INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

Bell & Howell Information and Learning
300 North Zeeb Road, Ann Arbor, MI 48106-1346 USA
800-521-0600

UMI®

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

A

THE FUNCTIONAL MORPHOLOGY OF THE POSTCRANIUM OF *PTILOCERCUS* AND TUPAIINES (SCANDENTIA, TUPAIIDAE): IMPLICATIONS FOR THE RELATIONSHIPS OF PRIMATES AND OTHER ARCHONTAN MAMMALS

by

ERIC J. SARGIS

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

2000

Bell & Howell Information and Learning Company
300 North Zeeb Road
P.O. Box 1346
Ann Arbor, MI 48106-1346

This manuscript has been read and accepted for the Graduate Faculty in Anthropology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

8/11/00
Date

Chair of Examining Committee

8/11/00
Date

Executive Officer

Dr. Eric Delson

Dr. John H. Wahlert

Dr. Richard L. Cifelli

Supervisory Committee

The City University of New York

Abstract

THE FUNCTIONAL MORPHOLOGY OF THE POSTCRANIUM OF *PTILOCERCUS* AND TUPAIINES (SCANDENTIA, TUPAIIDAE): IMPLICATIONS FOR THE RELATIONSHIPS OF PRIMATES AND OTHER ARCHONTAN MAMMALS

by

Eric J. Sargis

Advisor: Professor Frederick S. Szalay

In this study, the postcranial morphology of tupaiids was analyzed from both a functional and phylogenetic perspective. The grasping behavior of some tupaiids was also investigated, and *Tupaia minor* was frequently observed grasping. Arboreal tupaiids, such as *Ptilocercus* and *T. minor*, may represent better models for early primates than didelphid marsupials because they are capable of grasping and are more closely related to primates.

The axial skeleton of *Ptilocercus* exhibits adaptations for a stable thorax that may facilitate bridging locomotion. The vertebral columns of tupaiines are more mobile and allow more flexion and extension of the spine; this increases stride length, which increases speed in bounding mammals like terrestrial tupaiines. The attributes of *Ptilocercus*' thorax are probably primitive for Tupaiidae and the ancestral tupaiid was likely arboreal, whereas the tupaiine condition is derived and the ancestral tupaiine was likely terrestrial. *Ptilocercus* may also be primitive for Archonta, and a stable thorax may have first evolved in an arboreal ancestral archontan. The adaptations for stability of the thorax were retained in volitantians, and a mobile thorax likely evolved in conjunction with the shift to graspleaping in the ancestral euprimate.

The limbs of *Ptilocercus* are more adapted for arboreality, while those of tupaiines are more adapted for terrestriality. While *Ptilocercus'* limbs appear to be habitually flexed and exhibit more mobility in their joints, tupaiines are characterized by more extended limbs and more stability in their joints. The latter restricts movements more to the parasagittal plane, which increases the efficiency of terrestrial locomotion. Tupaiine limbs are more adapted for powerful flexion and extension and, consequently, for rapid terrestrial locomotion. Even the most arboreal tupaiines remain similar to their terrestrial relatives, providing strong evidence for the terrestrial ancestry of Tupaiinae.

A character analysis showed that many of Beard's postcranial characters should be interpreted differently when *Ptilocercus* is used to represent Scandentia. This further reduces the evidence for Primatomorpha, which likely represents an unnatural grouping. Alternatively, Volitantia has been corroborated by several other studies. Hence, the sister taxon of Dermoptera is likely Chiroptera, not Primates. The relationships of Scandentia and Primates within Archonta remain unclear.

ACKNOWLEDGEMENTS

For access to specimens, I am grateful to the following people and institutions: Ross MacPhee and Darrin Lunde, Department of Mammalogy, and Mark Norell, Malcolm McKenna, and John Alexander, Department of Vertebrate Paleontology, American Museum of Natural History, New York; Larry Heaney, Bill Stanley, and Michi Solomon, Field Museum of Natural History, Chicago; Richard Thorington and Linda Gordon, National Museum of Natural History, Washington, D.C.; Maria Rutzmoser, Museum of Comparative Zoology at Harvard University, Cambridge; Chris Beard, Carnegie Museum of Natural History, Pittsburgh; Marc Godinot, Christian de Muizon, Pascal Tassy, and Brigitte Senut, Department of Paleontology, and Michel Tranier and Jacques Cuisin, Department of Mammalogy, Muséum National d'Histoire Naturelle, Paris; Paula Jenkins, Natural History Museum, London; Chris Smeenk, Nationaal Natuurhistorisch Museum, Leiden; Louis de Roguin and Albert Keller, Muséum d'Histoire Naturelle, Geneva; Gerhard Storch, Naturmuseum Senckenberg, Frankfurt; Richard Kraft and Michael Hiermeier, Zoologische Staatssammlung, Munich; and Olavi Grönwall, Swedish Museum of Natural History, Stockholm. I wish to further thank Richard Thorington for the use of his imaging equipment in D.C., and I thank Brian Stafford for instructing me how to use this equipment.

I thank Miles Roberts of the Department of Zoological Research at the National Zoological Park in Washington, D.C. for permission to carry out behavioral research on the two tupaiid colonies under his supervision. I also thank Mike Deal of the Department of Zoological Research at the National Zoological Park for his assistance in the animal lab for the entire duration of my research there.

I thank Louise Emmons for providing body weight data on several tupaiid species, as well as for contributing a great deal of information on tupaiid substrate use. I also thank Annette Zitzmann for providing unpublished body weights of *Ptilocercus lowii*, and for sharing information on the locomotor and grasping behavior of this poorly known species. Finally, I thank Larry Heaney for providing unpublished body weights of *Urogale everetti.*

I thank my graduate advisor, Fred Szalay, for his constant support, advice, encouragement, and friendship over the years. His knowledge of mammalian evolution and his continued pursuit of more information on this topic has been an inspiration, and I must thank him for helping to broaden my horizons into the realms of archontan and metatherian biology. From the inception of this project, he has been an invaluable resource particularly insofar as his understanding of evolutionary theory, systematics, and functional morphology is concerned. I can't thank him enough for all his help and guidance over the years. I also thank Eric Delson for the many roles he has served during my graduate career. Eric has been like a co-advisor to me and has provided endless support, encouragement, and assistance. He has never hesitated to help, has always attempted to accommodate my innumerable requests over the years, and has provided numerous helpful comments that have improved this work. Finally, I thank John Wahlert and Rich Cifelli for serving on my dissertation committee and for giving me many helpful suggestions that improved this work.

Several members of the NYCEP faculty have contributed greatly to my graduate education. I would particularly like to thank Fred Szalay, Eric Delson, John Oates, Terry Harrison, and Carl Terranova for teaching me so much over the years. I thank John

Oates for helping me navigate through the politics of CUNY during my early years and for helping me navigate through the bars of the upper east side during my later years. I thank him particularly for his friendship over the years. I thank Tim Bromage for the use of the equipment of the Analytical Microscopy and Imaging Center in Anthropology (AMICA) at Hunter College, which was essential to this study. I thank Terry Harrison for contributing greatly to my understanding of functional morphology, especially during the early part of my graduate education. I also thank both Tim and Terry for serving on my examination committee. I thank Carl Terranova for the many educational debates about allometry vs adaptation when he was a NYCEP postdoctoral fellow (and after). We rarely agreed, but the discussions were always entertaining (as were the venues). I also thank Carl for all of his advice concerning statistics and for his hospitality during my stay in D.C. Finally, I thank my undergraduate advisor, Dan Gebo, for sparking my initial interest in biological anthropology and especially primate postcranial morphology. I also thank him for his constant and continued support during my graduate career. I can't thank him enough for all he has done for me.

Four years of my graduate studies were supported by a graduate fellowship from the New York Consortium in Evolutionary Primatology (NYCEP). During the years when I was not receiving fellowship support, Fred Szalay, Eric Delson, and John Oates always provided me with teaching opportunities at Hunter College and Lehman College. My dissertation research was funded by a Doctoral Dissertation Improvement Grant from the National Science Foundation (SBR-9616194), a Grant-in-Aid of Research from the Sigma Xi Scientific Research Society, and a Visiting Scholarship from the Field Museum

of Natural History. I am grateful to Larry Heaney for sponsoring me for the Field Museum Visiting Scholarship.

I thank all the members of my family who have been so supportive during my graduate years, especially my parents, Donna & Don Peterson and Jim & Bertie Sargis. I thank my brother, Matthew Sargis, for serving as my confidant, as well as for always providing an alternative perspective in our great conversations over the years. I thank the following friends and colleagues for their friendship, assistance, and support during graduate school: Haviva Goldman & Greg Lattanzi, Sebastian Fernandez & Mara Leventhal, John Krigbaum & Wendy Haller, Carl Terranova, Jay O'Sullivan, Katerina Harvati, Steve Frost, Kieran McNulty, Peter Fashing, Michael Yuan, Johanna Warshaw, Shannon McFarlin, Justine Salton, Sam Marquez, and Link Olson.

Finally, I particularly wish to thank my wife, Larissa Swedell, without whom this work could not have been completed. I thank her for her unwavering support, patience, encouragement, and confidence in my abilities. I also thank her for all our great years in New York City. I am happy to dedicate this work in part to her. I also wish to dedicate this in part to my late grandfather, Ned Bostedo, who fostered my initial interest in science, evolutionary biology, and paleontology.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1: BACKGROUND AND INTRODUCTION

"[I]t is certain that the *tree shrews represent a highly important group of mammals*, and, for this reason, *they demand an intensive study from all aspects.*"
Le Gros Clark (1927, p. 255, italics added)

"Among living non-primates the tupaiids are apparently the closest primate relatives, and *these conclusions in no way lessen the value of tupaiids to primatology.*"
McKenna (1966, p. 9, italics added)

"Szalay's interesting argument that the glissant dermopteran and volant chiropteran roles resulted from arboreal adaptation like those of primates and tupaiids requires more detailed comparisons of limb osteology in archontans with that of other eutherians. *This aspect of the skeleton is so much more intensively studied in primates than in most other mammalian groups that it defies an objective basis for comparison.*"
Novacek (1986, p. 73, italics added)

"[A] renewed focus on obtaining additional molecular, neurobiological, cranial, and ***postcranial*** *data from 'key' taxa, including* ***Ptilocercus***, *Cynocephalus*, and a wider range of microchiropteran families, *will lead to a further refinement and possible resolution of hypotheses concerning the superordinal affinities of Primates and other 'archontans'.*"
Luckett (1993, p. 181, italics and bold added)

Tree shrews (Scandentia, Tupaiidae), small bodied (Table 1.1) mammals from South and Southeast Asia, vary in their substrate use from completely arboreal to predominantly terrestrial. While their ordinal status has long been debated, they have long been considered to have close affinities with primates. Despite much recent debate concerning their relationships to primates and other mammals (see volumes edited by Luckett, 1980a, and MacPhee, 1993), the supraordinal relationships of tree shrews remain poorly understood. A better understanding of the evolutionary relationships of tupaiids is further confounded by their poor fossil record, which consists of only teeth and skull fragments from the Miocene of India, Pakistan, (Chopra and Vasishat, 1979; Chopra *et al.*, 1979; Jacobs, 1980), China (Qiu, 1986), and Thailand (Mein and Ginsburg, 1997), as well as the Eocene of China (Tong, 1988). Only one postcranial specimen, a rib cage

Table 1.1: Tupaiid body weights* in grams.

TAXON		MEAN	MIN	MAX	n	REFERENCES
Ptilocercinae						
Ptilocercus	*lowii*	37.5	23	54.5	31	Muul and Lim, 1971
Ptilocercus	*lowii*	51	40	62		Gould, 1978
Ptilocercus	*lowii*	40				Harrison, 1964
Ptilocercus	*lowii*	46.4			4	Le Gros Clark, 1926
Ptilocercus	*lowii*	37	34	40	2	Napier and Napier, 1967
Ptilocercus	*lowii*	57.5	55.1	59.9	3	Whittow and Gould, 1976
Ptilocercus	*lowii*	42.5	25	60		Lekagul and McNeely, 1977
Ptilocercus	*lowii*	48			11	Emmons, in press
Ptilocercus	*lowii*	47.5	42	53	10	Zitzmann, pers. comm.
Ptilocercus	***lowii***	**45.3**	23	62		**MEAN of weights above**
Tupaiinae						
Dendrogale	***murina***	**45**	35	55		Lekagul and McNeely, 1977
Tupaia	*glis*	145	88	173		D'Souza, 1974
Tupaia	*glis*	160	147	183	6	Kawamichi & Kawamichi, 1979
Tupaia	*glis*	148.7			89	Langham, 1982
Tupaia	*glis*	173	150	190	12	Davis, 1962
Tupaia	*glis*	180				Harrison, 1974
Tupaia	*glis*	168	159	177		Napier and Napier, 1967
Tupaia	*glis*	117.25	91.8	126.6	4	Rudd, 1965
Tupaia	*glis*	121.35	91.2	147.3	4	Elliot and Wong, 1969
Tupaia	*glis*	135	85	185		Lekagul and McNeely, 1977
Tupaia	*glis*	160			1	Rabinowitz, 1990
Tupaia	*glis*	165.5			50	Emmons, in press
Tupaia	***glis***	**152.2**	85	190		**MEAN of weights above**
Tupaia	*gracilis*	69.75	62	79	4	Shukor, 1996
Tupaia	*gracilis*	60			1	Davis, 1962
Tupaia	*gracilis*	71.5			11	Emmons, in press
Tupaia	***gracilis***	**67.1**	60	79		**MEAN of weights above**
Tupaia	*minor*	63.79			1	Banks, 1931
Tupaia	*minor*	64.38	53	77	10	Shukor, 1996
Tupaia	*minor*	44	33	59		D'Souza, 1974
Tupaia	*minor*	47	30	60	10	Davis, 1962
Tupaia	*minor*	50				Harrison, 1964
Tupaia	*minor*	70				Harrison, 1974
Tupaia	*minor*	45	30	60		Lekagul and McNeely, 1977
Tupaia	*minor*	51			27	Emmons, in press
Tupaia	***minor***	**54.4**	30	77		**MEAN of weights above**

Table 1.1 (con.)

