height
length of ATiL(A)	long	long
ATiM(A) ATiL(A)	moderately curved	strongly curved
ATiM(Ti)	curved, faces 30-40 from sagittal plane	curved, faces 30-40 from sagittal plane
AFi(A)	gently and gradually flared	gently and gradually flared
fl. fibularis groove	deep	deep
posterior trochlear shelf	present	present
pAC(A) pAC(C)	long, aligned parallel to long axes of bones	long, aligned parallel to long axes of bones
aAC(A) aAC(C)	long	long
aAC(A)	confluent with AN(A) and spring ligament facets	confluent with AN(A) and spring ligament facets
AN	dorsomedial orientation, lateral side = medial side	dorsomedial orientation, lateral side = medial side
CCu	perpendicular to long axis of calcaneus, pivot type articulation	perpendicular to long axis of calcaneus, pivot type articulation

continued

Table 28, continued.

FEATURE	STREPSIRHINI	LEMURIFORMES
CuN	CuN(N) plantad to NEc(N) and NMe(N)	CuN(N) plantad to NEc(N) and NMe(N)
EnMT1	sellar joint, opposable	sellar joint, opposable
length of tarsals	long	long
relative length of load arm of calcaneus	40.00	45.00
functional axis of foot	ectaxony	ectaxony
claws	nails	nails
toilet claw on digit two	yes	yes

Table 29. A summary of features of the foot in extant lemuriform primates discussed in this chapter. The condition of the trait which is primitive for lemuriform primates is given in column 1. Derived conditions for these features are listed under the appropriate taxon. Blanks indicate that the taxon at the head of the column does not differ from the primitive lemuriform condition.

LEMURIFORMES	LEMURIDAE	INDRIINAE	DAUBENTONIA
ATiM and ATiL moderately curved		less curved	less curved
UAJ angle 175			
posterior trochlear shelf large, not twisted		very large, twisted	
pAC facets slightly oblique to long axes of bones		more parallel to long axes of bones	more parallel to long axes of bones
pAC(C) angle moderate			
aAC(A) horizontal		plantarly bent	
CCu-moderate pivot		reduce pivot	
AN joint spherical		more spherical	
AN dorsomedial orientation	dorsolateral	dorsolateral	
CuN ovoid		sellar	
CuMe contact present		very large	absent
navicular-cuneiform joints primitive (see text)			

continued

Table 29, continued.

LEMURIFORMES	LEMURIDAE	INDRIINAE	DAUBENTONIA
tarsometatarsal joint and adductor hallucis primitive (see text)	derived (see text)	derived (see text)	
tarsus relatively long		short	short
relative length of load arm of calcaneus 45.00			

continued

Table 29, continued.

LEMURIFORMES	CHEIROGALEIDAE	GALAGINAE	LORISINAE
ATiM and ATiL moderately curved	less curved*	less curved	more curved
UAJ angle 175	180*	180	154
posterior trochlear shelf large, not twisted		absent	absent
pAC facets slightly oblique to long axis of bones			more oblique
pAC angle moderate			higher
aAC(A) horizontal			
CCu moderate pivot		large pivot	large pivot
AN joint spherical		laterally flattened	dorso-plantarly constricted
AN dorsomedial orientation			strongly dorsomedial
CuN ovoid	sellar*	sellar	
CuMe contact present	lost in some	lost	lost in some
navicular-cuneiform joints	derived, see text*	derived, see text	derived, see text
tarsometatarsal joints and adductor hallucis primitive (see text)			
tarsus relatively long	longer*	very long	short

*Except *Cheirogaleus*, which has the primitive condition.

continued

Table 29, continued.

LEMURIFORMES	CHEIROGALEIDAE	GALAGINAE	LORISINAE
relative length of load arm of calcaneus 45.00	45.00-60.00	65.00-75.00	35.00-40.00

Figure 67. Hypothesis of relationships in primates based mainly on features of the foot discussed in this work. Only synapomorphies of nodes are listed below, not the complete morphotype.