TAXON		MEAN	MIN	MAX	n	REFERENCES
Tupaia	***montana***	**126**			43	Emmons, in press
Tupaia	***nicobarica***	**170**				Roonwal and Mohnot, 1977
Tupaia	*tana*	166.15	120	240	8	Shukor, 1996
Tupaia	*tana*	200				D'Souza, 1974
Tupaia	*tana*	240.97			1	Banks, 1931
Tupaia	*tana*	221	160	260	25	Davis, 1962
Tupaia	*tana*	200				Harrison, 1964
Tupaia	*tana*	203.5			45	Emmons, in press
Tupaia	***tana***	**205.3**	120	260		**MEAN of weights above**
Urogale	*everetti*	190	180	195	3	Heaney pers. comm.
Urogale	*everetti*	275	235	315	2	Bauchot and Stephan, 1966
Urogale	***everetti***	**224**	180	315	5	**MEAN of weights above**

*body weights in bold are the means of all the weights known for that taxon

from the Pliocene of India reported by Dutta (1975), has been suggested to represent a tupaiid (see Sargis, 1999 for a review of tupaiid fossils). Prior to the present study, tupaiid postcranial morphology was poorly known, had been largely ignored, and had not been studied from a modern functional-adaptive perspective. Hence, this study represents the first comprehensive functional-adaptive analysis of the tupaiid postcranium. An attempt was made to document variation in postcranial morphology in relation to differential substrate use, as well as to consider the adaptive variation of tupaiid postcranial morphology in a character analysis of scandentian, "primatomorphan," volitantian, and archontan features.

Taxonomy of the Family Tupaiidae

A formal revision of the Tupaiidae has not been attempted since Lyon's (1913) analysis of tupaiid skulls, teeth, and skins, and since then the number of species, genera, and subfamilies has been debated. The only taxonomic statement that all researchers seem to agree on is that the family Tupaiidae represents a monophyletic group (*e.g.*, Martin, 1984, 1990; Corbet and Hill, 1992; Wilson, 1993; Nowak, 1999). Lyon's (1913) division of the family into two subfamilies (Tupaiinae and Ptilocercinae), though once challenged by Davis (1938) based on his interpretation of *Dendrogale* as being morphologically intermediate between *Ptilocercus* and tupaiines (*Tupaia*, *Anathana*, *Urogale*, and *Dendrogale*), has subsequently been reaffirmed by Le Gros Clark (1926), Steele (1973), Butler (1980), Luckett (1980b), and Zeller (1986a,b).

Although Lyon (1913) described 46 species of tupaiids in his classification, many of them are no longer recognized, and the separation of the genus *Lyonogale* from *Tupaia* has also been much disputed (see Napier and Napier, 1967; Martin, 1968b, 1984, 1990; Dene *et al.*, 1978, 1980; Butler, 1980; Luckett, 1980b; Corbet and Hill, 1992; Wilson, 1993; Nowak, 1999). Today it is agreed that there is one species of *Ptilocercus*, one of *Anathana*, one of *Urogale*, two of *Dendrogale*, and eleven to fourteen species of *Tupaia*, two to four of which may be included in the genus or subgenus *Lyonogale* (*i.e.*, 16-19 species total: see Napier and Napier, 1967; Martin, 1984, 1990; Corbet and Hill, 1992; Wilson, 1993; Nowak, 1999). I followed Corbet and Hill (1992), Wilson (1993), and Nowak (1999) in including *Lyonogale* within *Tupaia*, and hence only recognize five genera. I also followed Wilson (1993) who recognized fourteen species of *Tupaia*, but I did include *T. belangeri* and *T. longipes* in *T. glis* because they were not distinct postcranially (with the possible exception of a single character) and because they were occasionally lumped in museum collections.

Natural History

All tupaiids are diurnal except for *Ptilocercus lowii*, and most live in tropical forests (see Nowak, 1999). Substrate use has been studied thoroughly in some tupaiid species, while information concerning other species is based largely on qualitative observations and descriptions rather than quantitative data. L. Emmons (pers. comm.) has recently completed a detailed behavioral ecological study of five tupaiid species at the Danum Valley Field Center and one species at Poring Hot Springs in Kinabalu Park, both in Sabah, Malaysia. She concluded that *Ptilocercus* and *Tupaia minor* are arboreal, while *T. tana* (whose common name is the terrestrial tree shrew), *T. gracilis*, *T. longipes*, and *T. montana* are terrestrial. She also acquired anecdotal evidence that *Dendrogale melanura*, present at Poring Hot Springs in Kinabalu Park with *T. montana*, is terrestrial. Apparently, *T. longipes* is more terrestrial than *T. gracilis*: the former species digs and nests in burrows, while the latter species does not (L. Emmons, pers. comm.). The terrestriality of *Tupaia longipes* is somewhat expected because its close relative, *T. glis* (see Dene *et al*., 1978, 1980), has been shown to be much more terrestrial than was previously believed (Vandenbergh, 1963; Kaufmann, 1965; Lim, 1969; Kawamichi and Kawamichi, 1979; Langham, 1982), and seems to escape predators on the ground (Ridley, 1895; Le Gros Clark, 1927; Lekagul and McNeely, 1977; Langham, 1982). Emmons' extensive study confirms previous observations that *Ptilocercus* is completely arboreal and that *T. minor* is predominantly arboreal (Table 1.2). That *T. gracilis* is terrestrial contradicts captive studies, which have shown this species to be very arboreal (Sorenson and Conaway, 1964; Sorenson, 1970). *Urogale everetti* is considered to be one of the most terrestrial species (Martin 1984, 1990), and it has been shown to be terrestrial in the wild (Wharton, 1950). Finally, little is known about *Anathana ellioti*; Chorazyna and Kurup (1975) stated that it is terrestrial, while Martin (1984) claimed that it is semiterrestrial.

Table 1.2: Tupaiid substrate preferences.*

TAXON	SUBSTRATE PREFERENCE	REFERENCES
Ptilocercus lowii	Arboreal	Lim (1967, 1969), Muul and Lim (1971), Gould (1978), Emmons (pers. comm.)
Anathana ellioti	Terrestrial or Semiterrestrial	Chorazyna and Kurup (1975), Martin (1984)
Dendrogale melanura	Terrestrial?	Emmons (pers. comm.)
Tupaia glis	Terrestrial or Semiterrestrial (Scansorial)	Vandenbergh (1963), Kaufmann (1965), Lim (1969), D'Souza (1974), Kawamichi and Kawamichi (1979), Langham (1982)
Tupaia gracilis	Terrestrial	Emmons (pers. comm.)
Tupaia minor	Arboreal	Lim (1969), D'Souza (1974), Emmons (pers. comm.)
Tupaia montana	Terrestrial	Emmons (pers. comm.)
Tupaia nicobarica	Arboreal to	Kloss (1903), Prashanth and Veenakumari (1996)
	Semiterrestrial	Martin (1984)
Tupaia tana	Terrestrial	D'Souza (1974), Emmons (pers. comm.)
Urogale everetti	Terrestrial	Wharton (1950)

*the substrate preferences of *D. murina*, *T. javanica*, and *T. palawanensis* are not known

Morphology

Some morphological features in tupaiids have been proposed to relate to their differential substrate use. For example, *Ptilocercus* and *T. minor* are completely or predominantly arboreal, and, correspondingly, are smaller in body size and have longer tails than terrestrial tupaiids for balance on branches (Martin, 1968b, 1984, 1990; D'Souza, 1974). On the other hand, terrestrial tupaiids have longer snouts and better developed claws than arboreal species for rooting in the leaf litter (Martin, 1968b, 1984, 1990; D'Souza, 1974).

The only study that has examined several tupaiid species in relation to their differential substrate use is George's (1973, 1977) comparison of the limb myology of

Tupaia glis, *T. nicobarica*, *T. tana*, and *Urogale everetti*. George, however, did not find any differences in limb myology that related to differences in substrate preference. He attributed this to Jenkins' (1974) proposal that small mammals are faced with similar obstacles whether they move on the forest floor or in the trees. Jenkins argued that the distinction between arboreal and terrestrial habits is an artificial one when small mammals like tupaiids are being considered (but see Szalay and Drawhorn, 1980, and Szalay and Sargis, submitted, for a contrasting point of view). However, all four of the species George studied may actually be predominantly terrestrial. *T. glis* has been shown to be more terrestrial than previously believed (see above), and Martin (1984) stated that *T. nicobarica* is semiterrestrial to arboreal.

Other morphological studies of tupaiids include early descriptions such as Le Gros Clark's of *Tupaia minor* (1924a,b) and *Ptilocercus lowii* (1926), Davis' (1938) of *Dendrogale murina*, Verma's (1965) of *Anathana ellioti*, and Haines' (1955) of the hand myology of *Ptilocercus* and *Tupaia tana*. More recent analyses of tupaiids have primarily focused on cranio-dental morphology (*e.g.*, Steele, 1973; Wöhrmann-Repenning, 1979; Butler, 1980; Cartmill and MacPhee, 1980; MacPhee, 1981; Zeller, 1986a,b, 1987; Wible and Martin, 1993; Wible and Zeller, 1994), while studies that have included an examination of the postcranium have been restricted to phylogenetic analysis (*e.g.*, Novacek, 1980) or to a specific part of the postcranium such as the tarsus (*e.g.*, Szalay and Drawhorn, 1980; Szalay and Dagosto, 1988) or the carpus (*e.g.*, Stafford and Thorington, 1998). Most recently, Endo *et al.* (1999) examined the scapular morphology and limb myology of *Dendrogale murina*, and claimed to have discovered several adaptations for arboreality in this species. However, they neither explained how these features are specifically related to arboreality, nor did they attempt to differentiate the relevant habitus features from the context of heritage. They also made several erroneous observations in their analysis, and *Dendrogale* is likely more terrestrial than arboreal (Emmons, pers. comm.).

Supraordinal Relationships

Wagner (1855) included tree shrews in the Insectivora, and Haeckel (1866) grouped them in the insectivoran suborder Menotyphla with the elephant shrews (see Butler, 1972). A close relationship between tupaiids and primates was first suggested in 1910 when Gregory proposed the superorder Archonta, which included Chiroptera, Dermoptera, Primates, and Menotyphla (which he recognized as an order). Carlsson (1922) included tupaiids in the order Primates, and Le Gros Clark (1924a,b, 1925, 1926) strongly supported this grouping with his studies of tupaiid anatomy. Simpson (1945) considered Archonta to be an unnatural group, but at the same time he included tupaiids in the order Primates. Tupaiids continued to be classified as Primates until the 1960's (see Napier and Napier, 1967), when they were removed from the order by Van Valen (1965), Jane *et al.* (1965), McKenna (1966), Campbell (1966a,b), Martin (1966, 1968a,b), and Szalay (1968, 1969). Most similarities between the two groups were deemed to be either erroneous observations, shared primitive characters, or convergences found only in derived representatives of the groups rather than in ancestral morphotypes. Once the Tupaiidae were removed from the order Primates, Butler (1972) classified them in their own order Scandentia, a name used (at the family level) by Wagner (1855) for tupaiids. In 1975 McKenna accepted Butler's (1972) classification of tupaiids as an independent order Scandentia, and he revised Gregory's (1910) superorder Archonta by including the orders Scandentia, Primates, Chiroptera, and Dermoptera and excluding the Macroscelididae. Szalay (1977) supported this grouping with evidence from the tarsus, and within the Archonta he recognized a Primate-Scandentia clade and a Chiroptera-Dermoptera clade (called Volitantia). Szalay and Drawhorn (1980) found further support for the archontan hypothesis in the tarsus of fossil plesiadapiforms and other archontan mammals. Novacek and Wyss (1986) came to support the archontan hypothesis based on one tarsal character (from Szalay and Drawhorn, 1980) and one penial character (from Smith and Madkour, 1980), despite Novacek's (1980, 1982, 1986) previous agreement with Cartmill and MacPhee (1980) that this hypothesis was not supported by cranial or postcranial evidence. Since 1986, Novacek has become one of the major proponents of both the Archonta and Volitantia hypotheses (Novacek *et al.*, 1988; Novacek, 1989, 1990, 1992, 1993, 1994). Wible (Wible and Covert, 1987; Wible and Novacek, 1988) has also supported these hypotheses, and has provided evidence for a Scandentia-Euprimates clade that does not include the "archaic primates" (Plesiadapiformes) (also supported by Kay *et al.*, 1992). Some subsequent studies have continued to bolster support for the Archonta hypothesis (Johnson and Kirsch, 1993; Szalay and Lucas, 1993, 1996; Shoshani and McKenna, 1998), while others have rejected it (*e.g.*, Kay *et al.*, 1990, 1992). Recently, McKenna has reconfirmed his support of the Archonta in his classification of mammals (McKenna and Bell, 1997).

Beard's (1989) detailed functional-adaptive analysis of archontan mammal postcranial morphology led him to conclude that plesiadapiforms should be included in the order Dermoptera (a hypothesis also supported by Kay *et al.*, 1990, 1992). Beard (1989) also concluded that Dermoptera and Primates form a natural group, which he named Primatomorpha. The evidence for this grouping consists mainly of similarities between the morphology of the intermediate manual phalanges of dermopterans and paromomyids that may be related to gliding (Beard, 1990, 1993a), although other characters can be interpreted as supporting this hypothesis as well (Beard, 1993b). This grouping of Dermoptera with Primates is in sharp contrast to the grouping of Dermoptera with Chiroptera in Volitantia, which has been strongly supported in numerous morphological studies using extremely varied databases and phylogenetic methods (see Szalay, 1977; Novacek, 1982, 1986, 1989, 1990, 1992, 1993, 1994; Novacek and Wyss, 1986; Wible and Covert, 1987; Novacek *et al.*, 1988; Wible and Novacek, 1988; Thewissen and Babcock, 1991, 1993; Johnson and Kirsch, 1993; Szalay and Lucas, 1993, 1996; Wible, 1993; Shoshani and McKenna, 1998). Thewissen and Babcock (1992), Simmons and Quinn (1994), and Simmons (1995) have also supported Volitantia rather than Primatomorpha, but they incorporated Beard's (1990, 1993a) contribution by including the paromomyids in the order Dermoptera. McKenna and Bell (1997), while not recognizing Beard's Primatomorpha, also included the Paromomyidae in Dermoptera, but they further recognized Beard's (1993a,b) contribution by including Dermoptera as a suborder of the order Primates (however, see Szalay, 1999, for criticisms). Most of the other plesiadapiform families were placed in the order Primates, but not specifically in the suborder Dermoptera. A curious exception was the placement of the Carpolestidae within the Tarsiiformes in the suborder Euprimates (see Szalay, 1999). Shoshani and McKenna (1998) recognized both Volitantia and Beard's Primatomorpha, but their "Primatomorpha" was a grouping of Volitantia and Primates. This concept of Primatomorpha has surely lost the meaning that Beard (1993a,b) intended because

Shoshani and McKenna (1998) argued that Chiroptera was the closest relative of Dermoptera, while Beard (1993a,b) believed that Primates represented the sister taxon of Dermoptera. It is significant that when Beard's data set was incorporated into the much larger data set of Shoshani and McKenna (1998) the signal for a Dermoptera-Primates clade was lost, whereas a Dermoptera-Chiroptera clade was supported.

Beard (1989, 1990, 1991, 1993a,b) has clearly advanced the debate about archontan phylogenetics, but there are several problems with his studies. Krause (1991) immediately questioned the identifications and associations of the paromomyid specimens that Beard (1989, 1990) analyzed. Szalay and Lucas (1993, 1996) questioned and reevaluated many of the postcranial characters that Beard used to support both his concept of Primatomorpha, as well as his hypothesis concerning the "mitten" or finger-gliding capabilities of paromomyids (based on intermediate phalangeal proportions). Runestad and Ruff (1995) rejected Beard's gliding interpretation of paromomyids based on evidence from the long bones, and they showed that the intermediate phalangeal length to average diameter ratios for paromomyids (9-10) are more similar to those of the non-gliding *Tarsius* (8.5) and *Microcebus* (9) than to dermopterans (15-17). Simmons (1994) showed that two of Beard's (1993b) 29 characters included erroneous observations, while Stafford and Thorington (1998) showed that two additional characters included erroneous observations and another character was misinterpreted. Shoshani and McKenna (1998) only used 12 of Beard's (1993b) 29 characters in their phylogenetic analysis because they said that Beard himself stated that the others were questionable. Recently, Hamrick *et al.* (1999) rejected the "mitten" or finger-gliding capabilities of paromomyids based on their analysis of phalangeal proportions. They did recognize several similarities between the phalanges of dermopterans and paromomyids; however, they interpreted these features not as gliding adaptations, but as adaptations for vertical clinging and climbing on large arboreal supports. They also showed that a phalangeal feature previously believed to be unique to paromomyids and dermopterans (Beard, 1993b) is also found in chiropterans (see also Thewissen and Babcock, 1992), and they identified an additional derived phalangeal character shared by chiropterans, dermopterans, and paromomyids (Hamrick *et al.*, 1999). These characters support the emended volitantian concept (where paromomyids are included in Dermoptera) of Thewissen and Babcock (1992), Simmons and Quinn (1994), and Simmons (1995), rather than Beard's (1993a,b) Primatomorpha. Most recently, Lemelin (2000) further supported Volitantia rather than Primatomorpha with a unique feature of the volar skin that is shared by dermopterans and chiropterans. Perhaps most importantly for this study, Beard (1989, 1993b) did not include *Ptilocercus* in his assessment of the postcranium of archontan mammals, but instead used *T. glis* to represent Tupaiidae. *Ptilocercus*, however, has been considered to be the living taxon that most closely resembles the ancestral tupaiid in both its ecology and its morphological attributes (Le Gros Clark, 1926; Szalay, 1969; Campbell, 1974; Gould, 1978; Butler, 1980; Szalay and Drawhorn, 1980; Martin, 1990; Szalay and Lucas, 1993, 1996), and thus it has a paramount role in any supraordinal phylogenetic analysis that includes the Tupaiidae.

In contrast to many of these morphological studies, molecular studies have consistently supported a group that includes Dermoptera, Scandentia, and Primates but excludes Chiroptera (Cronin and Sarich, 1980; Adkins and Honeycutt, 1991, 1993; Honeycutt and Adkins, 1993; Allard *et al.*, 1996; Porter *et al.*, 1996; Liu and Miyamoto, 1999; Waddell *et al.*, 1999); this group has been called Euarchonta by Waddell *et al.* (1999). Despite this apparent consensus regarding the exclusion of bats from the Archonta based on molecular evidence, there has been little agreement concerning which order represents the closest relative of the remaining archontan orders (see Allard *et al.*, 1996). Several orders, including Macroscelidea, Lagomorpha, Rodentia, and occasionally both Lagomorpha and Rodentia (placed in the supraordinal grouping Glires), have been proposed to be more closely related to the remaining members of the Archonta than are bats (Bailey *et al.*, 1992; Honeycutt and Adkins, 1993; Stanhope *et al.*, 1993, 1996; Goodman *et al.*, 1994; Allard *et al.*, 1996; Miyamoto, 1996; Porter *et al.*, 1996; Waddell *et al.*, 1999). Graur *et al.* (1996) argued that lagomorphs are very closely related to primates and tree shrews, and they tentatively concluded that Lagomorpha represents the sister taxon of Scandentia. However, Liu and Miyamoto (1999) recently found the most support for a Dermoptera-Scandentia clade, while Waddell *et al.* (1999), in the same volume, had Dermoptera grouped with Primates in the Primatomorpha.

In summary, the existence of a clade Archonta and the relationships of archontan mammals have by no means been agreed upon, and a major conflict exists between molecular and morphological approaches. A study of the postcranium of the least well known order in this group, Scandentia, was undertaken in order to provide additional information for the understanding of the relationships between these different orders of mammals (see below).

RESEARCH OBJECTIVES

The primary aim of this study was to document variation in postcranial morphology in relation to differential substrate use within the order Scandentia (chapter

4: axial skeleton; chapter 5: forelimb; chapter 6: hindlimb). This effort should contribute to a better understanding of this order of mammals (compared to the relatively better known orders Primates, Chiroptera, and Dermoptera). By analyzing the postcranial morphology of tupaiids, I also specifically examined Jenkins' (1974) proposal that the distinction between arboreality and terrestriality is artificial in the case of small, forest-dwelling mammals. In order to further examine this proposition, I included postcranial attributes of small marsupials in my comparisons (from Szalay and Sargis, submitted). Such comparisons allowed me to analyze the functional-adaptive aspects of postcranial features in selected therian mammals, as well as to examine the specificity of postcranial adaptations in a group of eutherians. I also examined the grasping capabilities of tupaiids, which have been debated in the literature since 1927 and which are significant to the use of tupaiids as models for early primates (chapter 3).

Finally, I considered tupaiid postcranial morphology from a phylogenetic perspective (chapter 7). The inclusion of *Ptilocercus* in this study was pivotal because *Ptilocercus* has been proposed in the past to be the living tupaiid taxon that retains the most conservative skeletal features for Scandentia (see above). However, in most of the past phylogenetic studies it was *Tupaia*, rather than *Ptilocercus*, that was often used as an outgroup when the relationships among various groups of primates were examined (*e.g.*, Shoshani *et al.*, 1996), and it was also *Tupaia* that represented Scandentia in studies of mammalian supraordinal relationships (*e.g.*, Beard, 1989, 1993b; Rose, 1999; Rose and Lucas, 2000). To gain a better understanding of the character states found in the Tupaiidae, which, in turn, should provide primate systematists with a better understanding of this often-used outgroup, I performed a functional-adaptive study of the tupaiid postcranium. The inclusion of *Ptilocercus* in this study allows a more robust (with greater taxonomic sampling) character analysis to be performed on scandentian, "primatomorphan," volitantian, and archontan features in light of an understanding of the polymorphic nature of tupaiid postcranial morphology.

CHAPTER 2: MATERIALS AND METHODS

Materials

Tupaiid skeletal specimens were examined at the following institutions: American Museum of Natural History (AMNH), New York; Field Museum of Natural History (FMNH), Chicago; United States National Museum of Natural History (USNM), Washington, D.C.; Museum of Comparative Zoology (MCZ) at Harvard University, Cambridge; Natural History Museum (NHM), London; Muséum national d'Histoire naturelle (MNHN), Paris; Nationaal Natuurhistorisch Museum (NNM), Leiden; Muséum d'Histoire Naturelle (MHN), Geneva; Forschungsintitut Senckenberg (FS), Frankfurt; Zoologische Staatssammlung (ZS), Munich; and the Swedish Museum of Natural History (SMNH), Stockholm. In addition, plesiadapiform postcranial specimens were studied at the AMNH, the MNHN, and the Carnegie Museum of Natural History (CMNH) in Pittsburgh. The specimens housed at the CMNH were USNM and United States Geological Survey (USGS) specimens. Postcranial specimens of other archontans were examined at the AMNH, MCZ, and in the research collection of F. S. Szalay (FSS). The number of tupaiid specimens from each museum and the number of specimens of each taxon are summarized in Table 2.1, and all of the tupaiid specimens examined in this study are listed in Table 2.2. Additional qualitative comparisons were made to other archontan mammals (see Table 2.2), including a small-bodied cheirogaleid (*Microcebus murinus*), a dermopteran (*Cynocephalus volans*), a chiropteran (*Pteropus* sp.), and several plesiadapiforms (*Plesiadapis*, *Ignacius*, *Phenacolemur*, and *Tinimomys*).

Table 2.1: Number of specimens per taxon in American and European museums.

Museum	*Ptilocercus lowii*	*Dendrogale* sp.	*Tupaia glis*[a]	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*	Totals
AMNH	0	0	3	0	3	0	0	0	0	3	0	9
FMNH	1	1[b]	9	2	0	2	0	0	11	7	11	44
MCZ	1	1[c]	0	0	1	0	0	0	0	0	0	3
USNM	1	0	3	1	1	4	1	1	0	9	0	21
MHN	0	0	1	0	1	1	0	0	0	1	0	4
MNHN	0	0	1	0	0	1	0	0	0	1	0	3
NHM	3	0	0	0	0	0	0	0	0	0	0	3
NNM	1	0	0	0	0	1	0	0	0	0	0	2
FS	0	0	0	0	0	0	1	0	0	0	0	1
SMNH	0	0	1	0	1	0	0	0	0	0	0	2
ZS	0	0	1	0	0	0	0	0	0	1	0	2
Totals	7	2	19	3	7	9	2	1	11	22	11	94

[a] *Tupaia glis* specimens include *T. g. belangeri* and *T. g. longipes*.