Node A: Archonta
loss of calcaneofibular contact
body of astragalus deepens laterally
increased length and thus relative narrowness ATi(L)A
pAC facets are longer and more closely aligned to the long axes of the astragalus and calcaneus
aAC facets are longer, more helically shaped, and tend to become confluent with the AN and spring ligament facets
AN joint dorsomedially oriented, larger on medial than lateral side
CCu joint aligned more perpendicular to the long axis of the calcaneus, more circular in outline

Node B: Primates
larger groove for flexor fibularis muscle

Node C: Plesiadapiformes
no differences from Node B.

Node D: Euprimates
medial and lateral crests of ATiL(A) are equal in height
body of astragalus deepens both laterally and medially
posterior trochlear shelf moderately developed
depth of the trochlea increases
elongation of tarsal bones (astragalar neck, distal part of calcaneus, navicular, cuboid)
ATiM(Ti), ATiM(A), ATiL(A) moderately medially rotated
more nearly spherical AN joint
develop sellar CCu joint (pivot joint)
reduction and more proximal placement of peroneal tubercle
sellar En-MT1 joint
enlarged hallux
claws replaced by nails
?ectaxony
?toilet claw on digit two

Node E: Strepsirhini
large amount of lateral flare and gentle slope of AFi(A)
CuN(N) facet is related to the NMe(N) and NEc(N) facets
separateness and greater curvature of navicular-cuneiform facets
?ectaxony
?toilet claw on second digit

continued

Node F: Notharctinae
- reduce medial rotation of ATiM(A) and ATiL(A) facets
- increase size of the posterior trochlear shelf
- elongate pAC facets

Node G: Adapini (Adapinae unknown)
- increase medial rotation of ATiM(A) and ATiL(A)
- increase relative length of ATiL(A)
- decrease height of astragalus
- short astragalar neck
- short distal calcaneus
- reduce/lose posterior trochlear shelf

Node H: Lemuriformes
- increase medial rotation of ATiM(A) and ATi(L)A
- increase medial extent of CuN joint so that it lies under the NMe(N) joint
- reduce plantar keel on ectocuneiform; mesocuneiform contacts cuboid

Node I: Lemuroidea
- reorientation of tarsometatarsal joint
- moderate to strong dorsolateral orientation of astragalar head

Node J: Indriidae (no pedal synapomorphies)

Node K: Indriinae
- large, plantarly twisted posterior trochlear shelf
- pAC facets elongate, and are more nearly parallel to the long axes of the astragalus and calcaneus
- more spherical AN(A)
- higher, flatter CCu(C)
- plantarly bent aAC facet
- CuN more sellar shaped
- CuMe contact expanded
- serial tarsus
- relatively short tarsus

Node L: Archaeolemurinae
- large proximolateral tubercle on calcaneus
- short, flat pAC facets
- short distal calcaneus
- lose medial extension of CuN(N)

Node M: Lemuridae
- no distinctions from Node H

continued

Node N: *Lepilemur*
(all of these features are shared with indriines)
reduce ATiM(A) and ATiL(A) curvatures
less rotation of tibial malleolus
high astragalar body
long UAJ arc
large CuMe articulation
CuN more sellar shaped
strong dorsolateral orientation of astragalar head
plantarly bent aAC facet

Node O: *Megaladapis*
lose posterior trochlear shelf
ATiL(A) and ATiM(A) highly curved
ATiL(A) long relative to astragalar length
ATiM(A) dorsoplantarly short
highly flared, but short AFi(A)
low angle of UAJ
dorsomedial orientation of astragalar head
dorsoplantarly constricted AN(A)
short, flat pAC(A)
laterally restricted aAC(A)
short astragalar neck

Node P: Lorisoidea
slight exaggeration of dorsomedial tilt of astragalar head

Node Q: Cheirogaleidae
no pedal synapomorphies

Node R: Lorisidae
deep C-Cu joint
lose posterior trochlear shelf

Node S: Galaginae
develop C-N synovial articulation
highly sellar CuN joint
high pAC(C) arc

(all characters below this line are also shared with *Mirza*, *Microcebus*, and *Phaner*)
elongate distal calcaneus
elongate navicular
CuN facet shifts laterally; is plantarlateral to NEc(N); loses most contact with NMe(N)
NEc(N) surface enlarges, rotates laterally to lie dorsal to NMe(N); NMe(N) small, plantarly restricted, but highly curved; NEn(N) highly curved; small non-articular gap between NEn(N) and NMe(N) facets.

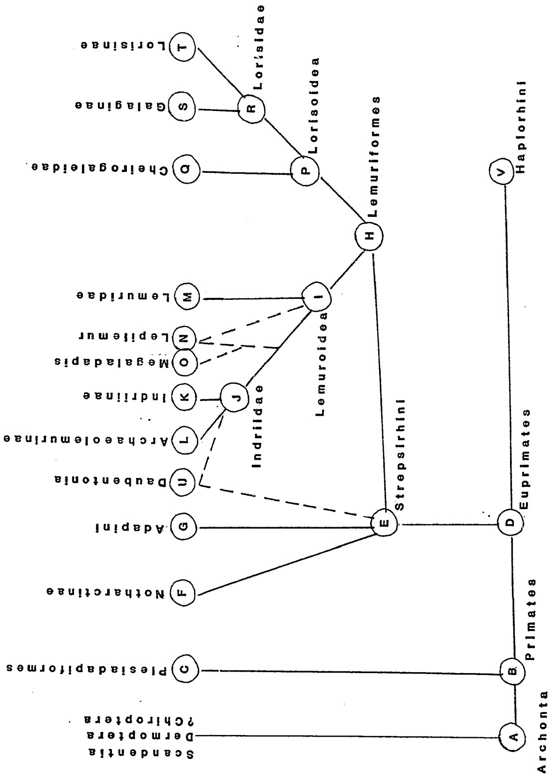
continued

Node S: Galaginae (continued)
lose Cu-Me contact
AN(A) flattened laterally
AN(N) proximally extensive

Node T: Lorisinae
shorten cuboid and navicular
shorten distal calcaneus
short ATiL(A)
low astragalar body
strongly medially rotated ATiL(A) and ATiM(A)
large degree of lateral flare of AFi(A)
lower UAJ arc of curvature; lower length of arc
more marked medial angle of STJ
high cuboid angle
serial tarsus
dorsoplantarly flattened AN(A)
strong dorsomedial orientation of astragalar head
flat navicular-cuneiform facets
NEc facet mediolaterally narrow, horizontally oriented
NEn very flat, elongate mediolaterally and compressed dorsoplantarly, horizontally oriented

Node U: *Daubentonia*
flat ATiL(A)
wedged ATiL(A)
dorsoplantarly flattened A-N(A)
NEc(N) more medially extensive
NEn(N) more horizontally oriented, wraps around medial edge of navicular

Node V: Haplorhini
reduce rotation of medial malleolus
only anterior ATiM(Ti) is medially rotated
ATiM(A) less concave, less cupped
ATiL(A) does not curve medially
inferior tibiofibular joint relatively rigid
reduce/lose posterior trochlear shelf


Scandentia
Dermoptera
?Chiroptera
A
Archonta
B
Primates
C
Plesiadapiformes
D
Euprimates
E
Strepsirhini
F
Notharctinae
G
Adapini
U
Daubentonia
L
Archaeolemurinae
K
Indriinae
J
Indriidae
O
Megaladapis
N
Lepilemur
M
Lemuridae
I
Lemuroidea
H
Lemuriformes
P
Lorisoidea
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Cheirogaleidae
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Lorisidae
S
Galaginae
T
Lorisinae
V
Haplorhini