[b] *Dendrogale murina* specimen

[c] *Dendrogale melanura* specimen

Table 2.2: Tupaiid* specimens examined (listed by museum).

Genus	Species	Subspecies	Museum	Number	Sex	Country	Notes
Ptilocercinae							
Ptilocercus	*lowii*	*lowii*	FMNH	76855	M	Borneo, Malaysia	
Ptilocercus	*lowii*		MCZ	51736	?	Peninsular Malaysia	
Ptilocercus	*lowii*		NHM	1934.5.6.1	M	Borneo, Malaysia	
Ptilocercus	*lowii*		NHM	67.1479	F	Peninsular Malaysia	
Ptilocercus	*lowii*		NHM	1960.8.4.6	?	Peninsular Malaysia	
Ptilocercus	*lowii*		NNM	a	?	Sumatra, Indonesia	
Ptilocercus	*lowii*		USNM	121885	M	Batu Islands, Indonesia	Manus & Pes
Tupaiinae							
Dendrogale	*melanura*		MCZ	36746	?	Borneo, Malaysia	
Dendrogale	*murina*	*frenata*	FMNH	46630	M	Vietnam	
Tupaia	*glis*		AMNH	55561	?	Thailand	
Tupaia	*glis*		AMNH	55562	?	Thailand	
Tupaia	*glis*	*belangeri*	AMNH	113135	M	Burma	
Tupaia	*glis*	*belangeri*	FMNH	46642	M	Vietnam	
Tupaia	*glis*	*glis*	FMNH	98468	M	Pinang Island, Malaysia	
Tupaia	*glis*	*glis*	FMNH	98469	F	Pinang Island, Malaysia	
Tupaia	*glis*	*glis*	FMNH	98470	M	Pinang Island, Malaysia	
Tupaia	*glis*	*longipes*	FMNH	76815	F	Borneo, Malaysia	
Tupaia	*glis*	*longipes*	FMNH	76819	M	Borneo, Malaysia	
Tupaia	*glis*	*longipes*	FMNH	76824	M	Borneo, Malaysia	
Tupaia	*glis*	*longipes*	FMNH	76825	M	Borneo, Malaysia	
Tupaia	*glis*	*wilkinsoni*	FMNH	66019	M	Thailand	
Tupaia	*glis*	*demissa*	MHN	801.95	M	Sumatra, Indonesia	
Tupaia	*glis*	*belangeri*	MNHN	1990-510	F	Thailand	
Tupaia	*glis*		SMNH	A620505	M	Sumatra, Indonesia	
Tupaia	*glis*	*longipes*	USNM	198043	F	Borneo, Malaysia	

Table 2.2 (con.)

Genus	Species	Subspecies	Museum	Number	Sex	Country	Notes
Tupaia	*glis*	*longipes*	USNM	396665	M	Borneo, Malaysia	
Tupaia	*glis*	*longipes*	USNM	396673	F	Borneo, Malaysia	
Tupaia	*glis*	*discolor*	ZS	1905/13	M	Simpang Banka	
Tupaia	*gracilis*	*gracilis*	FMNH	140925	F	Borneo, Malaysia	
Tupaia	*gracilis*	*gracilis*	FMNH	140928	F	Borneo, Malaysia	
Tupaia	*gracilis*		USNM	449963	F	Borneo, Malaysia	
Tupaia	*javanica*	*occidentalis*	AMNH	106505	F	Sumatra, Indonesia	
Tupaia	*javanica*	*occidentalis*	AMNH	106506	F	Sumatra, Indonesia	
Tupaia	*javanica*	*occidentalis*	AMNH	106507	M	Sumatra, Indonesia	
Tupaia	*javanica*		MCZ	12949	?	Java, Indonesia	
Tupaia	*javanica*		MHN	450.15	?	Java, Indonesia	
Tupaia	*javanica*		SMNH	A630506	?	?	
Tupaia	*javanica*		USNM	154593	F	Java, Indonesia	
Tupaia	*minor*	*caedis*	FMNH	140929	F	Banggi Island, Malaysia	
Tupaia	*minor*	*caedis*	FMNH	76865	M	Borneo, Malaysia	
Tupaia	*minor*	*malaccana*	MHN	801.94	M	Sumatra, Indonesia	
Tupaia	*minor*		MNHN	1981-186	F	Peninsular Malaysia	
Tupaia	*minor*		NNM	36048(a)	?	Borneo, Indonesia	
Tupaia	*minor*	*minor*	USNM	145575	F	Borneo, Indonesia	Pes
Tupaia	*minor*		USNM	396668	M	Borneo, Malaysia	
Tupaia	*minor*		USNM	396669	F	Borneo, Malaysia	
Tupaia	*minor*		USNM	396672	F	Borneo, Malaysia	
Tupaia	*montana*	*baluensis*	FS	82081	M	Borneo, Malaysia	
Tupaia	*montana*		USNM	449964	M	Borneo, Malaysia	
Tupaia	*nicobarica*	*nicobarica*	USNM	111782	?	Nicobar Islands	
Tupaia	*palawanensis*	*palawanensis*	FMNH	62950	F	Palawan Island, Philippines	
Tupaia	*palawanensis*	*palawanensis*	FMNH	63018	M	Palawan Island, Philippines	
Tupaia	*palawanensis*	*palawanensis*	FMNH	62976	F	Palawan Island, Philippines	

Table 2.2 (con.)

Genus	Species	Subspecies	Museum	Number	Sex	Country	Notes
Tupaia	*palawanensis*	*palawanensis*	FMNH	63020	M	Palawan Island, Philippines	
Tupaia	*palawanensis*	*palawanensis*	FMNH	62977	F	Palawan Island, Philippines	
Tupaia	*palawanensis*	*palawanensis*	FMNH	62978	F	Palawan Island, Philippines	
Tupaia	*palawanensis*	*palawanensis*	FMNH	63019	F	Palawan Island, Philippines	
Tupaia	*palawanensis*	*palawanensis*	FMNH	63017	M	Palawan Island, Philippines	
Tupaia	*palawanensis*	*palawanensis*	FMNH	63016	M	Palawan Island, Philippines	
Tupaia	*palawanensis*	*palawanensis*	FMNH	63011	F	Palawan Island, Philippines	
Tupaia	*palawanensis*	*palawanensis*	FMNH	63010	F	Palawan Island, Philippines	
Tupaia	*tana*	*utara*	AMNH	35921	?	Borneo, Malaysia	
Tupaia	*tana*		AMNH	106483	M	Sumatra, Indonesia	
Tupaia	*tana*		AMNH	106485	F	Sumatra, Indonesia	
Tupaia	*tana*	*banguei*	FMNH	140935	M	Banggi Island, Malaysia	
Tupaia	*tana*	*banguei*	FMNH	140936	M	Banggi Island, Malaysia	
Tupaia	*tana*	*kretami*	FMNH	68793	M	Borneo, Malaysia	
Tupaia	*tana*	*kretami*	FMNH	68797	F	Borneo, Malaysia	
Tupaia	*tana*	*paitana*	FMNH	33031	M	Borneo, Malaysia	
Tupaia	*tana*	*paitana*	FMNH	76813	F	Borneo, Malaysia	
Tupaia	*tana*	*paitana*	FMNH	76892	F	Borneo, Malaysia	
Tupaia	*tana*		MHN	746.11	?	Borneo, Malaysia	
Tupaia	*tana*		MNHN	1977-361	M	Borneo, Malaysia	
Tupaia	*tana*	*paitana*	USNM	396660	M	Borneo, Malaysia	
Tupaia	*tana*	*tana*	USNM	151885	F	Borneo, Indonesia	Pes
Tupaia	*tana*	*tana*	USNM	154341	M	Borneo, Indonesia	
Tupaia	*tana*	*tana*	USNM	174611	M	Sumatra, Indonesia	
Tupaia	*tana*	*utara*	USNM	83938	F	Borneo, Malaysia	
Tupaia	*tana*		USNM	449965	F	Borneo, Malaysia	
Tupaia	*tana*		USNM	449966	F	Borneo, Malaysia	
Tupaia	*tana*		USNM	449968	F	Borneo, Malaysia	

Table 2.2 (con.)

Genus	Species	Subspecies	Museum	Number	Sex	Country	Notes
Tupaia	*tana*		USNM	449969	M	Borneo, Malaysia	
Tupaia	*tana*		ZS	1910/1462	F	Borneo	
Urogale	*everetti*		FMNH	57311	F	Mindanao, Philippines	
Urogale	*everetti*		FMNH	57312	M	Mindanao, Philippines	
Urogale	*everetti*		FMNH	57148	M	Mindanao, Philippines	
Urogale	*everetti*		FMNH	57307	M	Mindanao, Philippines	
Urogale	*everetti*		FMNH	57308	F	Mindanao, Philippines	
Urogale	*everetti*		FMNH	61418	M	Mindanao, Philippines	
Urogale	*everetti*		FMNH	61419	F	Mindanao, Philippines	
Urogale	*everetti*		FMNH	61420	M	Mindanao, Philippines	
Urogale	*everetti*		FMNH	57329	M	Mindanao, Philippines	
Urogale	*everetti*		FMNH	57464	?	Mindanao, Philippines	
Urogale	*everetti*		FMNH	57465	?	Mindanao, Philippines	

*Comparisons were made to *Cynocephalus volans* (n = 3; AMNH 207001, MCZ 6261-6264, FSS 1), *Microcebus murinus* (n = 17; especially AMNH 174398, but also AMNH 174383, 174385, 174415, 174424, 174428, 174430-174431, 174471-174472, 174499-174500, 185626-185630), and *Pteropus* sp. [n = 3; especially FSS 2, but also AMNH 202, 249992 (*P. tonganus tonganus*)], as well as to *Plesiadapis gidleyi* (AMNH 17379, 17409), *Plesiadapis intermedius* (USNM 442229), *Plesiadapis tricuspidens* (*e.g.*, MNHN R416, R613, R5337, R5357, R5359, R5361, R5381), *Ignacius graybullianus* (*e.g.*, USNM 442285), *Phenacolemur jepseni* (USGS 17847), *Phenacolemur simonsi* (*e.g.*, USNM 442243, 442257, 442266), and *Tinimomys graybulliensis* (*e.g.*, USNM 442277, 442280). Plesiadapiform specimens listed by Szalay *et al.* (1975) and Beard (1989, 1993b) were also examined in this study.

Methods

Due to the varied types of methods used in this study, only the quantitative morphological methods will be discussed here. These will be relevant to both chapters 5 and 6 on forelimb and hindlimb morphology, respectively. Each additional type of method will be discussed in the chapter for which it is relevant. The methods used to study behavior will be discussed in the chapter on grasping and locomotion (chapter 3) and the qualitative morphological methods will be discussed in the chapter on vertebral morphology (chapter 4).

While the axial skeleton, manus, and pes were all considered qualitatively, the limb bones were considered quantitatively. All measurements on the limb bones were either standard postcranial measurements or believed to have functional relevance to this study. They all refer to maximum lengths, widths, or depths. Initially, 77 measurements (see Figs. 2.1-2.2; Table 2.3) were taken on the postcranial bones of 19 specimens borrowed from the FMNH (7), MHN, MNHN, FS, ZS, and SMNH using a 3-D Mitutoyo MF 200 stage microscope with Measure Graph 1-2-3 software (Rose Technology Inc.). Using a Minolta RD-175 digital camera (Minolta Co. Ltd., Osaka, Japan), 34 images of postcranial joints and bony landmarks were collected on specimens at the FMNH (3), AMNH, USNM, MCZ, NHM, and NNM. Digital images were viewed and saved in Adobe Photoshop (Adobe Systems Inc., San Jose, CA), and 72 measurements (see Figs. 2.1-2.2; Table 2.3) were taken using Scion Image software (Scion Co., Frederick, MD). Six measurements (#9, 23, 30-32, and 49 from Table 2.3) were eliminated due to the difficulty of taking them from the images, and one measurement (#14 from Table 2.3) was added because of its potential functional relevance to this study. At the FMNH, 42

Figure 2.1. Forelimb measurements (see Table 2.3 for descriptions).