Figure 67

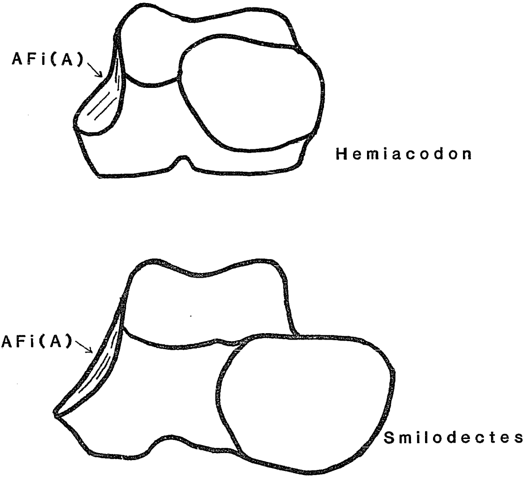


Figure 68. Shape of AFi(A) in haplorhines (top, represented by *Hemiacodon gracilis*) and strepsirhines (bottom, represented by *Smilodectes gracilis*). Arrow points to AFi(A) facet.

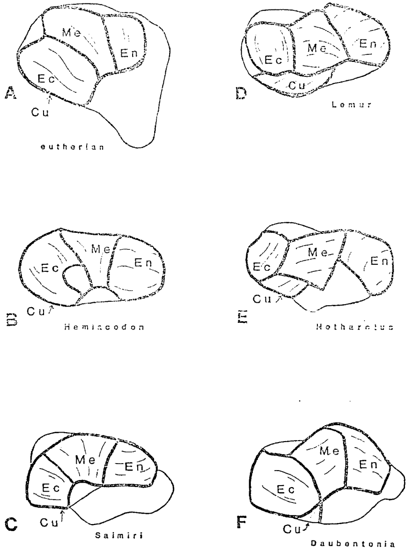


Figure 69. Distal view of navicular showing navicular-cuneiform facets and position of CuN(N) facet in A, most eutherians, represented by *Protictis*, an Eocene carnivoran; B, *Hemiacodon gracilis*; C, *Saimiri*; D, *Lemur fulvus*; E, *Notharctus*; F, *Daubentonia*.

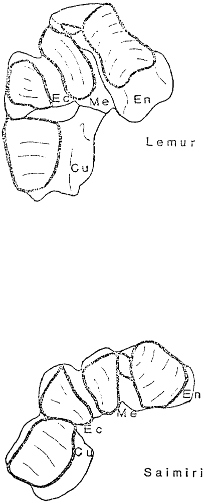
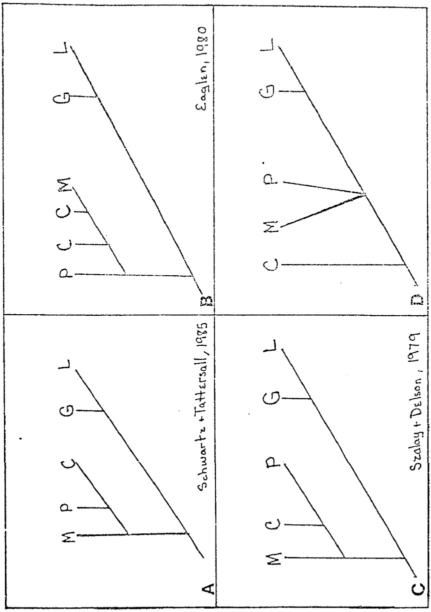


Figure 70. Distal view of cuboid and cuneiforms in *Lemur fulvus* (top) and *Saimiri* (bottom). Note Me-Cu contact in *Lemur*.

Figure 71. Hypotheses of lorisoid relationships. M, *Microcebus*; P, *Phaner*; C, *Cheirogaleus*; G, galagines; L, lorisines.



CHAPTER 11: SUMMARY

The purpose of this project is to analyze the functional, adaptive, and phylogenetic aspects of the tarsal joints in extant and extinct strepsirhine primates. Joint surfaces are described in terms of their linear dimensions, radius and degree of curvature, their placement relative to reference axes of the foot, their placement in the MacConaill joint classification system, and other nonmetrical aspects of form. The functional (in the sense of mechanical) attributes of joint surfaces are analyzed based on these components of form. Thus, the kinds and range of motion(s) allowed, the degrees of freedom, and the relative displacement of the foot or parts of the foot after motion at the joint are described.

An attempt is made to relate form-function complexes of joints to particular aspects of positional behavior. This is done by comparing the distribution of such traits with the distribution of differences in presence or frequency of positional behaviors. But, however suggestive these lines of evidence may be, the hypothesis of a relationship between a morphological feature and an aspect of positional behavior is considered weak unless the functions deriving from the form of the feature allow the organism to fulfill the selective demands of the behavior. Causal arguments are the only valid tests of these kinds of hypotheses.

The behaviors which seem to have the most impact on the form of the tarsus are, not surprisingly, leaping, climbing, and grasping. Strepsirhines in which leaping is the most frequent aspect of locomotor behavior (indriines, *Lepilemur*, galagines, non-*Cheirogaleus* cheirogaleids) increase stability at the upper ankle joint by reducing curvatures of the surfaces of the components of the upper ankle joint thus reducing the degree of conjunct and concomitant rotations occurring at this joint. Dorsiflexion and plantarflexion are restricted to a more purely sagittal plane. The range of motion is increased by a larger angle of curvature at the upper ankle joint (except in indriines). Leapers also have a higher radius of curvature at the upper ankle joint, but the significance of this is unclear. Due to these features, the body of the astragalus is high and short. Frequent leapers increase the length of the posterior astragalo-calcaneal articulation, but also reduce motion at this joint by increasing the overlap between the articulating surfaces. This stabilizes the subtalar joint, but necessitates reorganization of the transverse tarsal joint if rotation of the fore part of the foot (necessary for grasping) is to be maintained. Leapers tend to lengthen the elements of the tarsus; this trend reaches an extreme in galagines.

As climbing increases in frequency and importance one sees the opposite cline in the trends discussed above. The curvatures of the surfaces of the upper ankle joint increase, increasing the degree of conjunct and concomitant rotations at this joint, allowing greater variability in foot posture and placement on the support. Lorisines, which exhibit the most exaggerated form of these conditions, additionally have a very low radius of curvature and angle of the upper ankle joint, and a short tibioastragalar facet compared to skeletal trunk length. The body of the astragalus thus appears to be long and low. Motion at the subtalar joint allows for repositioning of the fore part of the tarsus into inversion and eversion. The range of motion is extreme in lorisines, due to a small overlap between the apposing surfaces, but the joint is stable only in the inverted position. The bones of the tarsus are short.

It thus seems that leaping and climbing exert opposing selective forces leading to antithetical morphological adaptations at the upper ankle joint and subtalar joint. Both behaviors, however, are performed by all extant strepsirhines except lorisines, thus some compromise solutions exist. Indriines, for example, conform to the expectations of leaping at these two joints, but modify the transverse tarsal joint and intertarsal articulations in ways which increase motion and thus facilitate the variable orientations of the distal foot which are necessary for climbing. Unlike indriines, galagines modify the transverse tarsal joint to increase stability (in an everted posiiton), not mobility. In order to allow repositioning of the digits in climbing and grasping galagines develop a synovial articulation between the calcaneus and navicular which permits rotation of the distal tarsus without motion at the subtalar joint. The galagine foot is also characterized by an extremely stable and reoriented calcaneonavicular articulation which flattens and stabilizes the midtarsus. The naviculocuneiform joints are highly modified to allow a great deal of flexion at the tarsometatarsal joint, which allows the lengthened proximal part of the foot to function as part of the leg in leaping. The differences in foot structure between galagines and indriines are most likely due to the influence of body size and the fact that they have convergently adopted vertical clinging and leaping as their mode of locomotion. It is extremely difficult to identify any morphological features of the foot which are clearly functionally related to the vertical clinging posture in either galagines or indriines.