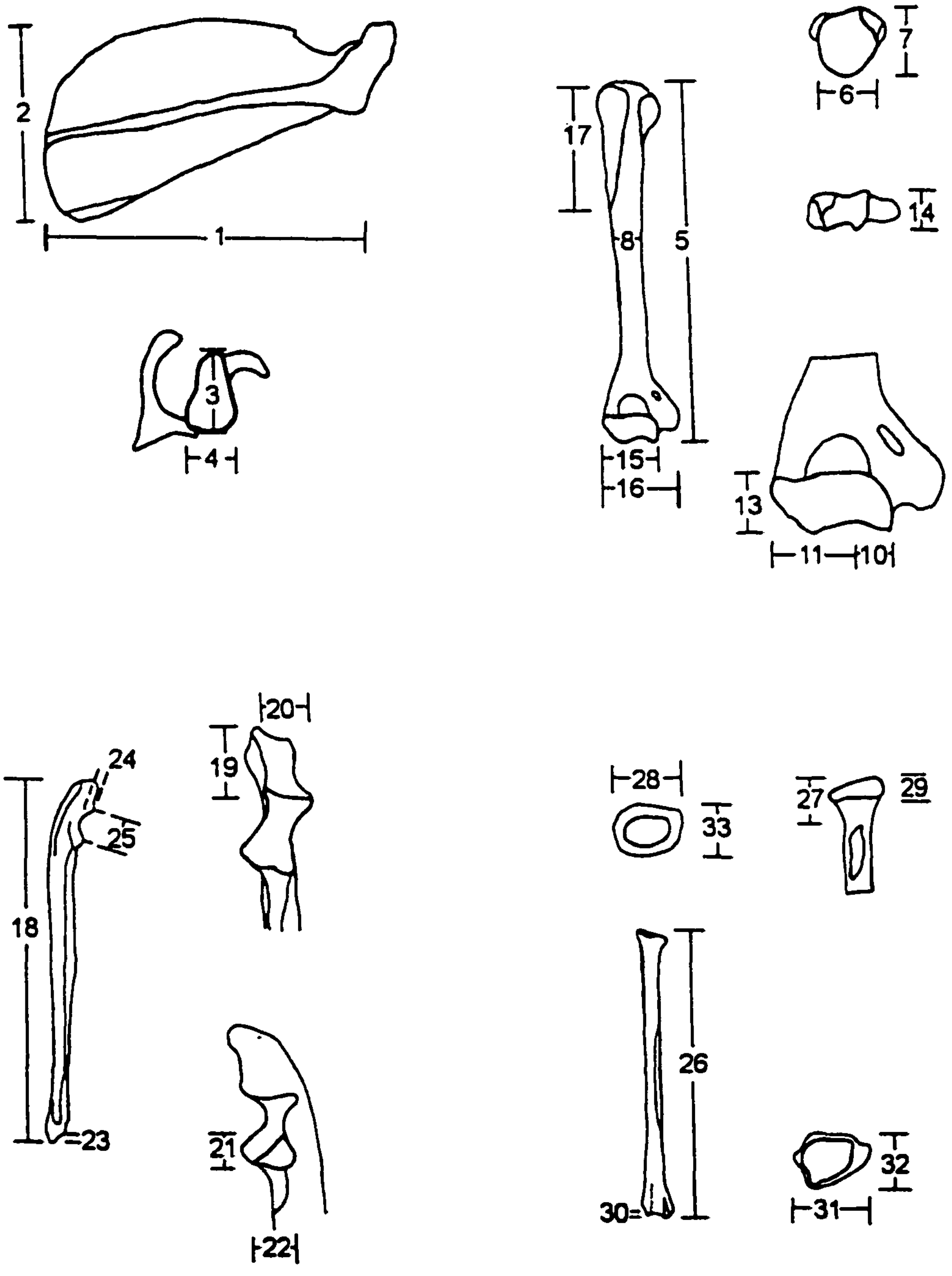


Figure 2.2. Hindlimb measurements (see Table 2.3 for descriptions).

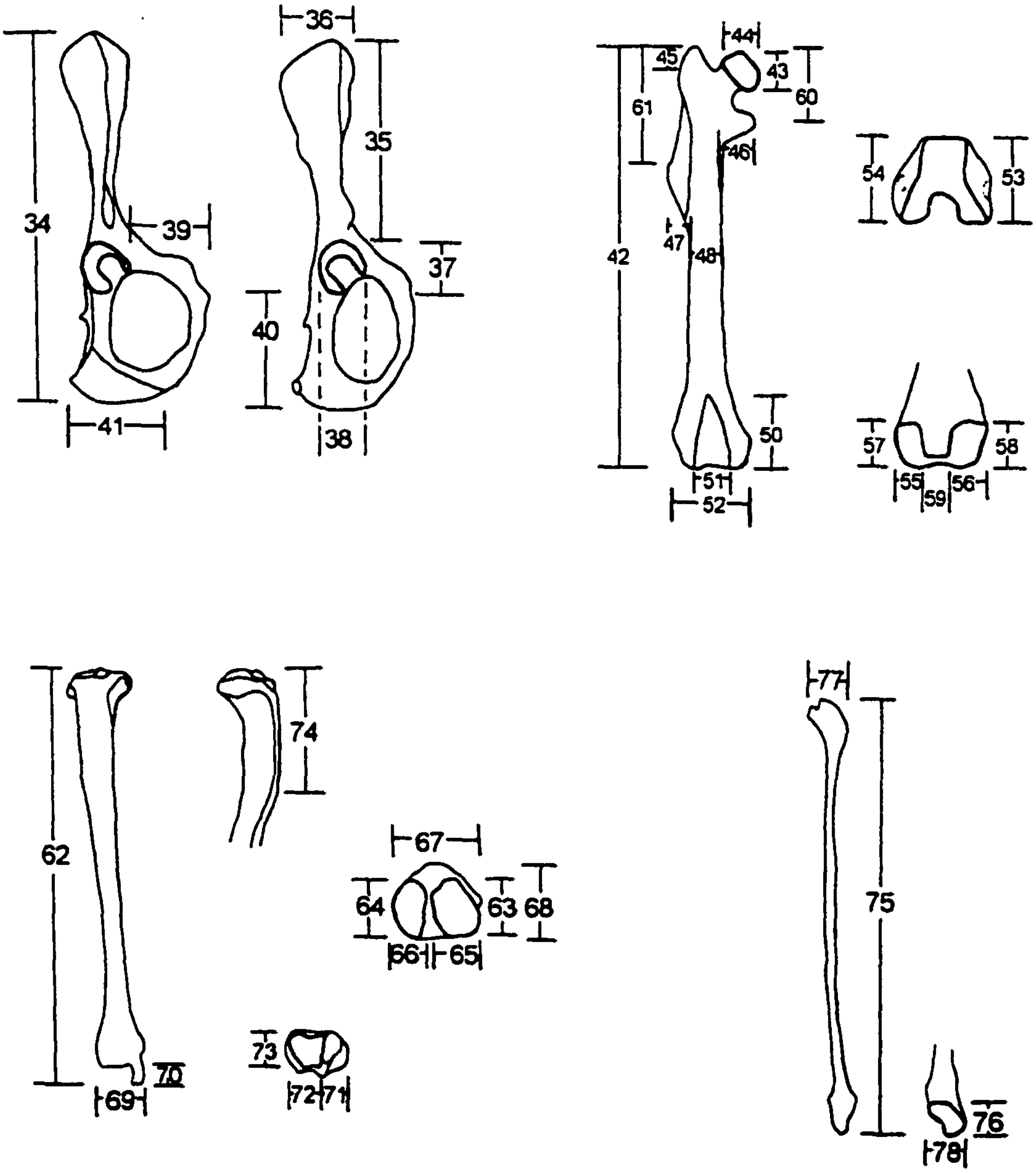


Table 2.3: Measurements (see Figs. 2.1-2.2 for illustrations).

1) Scapula Length (SL): glenoid fossa to vertebral border with vertebral border oriented vertically and the scapular spine oriented nearly horizontally
2) Scapula Width (SW): superior angle to inferior angle with vertebral border oriented vertically and the scapular spine oriented nearly horizontally
3) Glenoid Fossa Length (SGL): cranial edge to caudal edge
4) Glenoid Fossa Width (SGW): medial edge to lateral edge on caudal part of fossa
5) Humerus Length (HL): humeral head to distal trochlea
6) Humeral Head Width (HHW): medial edge of articular surface to lateral edge
7) Humeral Head Length (HHL): anterior edge of articular surface to posterior edge
8) Humeral Mid-shaft Medio-lateral Length (HMSML): medial edge of shaft to lateral edge (mid-shaft was located by measuring half the length of the humerus)
9) Humeral Mid-shaft Antero-Posterior Length (HMSAP): anterior edge of shaft to posterior edge (mid-shaft was located by measuring half the length of the humerus); not shown in Figure 2.1
10) Humeral Trochlea Width (HTW): medial edge of trochlea to end of slope of trochlea in tupaiines where the trochlea is continuous with the capitulum and to lateral edge of the trochlea in *Ptilocercus* where the trochlea is separated from the capitulum; does not include the zona conoidea because this region articulates with the radius in eutherians
11) Humeral Capitulum Width (HCW): lateral edge of capitulum to end of slope of trochlea in tupaiines where the trochlea is continuous with the capitulum and to medial edge of the capitulum in *Ptilocercus* where the trochlea is separated from the capitulum; includes the zona conoidea because this region articulates with the radius in eutherians
12) Humeral Trochlea Length (HTL): proximal edge of trochlea to distal edge
13) Humeral Capitulum Length (HCL): proximal edge of capitulum to distal edge
14) Humeral Trochlea Depth (HTD): anterior edge of trochlea to posterior edge
15) Humeral Distal Articular Surface Width (HDASW): medial edge of trochlea to lateral edge of capitulum
16) Humeral Distal End Width (HDEW): medial edge of medial epicondyle to lateral edge of lateral epicondyle
17) Humeral Delto-pectoral Crest Length (HDCL): proximal edge of greater tuberosity to distal extent of delto-pectoral crest
18) Ulna Length (UL): proximal edge of olecranon process to distal edge of styloid process
19) Ulnar Olecranon Process Length (UOPL): proximal edge of olecranon process to proximal edge of trochlear notch (olecranon beak)
20) Ulnar Trochlear Notch Width (UTNW): medial edge of trochlear notch to lateral edge along the olecranon beak (proximal edge of trochlear notch)
21) Ulnar Radial Facet Length (URFL): proximal edge of articular surface to distal edge
22) Ulnar Radial Facet Width (URFW): medial edge of articular surface to lateral edge
23) Ulnar Styloid Process Length (USPL): distal edge of process to proximal extent of process

Table 2.3 (con.)

24) Ulnar Trochlear Notch Depth (UTND): deepest point of notch to line extending from coronoid process (distal edge of trochlear notch) to olecranon beak (proximal edge of trochlear notch)
25) Ulnar Trochlear Notch Length (UTNL): proximal edge of trochlear notch (olecranon beak) to distal edge (coronoid process)
26) Radius Length (RL): proximal edge of radial head to distal edge of styloid process
27) Radial Neck Length (RNL): proximal edge of radial tuberosity to proximal edge of radial head
28) Radial Head Width (RHW): medial edge of head to lateral edge (from proximal view)
29) Radial Head Rim Length (RHRL): proximal edge of rim to distal edge
30) Radial Styloid Process Length (RSPL): distal edge of process to distal articular surface
31) Radial Distal End Width (RDEW): medial edge of distal end to lateral edge (from distal view)
32) Radial Distal End Length (RDEL): anterior edge of distal end to posterior edge (from distal view)
33) Radial Head Length (RHL): anterior edge of head to posterior edge (from proximal view)
34) Innominate Length (INL): superior edge of ilium (iliac crest) to inferior edge of ischium with ilium and ischium oriented vertically
35) Ilium Length (ILL): superior edge of ilium (iliac crest) to superior edge of acetabulum
36) Ilium Width (ILW): medial edge to lateral edge along iliac crest
37) Acetabulum Length (IAL): superior edge to inferior edge
38) Acetabulum Width (IAW): medial edge to lateral edge
39) Pubis Length (IPL): medial edge of acetabulum to medial edge of pubis (pubic symphysis) along the superior pubic ramus
40) Ischium Length (ISL): inferior edge of acetabulum to inferior edge of ischium
41) Ischium Width (ISW): lateral edge (ischial tuberosity) to medial extent of attachment area for the semimembranosus muscle along the ischial ramus
42) Femur Length (FEL): proximal edge of greater trochanter to distal edge of condyle
43) Femoral Head Length (FHL): proximal edge of head to distal edge
44) Femoral Head Width (FHW): medial edge of head to lateral edge
45) Proximal Extension of Greater Trochanter (FGTL): proximal edge of greater trochanter to point on femur where the greater trochanter meets the femoral neck and where the greater trochanter begins to protrude proximally (see Fig. 2.2)
46) Medial Extension of Lesser Trochanter (FLTL): medial edge of lesser trochanter to medial edge of femoral shaft
47) Lateral Extension of Third Trochanter (FTTL): lateral edge of third trochanter to lateral edge of femoral shaft
48) Femoral Mid-shaft Medio-lateral Length (FMSML): medial edge of shaft to lateral edge (mid-shaft was located by measuring half the length of the femur)

Table 2.3 (con.)