The influence of grapsing on the tarsus is directly evidenced in the saddle form of the entocuneiform-metatarsal 1 articulation, and more indirectly in the subtalar and transverse tarsal joints, which must be able to allow abduction and inversion of the foot for correct placement of the digits. Except in galagines and indriines, the long, anteroposteriorly oriented subtalar joint in strepsirhines permits the lamina pedis to reorient relative to the astragalus and leg. The ovoid form of the astragalonavicular joint and the "pivot" (sellar) articulation at the calcaneocuboid joint allow a great deal of pronation and supination at the transverse tarsal joint, but are also very stable. Another character complex which is probably related to grasping is the morphology of the joints of the midtarsus. Most strepsirhines have a highly arched midtarsal region in which the cuboid makes broad contact with the navicular. This reorients the naviculocuboid joint medially so that it lies plantad to the naviculoentocuneiform and naviculomesocuneiform articulations. This, plus the reduction of the ectocuneiform keel, allows cuboid-mesocuneiform contact in lemuriforms. The galagines (and non-*Cheirogaleus* cheirogaleids) reverse some of these conditions to flatten out the midtarsal region. In archaeolemurines the naviculocuboid facet does not contact the naviculomesocuneiform joint; the midtarsal arch is probably flatter in these terrestrially adapted species. *Daubentonia* is the only Malagasy strepsirhine which has none of these features (except for the more medial placement of the naviculocuboid joint); it is most similar to *Notharctus* in this regard.

The known notharctine primates (*Cantius*, *Notharctus*, and *Smilodectes*) are generally most like the extant lemurids in tarsal morphology, although they exhibit some features of the upper ankle joint which suggest that they were more frequent leapers than lemurids (but the load arm of the calcaneus is not very elongate). There are several features shared with indriines, but no feature of the foot strongly suggests vertical clinging in these primates, although limb proportions and elbow joint morphology imply this possibility. The range of variation in foot structure in notharctines is small; it is similar to that of extant lemurids. The most distinct taxon is a species of *Cantius* (or possibly *Pelycodus*) from the Wind River formation which has a relatively long calcaneal tuber.

Two morphologies are represented in adapine primates. An unallocated specimen from the middle Eocene of Messel resembles the contemporaneous notharctines (and thus lemurids) more than the later Eocene European adapids (only members of the Adapini are known), but cannot be clearly linked to either group. *Adapis parisiensis*, *Leptadapis magnus*, and *Caenopithecus lemuroides* have features of the upper ankle joint and foot proportions which suggest that quadrupedal slow climbing was the dominant form of locomotion. For *Adapis* and *Leptadapis* this hypothesis is strongly confirmed by other features of the postcranium.

Among the subfossil lemurs, *Varecia insignis*, archaeolemurines, *Daubentonia robusta*, *Megaladapis*, and possibly *Mesopropithecus* are represented by foot bones. *V. insignis* differs from its extant congener in its greater size and robusticity; relatively shorter foot bones; small range of motion at the subtalar joint; and expanded proximolateral tubercle of the calcaneus. These features, along with other aspects of the postcranium, indicate that leaping could not have been efficiently practiced, and that *V. insignis* may have utilized the terrestrial substrate more than extant lemurids.

Archaeolemurines (it is impossible to confidently assign bones to the species of *Archaeolemur* or *Hadropithecus*) exhibit an even greater commitment to terrestriality. In the foot this is evidenced by a small range of motion at the subtalar joint; very large proximolateral tubercle on the calcaneus; expanded Achilles tendon insertion, and a reduced hallux. The tarsus appears to have been more stable in everted than inverted positions.