49) Femoral Mid-shaft Antero-Posterior Length (FMSAP): anterior edge of shaft to posterior edge (mid-shaft was located by measuring half the length of the femur); not shown in Figure 2.2
50) Femoral Patellar Groove Length (FPGL): distal edge of groove (distal edge of condyle) to proximal extent of groove
51) Femoral Patellar Groove Width (FPGW): medial patellar ridge to lateral patellar ridge along distal edge (from anterior view)
52) Femoral Distal End Width (FDEW): medial edge of medial condyle to lateral edge of lateral condyle (from anterior view)
53) Femoral Medial Condyle Depth (FMCD): posterior edge of medial condyle to anterior edge of medial patellar ridge (from distal view)
54) Femoral Lateral Condyle Depth (FLCD): posterior edge of lateral condyle to anterior edge of lateral patellar ridge (from distal view)
55) Femoral Medial Condyle Width (FMCW): medial edge to lateral edge (from posterior view)
56) Femoral Lateral Condyle Width (FLCW): medial edge to lateral edge (from posterior view)
57) Femoral Medial Condyle Length (FMCL): proximal edge to distal edge (from posterior view)
58) Femoral Lateral Condyle Length (FLCL): proximal edge to distal edge (from posterior view)
59) Femoral Intercondylar Notch Width (FICNW): lateral edge of medial condyle to medial edge of lateral condyle (from posterior view)
60) Distal Extent of Lesser Trochanter (FLTLT): proximal edge of greater trochanter to midpoint of lesser trochanter
61) Distal Extent of Third Trochanter (FLTTT): proximal edge of greater trochanter to midpoint of third trochanter (corresponding to point of greatest lateral extension)
62) Tibia Length (TL): proximal edge of medial intercondylar tubercle to distal edge of medial malleolus
63) Tibial Lateral Condyle Length (TLCL): anterior edge to posterior edge (from proximal view)
64) Tibial Medial Condyle Length (TMCL): anterior edge to posterior edge (from proximal view)
65) Tibial Lateral Condyle Width (TLCW): medial edge to lateral edge
66) Tibial Medial Condyle Width (TMCW): medial edge to lateral edge
67) Tibial Proximal End Width (TPEW): medial edge of medial condyle to lateral edge of lateral condyle (from proximal view)
68) Tibial Proximal End Length (TPEL): anterior edge of tibial tuberosity to most posterior edge of tibial plateau, whether it be the medial condyle, lateral condyle, or intercondylar eminence (from proximal view)
69) Tibial Distal End Width (TDEW): medial edge of medial malleolus to lateral edge of distal fibular facet (from anterior view)
70) Tibial Medial Malleolus Length (TMML): distal edge of medial malleolus to distal articular surface (lateral astragalar facet)

Table 2.3 (con.)

71) Tibial Medial Malleolus Width (TMMW): medial edge to lateral edge (from distal view)
72) Tibial Distal Articular Surface (Lateral Astragalar Facet) Width (TDASW): lateral edge of medial malleolus to lateral edge of articular surface
73) Tibial Distal Articular Surface (Lateral Astragalar Facet) Length (TDASL): anterior edge to posterior edge
74) Tibial Crest Length (TCL): proximal edge of lateral condyle to distal extent of crest (from lateral view)
75) Fibula Length (FIL): proximal edge of head to distal edge of lateral malleolus
76) Fibular Lateral Malleolus Length (FILML): distal edge of lateral malleolus to proximal extent of articular surface of astragalar facet (from medial view)
77) Fibular Head Length (FIHL): anterior edge to posterior edge
78) Fibular Lateral Malleolus Width (FILMW): anterior edge to posterior edge (from medial view)

measurements (including #9 and 49 from Table 2.3) were initially taken on 34 specimens using Mitutoyo digital calipers. Later, seven images and 27 measurements (69 total) were collected on these 34 specimens. Some images and measurements (#14, 17, 59, 74, and 76 from Table 2.3) could not be taken on these specimens due to time restrictions. All images below are shown from the right side unless stated otherwise.

All statistical analyses were performed using Statistica (StatSoft Inc., Tulsa, OK). Forty-seven indices (see Table 2.4) were constructed; all were either standard postcranial indices or believed to have functional relevance to this study. These indices were plotted in box plots (see Table 2.5 for abbreviations) and were each compared between species using one-way ANOVA and the Tukey honest significant difference (HSD) post hoc test ($P < .05$).

Cluster analyses [unweighted pair-group average (UPGA)] for the scapula, humerus, ulna + radius, forelimb, innominate, femur, tibia + fibula, hindlimb, and forelimb + hindlimb were performed on the species means of the variables used to construct the indices. Trees are presented with Euclidean distances.

Table 2.4: Indices.

1) Intermembral Index: Humerus + Radius Length/Femur + Tibia Length * 100
2) Humerofemoral Index: Humerus Length/Femur Length * 100
3) Brachial Index: Radius Length/Humerus Length * 100
4) Crural Index: Tibia Length/Femur Length * 100
5) Scapula Shape Index: Scapula Width/Length * 100
6) Glenoid Fossa Shape Index: Glenoid Fossa Width/Length * 100
7) Humeral Head Shape Index: Humeral Head Width/Length * 100
8) Trochlea and Capitulum Width Index: Trochlea Width/Capitulum Width * 100
9) Trochlea Shape Index: Trochlea Width/Length * 100
10) Capitulum Shape Index: Capitulum Width/Length * 100
11) Trochlea and Capitulum Length Index: Trochlea Length/Capitulum Length * 100
12) Trochlea Depth Index: Trochlea Depth/Humerus Length * 100
13) Capitulum Width Index: Capitulum Width/Humeral Distal End Width * 100
14) Trochlea Length Index: Trochlea Length/Humeral Distal Articular Surface Width * 100
15) Capitulum Length Index: Capitulum Length/Humeral Distal Articular Surface Width * 100
16) Humeral Distal End Width Index: Humeral Distal End Width/Humerus Length * 100
17) Delto-pectoral Crest Length Index: Humeral Delto-pectoral Crest Length/Humerus Length * 100
18) Olecranon Process Length Index: Olecranon Process Length/Ulna Length * 100
19) Ulnar Radial Facet Shape Index: Ulnar Radial Facet Length/Width * 100
20) Ulnar Trochlear Notch Shape Index: Ulnar Trochlear Notch Depth/Length * 100
21) Radial Head Shape Index: Radial Head Length/Width * 100
22) Radial Neck Length Index: Radial Neck Length/Radius Length * 100
23) Radial Head Rim Length Index: Radial Head Rim Length/Radius Length * 100
24) Ilium Length Index: Ilium Length/Innominate Length * 100
25) Ilium Shape Index: Ilium Width/Length * 100
26) Acetabulum Shape Index: Acetabulum Width/Length * 100
27) Pubis Length Index: Pubis Length/Innominate Length * 100
28) Ischium Length Index: Ischium Length/Innominate Length * 100
29) Ischium Shape Index: Ischium Width/Length * 100
30) Femoral Head Shape Index: Femoral Head Width/Length * 100
31) Greater Trochanter Length Index: Proximal Extension of Greater Trochanter/Femur Length * 100
32) Lesser Trochanter Length Index: Medial Extension of Lesser Trochanter/Femur Length * 100
33) Third Trochanter Length Index: Lateral Extension of Third Trochanter/Femur Length * 100
34) Distal Extent of Lesser Trochanter Index: Distal Extent of Lesser Trochanter/Femur Length * 100
35) Distal Extent of Third Trochanter Index: Distal Extent of Third Trochanter/Femur Length * 100

Table 2.4 (con.)

36) Femoral Medial Condyle Depth Index: Femoral Medial Condyle Depth/Femur Length * 100 (1) & Femoral Medial Condyle Depth/Femoral Distal End Width * 100 (2)
37) Femoral Lateral Condyle Depth Index: Femoral Lateral Condyle Depth/Femur Length * 100 (1) & Femoral Lateral Condyle Depth/Femoral Distal End Width * 100 (2)
38) Femoral Condyle Width Index: Femoral Lateral Condyle Width/Medial Condyle Width * 100
39) Patellar Groove Shape Index: Patellar Groove Width/Length * 100
40) Tibial Crest Length Index: Tibial Crest Length/Tibia Length * 100
41) Tibial Proximal End Shape Index: Tibial Proximal End Length/Width * 100
42) Tibial Condyle Width Index: Tibial Lateral Condyle Width/Medial Condyle Width * 100
43) Tibial Lateral Condyle Length Index: Tibial Lateral Condyle Length/Tibia Length*100
44) Tibial Medial Condyle Length Index: Tibial Medial Condyle Length/Tibia Length*100
45) Tibial Medial Malleolus Length Index: Medial Malleolus Length/Tibia Length * 100
46) Tibial Distal Articular Surface (Lateral Astragalar Facet) Shape Index: Tibial Distal Articular Surface Length/Width * 100
47) Fibular Lateral Malleolus Length Index: Lateral Malleolus Length/Fibula Length * 100

Finally, a principal components analysis (PCA) was performed on a correlation matrix computed from the logged species means of 70 measurements. Eight measurements were excluded because they were missing in several taxa. Exclusion of these eight measurements allowed all but one of the twelve tupaiid species to be included in the analysis. Only the single specimen of *T. nicobarica*, which was missing several additional measurements, was excluded, although only ten taxa are included because the single specimens of each *Dendrogale* species were considered together as *Dendrogale* sp. No rotations were performed (see Neff and Marcus, 1980). The first three factors of the PCA (*i.e.*, those with eigenvalues greater than one) were compared in bivariate plots, and these are included with the eigenvalues, percent of total variance, factor scores, and factor loadings in chapter 6.

Table 2.5: Taxon abbreviations used for all plots.

ABBREVIATION	TAXON
PL	*Ptilocercus lowii*
DM	*Dendrogale* sp. (*D. melanura* and *D. murina*)
TG	*Tupaia glis*
TGr	*Tupaia gracilis*
TJ	*Tupaia javanica*
TM	*Tupaia minor*
TMo	*Tupaia montana*
TN	*Tupaia nicobarica*
TP	*Tupaia palawanensis*
TT	*Tupaia tana*
UE	*Urogale everetti*

CHAPTER 3: SUBSTRATE USE, LOCOMOTION, AND GRASPING

INTRODUCTION

The grasping capabilities of tree shrews have been in question since 1927, when Le Gros Clark reported that the pollex and hallux of *Tupaia minor* were opposable (see Table 3.1 for a definition of hand types and Table 3.2 for a review of grasping evidence). Napier (1961), however, concluded that tupaiids have a convergent, non-prehensile hand (with a non-opposable thumb; Table 3.1). He argued that the behavioral correlate of prehensility is the ability to hold food items in one hand, and he believed that evidence for habitual one-handed feeding in tupaiids was lacking. Napier (1993) also claimed that claws are incompatible with prehensile hands because they overgrow the fingertips, obstructing the grasping process. This implies that clawed mammals such as tupaiids would not be capable of grasping. D'Souza (1974) stated that tupaiines do not grasp (with either their hands or feet), nor do they possess a divergent pollex or hallux. *Ptilocercus* was not included in D'Souza's assessment, but several authors have concluded that this taxon, which is arboreal, has a divergent grasping pollex and hallux (Table 3.2; A. Zitzmann, pers. comm.). Furthermore, hallucial grasping in *Ptilocercus* has been demonstrated quite clearly in several figures (see Table 3.2 for descriptions). Most recently, however, Martin (1990) has claimed that there is no evidence that the hands or feet of tupaiids are adapted for grasping.

The inconsistencies in the understanding of tupaiid grasping capabilities may be due to the fact that *T. glis* (the common tree shrew), the species typically selected for observation, is not predominantly arboreal, but is instead terrestrial or at least scansorial (Table 1.2). The examination of a predominantly arboreal tupaiine may, therefore, clarify whether some tupaiines, in addition to *Ptilocercus*, are capable of grasping. For this study, I observed and compared the grasping behavior, locomotion, and substrate use of the arboreal *T. minor* (the lesser tree shrew) with that of the terrestrial *T. tana* (the terrestrial tree shrew) at the National Zoological Park in Washington, D.C. Prior to this study, the only locomotor studies of tupaiids were gait analyses of *T. glis* (Jenkins, 1974; Schilling and Fischer, 1999).

Table 3.1: Descriptions of mammalian hand types (after Napier, 1961).

CONVERGENT HAND: thumb is not independent of or divergent from other digits and one hand is incapable of grasping an object alone; possessed by two-handed feeders
PREHENSILE HAND: thumb is independent of and divergent from other digits and one hand is capable of grasping an object alone; possessed by one-handed feeders
OPPOSABLE THUMB: pollex capable of rotation so that it faces the other digits when grasping

MATERIALS AND METHODS SPECIFIC TO THIS CHAPTER

Behavioral observations were made on seven *T. minor* individuals (4 males, 3 females), housed in cages 1.22 m high by 1.22 m deep by 2.44 m wide, and five *T. tana* individuals (1 male, 4 females), housed in cages 3.05 m high by 1.83 m deep by 2.74 m wide, in the Department of Zoological Research at the National Zoological Park in Washington, D.C. All of the cages included branches of different sizes placed at various angles (horizontal, vertical, and oblique), and the floors of the cages were covered with wood shavings. Observations totaled 77 hours over a six-week period in December1997 and January 1998. In an attempt to determine whether these captive animals were behaving predominantly as they do in the wild (where *T. minor* is arboreal and *T. tana* is terrestrial), observations were made to document their substrate preferences, as well as their locomotor repertoire, in captivity. I conducted ten-minute focal animal samples and

Table 3.2: A review of observations and statements regarding tupaiid grasping.

BEHAVIORAL EVIDENCE SUPPORTING GRASPING HAND (POLLEX)		
Ptilocercus lowii	Capable of one-handed feeding	Le Gros Clark (1926)
Tupaia glis	Seen feeding with one hand (but rarely)	Bishop (1962, 1964)
Tupaia minor	Often holds food objects with one hand and grasps very small branches	THIS STUDY
MORPHOLOGICAL EVIDENCE SUPPORTING GRASPING HAND (POLLEX)		
Ptilocercus lowii	Pollex capable of marked divergence	Gregory (1913)
Ptilocercus lowii	Independence of extensor longus pollicis indicates mobility of the pollex; pollex is stout and capable of great freedom of movement	Le Gros Clark (1926)
Ptilocercus lowii	Claws on the pollex of a specimen worn down to stubs (giving them the appearance of nails), which would facilitate grasping	Le Gros Clark (1927)
Ptilocercus lowii	Contrahens to pollex independent of other contrahentes muscles	Haines (1955)
Ptilocercus lowii	Pollex widely divergent and contrahens I forms muscle which controls only the pollex; distal articular surface of trapezium for first metacarpal is saddle-shaped, indicating specialization of pollical movement	Haines (1958)
Ptilocercus lowii	Pollex more divergent than in *Tupaia*	Bishop (1964)
Ptilocercus lowii	Divergent and mobile thumb	Napier and Napier (1967)
Tupaia minor	Opposable pollex and described a photo (Fig. 6 in Elliot Smith, 1924) showing grasping hand	Le Gros Clark (1927)
Tupaia minor	Pollex often quite divergent	THIS STUDY
Tupaia	Hand with divergent pollex	Gregory (1913)
Tupaia	Contrahentes muscles allow independent movement of the thumb	Napier and Napier (1967)
BEHAVIORAL EVIDENCE SUPPORTING GRASPING FOOT (HALLUX)		
Tupaia glis	Hallux lies on top of branch and foot may actively grip the branch between the hallux and the other digits	Jenkins (1974)
Tupaia minor	Frequently grasps branches with foot	THIS STUDY
Ptilocercus lowii	Abducts hallux and grips small supports between hallux and other digits (illustrated in photo, Fig. 2)	Gould (1978)

Table 3.2 (con.)

Ptilocercus lowii	Photo shows grasping foot and divergent hallux	Martin (1982)
Tupaiidae	Cling to tree limbs with grasping feet	Miller (1935)
MORPHOLOGICAL EVIDENCE SUPPORTING GRASPING FOOT (HALLUX)		
Ptilocercus lowii	Hallux capable of marked divergence	Gregory (1913)
Ptilocercus lowii	Differentiation of extensor brevis hallucis is associated with freedom of movement of the hallux; hallux is stoutly built and independent of the other digits	Le Gros Clark (1926)
Ptilocercus lowii	Claws on the hallux of a specimen worn down to stubs (giving them the appearance of nails), which would facilitate grasping	Le Gros Clark (1927)
Ptilocercus lowii	Contrahens to hallux independent of other contrahentes muscles, forming muscle which controls only the hallux	Haines (1958)
Ptilocercus lowii	Photo (Plate Ib) shows divergent hallux	Lim (1967)
Ptilocercus lowii	Hallucial grasping possible based on arc of motion at entocuneiform-1st metatarsal joint	Szalay and Dagosto (1988)
Tupaia minor	Opposable hallux	Le Gros Clark (1927)
Tupaia minor	Hallux habitually divergent from other digits when moving on branches	THIS STUDY
Tupaia	Foot with divergent hallux	Gregory (1913)
BEHAVIORAL EVIDENCE REJECTING GRASPING HAND (POLLEX)		
Tupaia tana	Never observed feeding one-handed or grasping a branch	THIS STUDY
Tupaiinae	Non-grasping hand	D'Souza (1974)
MORPHOLOGICAL EVIDENCE REJECTING GRASPING HAND (POLLEX)		
Tupaia glis	Convergent, non-prehensile hand; pollex rarely observed in opposition to other digits	Bishop (1962, 1964)
Tupaia tana	Pollex not divergent	THIS STUDY
Tupaiinae	Non-divergent pollex	D'Souza (1974)
Tupaiidae	Convergent, non-prehensile hand with non-opposable thumb; carpo-metacarpal joint of pollex is a hinge joint (not saddle-shaped)	Napier (1961)
Tupaiidae	Pollex barely a "thumb" because not differentiated from other digits	Napier and Napier (1967)
Tupaiidae	Lost the opposable function of the pollex	Martin (1968a)
Tupaiidae	No evidence that hands are adapted to grasping	Martin (1990)
BEHAVIORAL EVIDENCE REJECTING GRASPING FOOT (HALLUX)		
Tupaia tana	Never observed grasping a branch	THIS STUDY

Table 3.2 (con.)

Tupaiinae	Non-grasping foot	D'Souza (1974)
MORPHOLOGICAL EVIDENCE REJECTING GRASPING FOOT (HALLUX)		
Tupaia tana	Hallux not divergent from other digits	THIS STUDY
Tupaiinae	Non-divergent hallux	D'Souza (1974)
Tupaiidae	Lost the opposable function of the hallux	Martin (1968a)
Tupaiidae	No evidence that feet are adapted to grasping	Martin (1990)

videotaped the animals with a Fujix-Hi 8 H80 8 mm camcorder with an 8X power zoom lens (Fuji Photo Film Co. Ltd., Tokyo, Japan). I scored bout data on locomotion and substrate use both from videotapes and directly into notebooks during observations (see Table 3.3 for locomotor categories). Because grasping was never observed in *T. tana*, this behavior was not investigated further in this species. *T. minor*, however, was often observed grasping the branches in its cages. In order to better observe this behavior, I introduced 9.5 mm and 6.5 mm dowels into the cages. I then videotaped *T. minor* crossing the dowels (occasionally individuals had to be enticed onto dowels with crickets), and the number of dowel crossings that included grasps with the feet or hands was scored from the videotapes. Finally, in order to illustrate this behavior, 65 images of

Table 3.3: Descriptions of behavioral categories (after Gebo, 1992).

QUADRUPEDALISM: movements in which all four limbs are used in a regular pattern above horizontal or slightly oblique supports (includes walking, running, and bounding)

CLIMBING: movements up or down vertical or strongly oblique supports

LEAPING: movements in which the hindlimbs are extended to propel an individual across a gap between two supports

SUSPENSORY LOCOMOTION: movements in which three or four limbs are used below a support

---

GRASPING: a behavior in which a support is actively gripped between the pollex and the other manual digits or between the hallux and the other pedal digits

ROOTING: a behavior in which an individual moves its snout through litter (leaves in the wild, but wood chips in this captive situation) in search of food (live crickets and mealworms in this study); this behavior occurs only on the ground and only during quadrupedal locomotion and in standing or sitting postures

T. minor grasping were captured from videotapes using VideoPort Professional with Image Wizard software (MRT micro as., Strømmen, Norway).

RESULTS

Qualitative and quantitative behavioral results are summarized in Tables 3.4 and 3.5, respectively. *Tupaia tana* predominantly moved on the ground, whereas *T. minor* preferred arboreal supports. *T. minor* leapt, climbed, and used suspensory locomotion more frequently than *T. tana*, whereas *T. tana* preferred quadrupedal locomotion. *T. minor* moved more quickly and was far more active than *T. tana*: the bout total for *T. minor* was six times higher than that of *T. tana* despite an equal amount of observation time (Table 3.5). *T. minor* was observed reversing its feet (Figs. 3.1c-e) more often than *T. tana*, while *T. tana* was seen rooting in the wood chips on the ground more frequently than *T. minor*. The forelimbs of *T. minor* were habitually flexed (and abducted) and its feet were often observed in a semi-plantigrade posture (Fig. 3.2a), while the forelimbs of *T. tana* were often extended more fully and its feet were typically in a digitigrade posture. Finally, *T. minor* individuals were observed grasping with their feet (or, less

Table 3.4: Qualitative results from analysis of locomotor behavior.

Tupaia tana	*Tupaia minor*
Larger body size	Smaller body size
Less active	More active
Moves more slowly	Moves more quickly
More terrestrial	More arboreal
No grasping observed	Grasps small branches
Rarely reverses hindfoot	Frequently reverses hindfoot
More rooting	Less rooting
Forelimbs more extended	Forelimbs more flexed
More digitigrade	More (semi) plantigrade

Table 3.5: Quantitative results from analyses of locomotion, substrate use, and grasping behavior.

LOCOMOTION

Species	n	Body Weight[a]	Quadrupedalism	Climbing	Leaping	Suspension	Total		Rooting
Tupaia minor	7	65.7 g	2792	958	2080	302	6132	bouts	64
			45%	16%	34%	5%	100%		1%
Tupaia tana	5	267.2 g	800	70	152	2	1024	bouts	224
			78%	7%	15%	0.2%	100%		22%

SUBSTRATE USE

Species	n	Arboreal[b]	Terrestrial[c]	Total	
Tupaia minor	7	5860	272	6132	bouts
		96%	4%	100%	
Tupaia tana	5	224	800	1024	bouts
		22%	78%	100%	

GRASPING

Species	n	Crosses[d]	Grasps[e]	Percent[f]
Tupaia minor	6	652	546	84%
Tupaia tana	5	(never	observed	grasping)

[a] average body weight of all captive individuals

[b] movements on branches in cages

[c] movements on floors of cages

[d] total number of dowel crossings

[e] number of dowel crossings that included grasping with either the feet or hands

[f] percentage of dowel crossings that included grasping

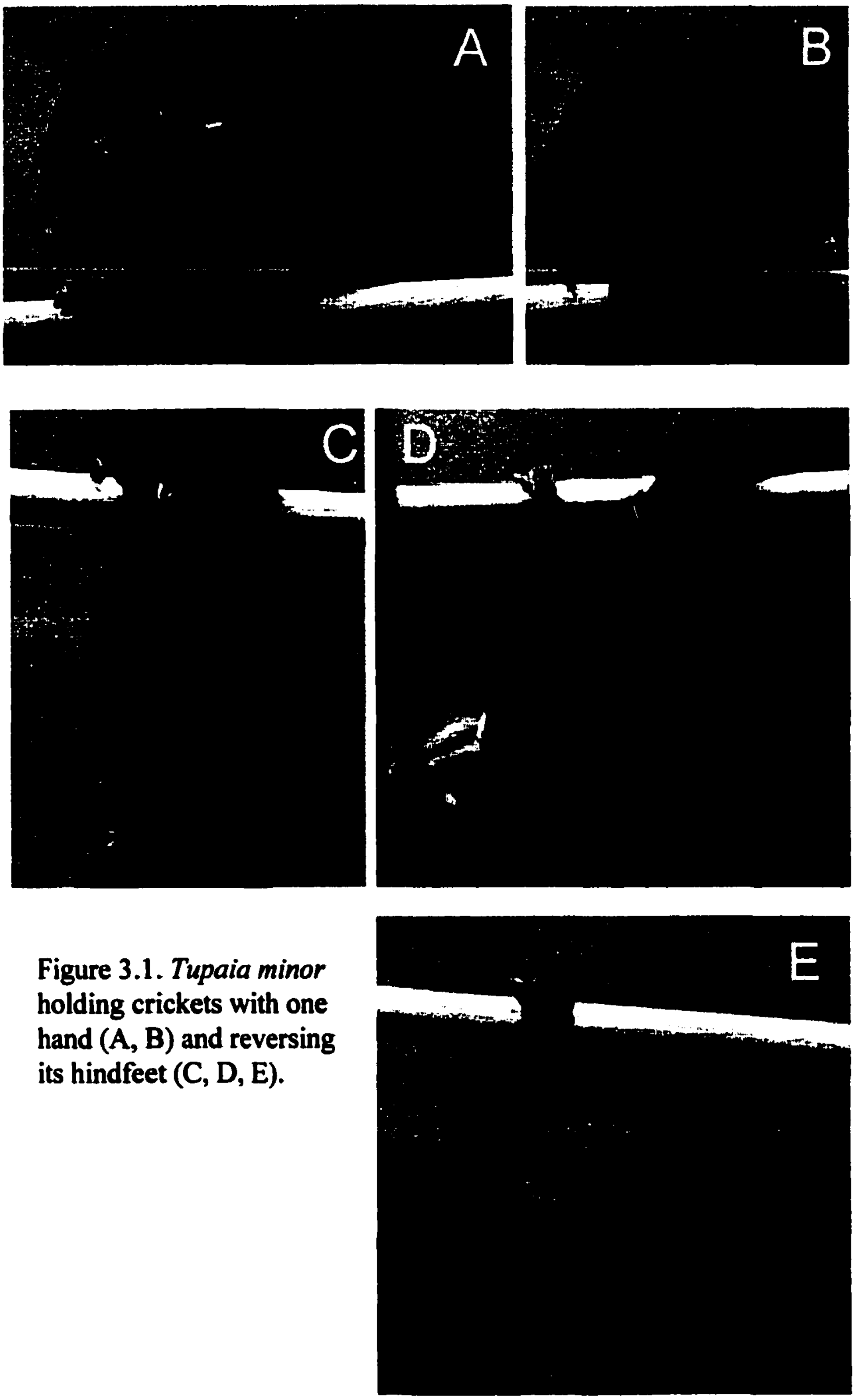


Figure 3.1. *Tupaia minor* holding crickets with one hand (A, B) and reversing its hindfeet (C, D, E).