A calcaneus and navicular can be reasonably surely assigned to *D. robusta*. These bones are not significantly different from extant *Daubentonia* except in calcaneal proportions and in the development of a moderate proximolateral tubercle on the calcaneus. The astragalus Lamberton attributed to *D. robusta* resembles indriines much more than *Daubentonia* and may in fact belong to *Mesopropithecus*. If it is indeed *Mesopropithecus*, this animal differs from extant indriines in ways which suggest that it was not a frequent leaper; this hypothesis is supported by other aspects of its postcranium.

Only the astragalus of *Megaladapis* was studied. It shares many features with the extant lorisines, supporting a hypothesis that some sort of climbing was the predominant mode of locomotion.

A phylogenetic analysis of the tarsus corroborates generally accepted hypotheses of primate and strepsirhine relationships. Strepsirhines and haplorhines are united into a monophyletic taxon Euprimates since they share several derived characters of the upper ankle joint, transverse tarsal joint, and entocuneiform-metatarsal 1 joint, in addition to other features like nails and elongate tarsal bones. The ancestral euprimate was most likely to have been an accomplished leaper and grasper. Two synapomorphies of strepsirhines (adapiforms and lemuriforms) are identified: one is a gradual and gentle lateral flare of the astragalofibular joint; the other is the more medial placement of the naviculocuboid joint so that it lies plantad to the naviculoectocuneiform or naviculomesocuneiform articulation, rather than lateral to the naviculoectocuneiform joint. Both features are most likely the result of selective pressures for climbing and/or grasping in large animals. No feature of the foot is exclusively shared by notharctine and adapine primates; the concept of a taxon Adapiformes is not supported by any postcranial evidence. Links between specific adapid taxa and specific lemuriform taxa are not supported by any evdience from the foot or postcranium.

The only differences in foot structure between adapiforms and tooth combed strepsirhines are a slightly increased degree of lengthening of the distal calcaneus, and a greater degree of midtarsal folding leading to cuboid-mesocuneiform contact. The extant and subfossil lemuriforms can be divided into two distinct monophyletic groups. The lemuroids (lemurids and indriids) are united by modifications of the tarsometatarsal and astragalonavicular joints which are related to large body size and increased use of vertical supports. The lorisoids (cheirogaleids and lorisids) are not defined by any postcranial synapomorphies.

Within the lemuroids, the indriines are the most derived extant group, and have a foot which morphologically is an interesting compromise between the demands of leaping and climbing. *Lepilemur* shares some pedal features with the indriines implying that it may be an early derivative from this group, and not a lemurid. Except for *Cheirogaleus* and lorisines, all lorisoids share modifications of the naviculocuneiform and naviculocuboid joints and extreme tarsal lengthening which are interpreted as adaptations for frequent leaping. These features imply a much closer relationship between *Microcebus*, *Mirza*, *Phaner*, and galagines than is reflected in current classifications of strepsirhines. The differences in foot structure between galagines and these cheirogaleids are more of degree than of kind. The only features separating them are the excessive lengthening of the tarsals and the synovial naviculocalcaneal joint in galagines. Lorisines depart substantially from other strepsirhines in their very short tarsus and inverted set of the foot. If they are indeed the sister group of galagines, as cranial, dental, and even some postcranial evidence suggests, the changes and reversals in foot structure that have taken place are remarkable.

As in most other analyses of the relationships of strepsirhines, the placement of *Daubentonia* presents the greatest problem. It lacks derived features of foot structure which are present in all other lemuroids and lemuriforms, suggesting that it diverged very early in the history of strepsirhines. If *Daubentonia* does prove to be a lemuriform primate, its closest ties are likely to be with the subfossil indriids, the only other group of strepsirhines which have lost some (but not all) of these diagnostic features.

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