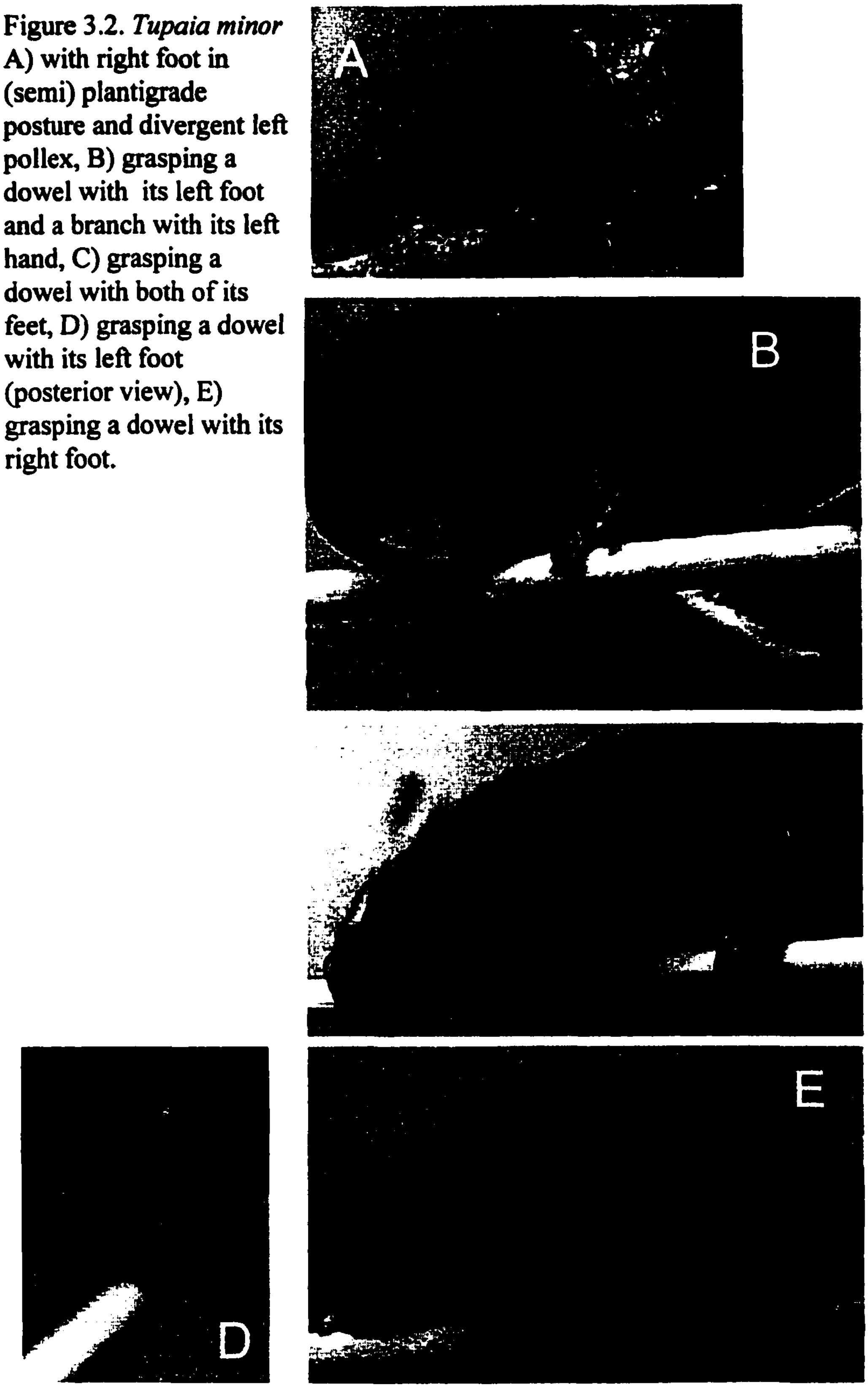


Figure 3.2. *Tupaia minor* A) with right foot in (semi) plantigrade posture and divergent left pollex, B) grasping a dowel with its left foot and a branch with its left hand, C) grasping a dowel with both of its feet, D) grasping a dowel with its left foot (posterior view), E) grasping a dowel with its right foot.

frequently, with their hands) in 84% of the dowel crossings (Table 3.5; Figs. 3.2b-e). They also often ate fruit, mealworms, and crickets with one hand rather than two (Figs. 3.1a-b).

DISCUSSION

Substrate Use

These data confirm reports from the wild that *T. minor* is predominantly arboreal and *T. tana* is predominantly terrestrial. *T. tana*'s preference for the ground may even have been underestimated in this study because *T. tana* individuals were almost always on the ground when I entered the animal lab and would move up into the branches when I approached their cages. Sorenson and Conaway (1964) and Sorenson (1970) reported similar differences in substrate use between these two species in captivity.

Tupaia minor habitually flexed (and abducted) its fore and hindlimbs and moved with its feet in a more semi-plantigrade posture (Fig. 3.2a) than did *T. tana*. These limb positions allow *T. minor* to keep its center of gravity close to the branch it is moving on, so that it does not topple to one side and fall off the branch (Napier, 1967; Cartmill, 1985). By contrast, *T. tana* extended its forelimbs more fully and moved with its feet in a more digitigrade posture, both of which would act to increase its stride length during terrestrial quadrupedal locomotion. In addition to these differences in the positions of the fore and hindlimbs, the tail length of these two species also reflects their differential substrate use in that *T. minor* has a relatively longer tail, helping it to balance on arboreal supports (Martin, 1968b, 1984, 1990). Not surprisingly, the more terrestrial *T. tana* rooted in the wood chips on the floors of its cages more often than did *T. minor*. This behavior is reflected in the skull morphology of these species in that *T. tana* has a relatively longer snout, which is presumably an adaptation for rooting in leaf litter (Martin, 1968b, 1984, 1990).

Locomotion

That *T. minor* climbed up and down branches, leapt between branches, and was suspended beneath branches more frequently than *T. tana* (Table 3.5) is not surprising because *T. minor* spent more time on branches than did *T. tana*. *T. minor* was observed reversing its feet (Figs. 3.1c-e; see Jenkins and McClearn, 1984) more often than *T. tana*, but this was expected because *T. minor* climbed and suspended itself more frequently than *T. tana*. Sorenson (1970) also reported that *T. minor* reverses its feet to a greater degree than *T. tana*. The body weight of *T. minor* is only about 25% that of *T. tana*, so it is not surprising that *T. minor* is more active and moves more quickly than *T. tana* (see Table 3.5 for average body weights).

Grasping

T. minor was often observed holding fruit, mealworms, and crickets with one hand (Figs. 3.1a-b). Holding food items in one hand, according to Napier (1961), is the behavioral correlate of prehensility. While this study did not include a systematic analysis of prehensile hands in relation to one-handed feeding, it does provide qualitative evidence for hand prehensility in clawed mammals (contra Napier, 1993) and supports the quantitative results of the exemplary experiment conducted by Lemelin and Grafton (1998) on callitrichid primates. In fact, Iwaniuk *et al.* (1998) showed that the claws of tree kangaroos actually help to facilitate one-handed grasping of food objects. Whishaw *et al.* (1998) found that clawed rodents are also capable of one-handed feeding.

While the terrestrial *T. tana* was never observed grasping, the arboreal *T. minor* was frequently observed grasping small branches and dowels in its cages, particularly with its feet (Figs. 3.2b-e) but occasionally with its hands (on the smaller dowel) as well (Fig. 3.2b). The hallux of *T. minor*, but not *T. tana*, was habitually divergent from its other digits (Figs. 3.2b-e). Even on larger branches that could not be grasped due to their large size, the four non-hallucial digits were typically held on the side of the branch and the hallux was placed on top of it. The pollex of *T. minor* was often quite divergent (Figs. 3.2a-b), particularly in certain positions, and the manual digits were often spread apart from one another (Fig. 3.2a). In contrast, those of *T. tana* were always less splayed. It is thus evident that in addition to *Ptilocercus* (Table 3.2; A. Zitzmann, pers. comm.), *T. minor*, an arboreal tupaiine, is indeed capable of grasping, while *T. tana*, a terrestrial tupaiine, is not. The grasping capability of *T. minor* is most likely an adaptation for moving on small branches, as Lim (1969) often observed *T. minor* "running upside down along thin branches of tall trees" (p. 125).

Models for Early Primates

The ability to grasp with the feet and hands has been proposed to be one of the defining features of primates (Le Gros Clark, 1962; Martin, 1990) and is therefore crucial to the understanding of the origin and early evolution of primates. Tupaiids have long been considered to represent a protoprimate stage of evolution, and Tattersall (1984) proposed *Tupaia* as a living ecological model of the ancestral primate. Rasmussen (1990), alternatively, used the didelphid marsupial *Caluromys* as a model for euprimate origins. However, based on postcranial morphology, *Caluromys* appears to be a poor choice for a model of the ancestral euprimate because while this taxon is arboreal, it does not possess any of the derived postcranial adaptations for graspleaping (a locomotor mode dominated by rapid leaping and climbing in which grasping is important during both climbing and landing: Szalay and Delson, 1979; Szalay and Dagosto, 1980, 1988; Dagosto, 1988; Szalay and Lucas, 1996) that characterize the first euprimates (Szalay and Sargis, submitted). Lemelin (1999), similarly, proposed didelphids as models for some aspects of early euprimates because, like primates, didelphids have evolved grasping extremities. The results reported here, however, suggest that arboreal tupaiids such as *T. minor* and especially *Ptilocercus* may represent better models for early primates (at least for plesiadapiforms) than didelphids. Arboreal tupaiids are not only far more closely related to primates than are didelphids, but they are also, as this study shows, capable of grasping. This is not to say that grasping in tupaiids is mechanically identical to that seen in primates. In fact, tupaiid grasping may be considered to be only "incipient" grasping in comparison to the more fully developed grasping of euprimates, and it is possible that the two conditions are not homologous. However, I propose that the type of grasping seen in tupaiids may represent the antecedent condition to that seen in primates, and I agree with Szalay and Dagosto (1988) that grasping may be primitive for archontan mammals. The first archontan may have evolved ("incipient") grasping capabilities similar to those of arboreal tupaiids, and the powerful grasping of primates may not have evolved until the origin of the first euprimates (for graspleaping; Szalay and Dagosto, 1980, 1988; Dagosto, 1988; Szalay and Lucas, 1996). Tupaiids can, at the very least, be used as living models for the extinct plesiadapiforms because both groups are clawed mammals, and they share similarities in their entocuneiform morphology that appear to be derived among eutherians (Szalay and Dagosto, 1988; see chapter 6).

The use of extant models is essential for the interpretation of extinct taxa such as plesiadapiforms and early euprimates, and the often difficult task of choosing an appropriate model is of the utmost importance as all paleobiological inferences concerning fossil taxa completely hinge upon it (Szalay, 1981; Szalay and Sargis, submitted). Simpson (1965) emphasized the significance of the choice of models for early primates when he stated that the "[u]se of [tupaiids] to represent the earliest primate or latest preprimate stage of evolution is as valid and useful, and subject to as much caution, as is any use of living animals to represent earlier phylogenetic stages" (p. 1397). Even with this cautious stance in mind, arboreal tupaiids still appear to represent the best living models for early primates, based on their shared grasping capabilities and their close phylogenetic relationships.

CHAPTER 4: AXIAL SKELETON

INTRODUCTION

Mammalian vertebral morphology has been analyzed in a few major studies (*e.g.*, Flower, 1885; Hatt, 1932; Gadow, 1933; Rockwell *et al.*, 1938; Slijper, 1946), but it is relatively poorly known compared to the morphology of the limbs. Much of the information on the mammalian vertebral column comes from studies of primates, and Shapiro's recent work (1993; 1995; Shapiro *et al.*, 1994; Shapiro and Demes, 1996; Johnson and Shapiro, 1998), in particular, has contributed greatly to the understanding of the function of mammalian vertebrae. Studies of mammalian ribs are even more rare than studies of vertebrae, although Jenkins' (1970) analysis of edentate and lorisine ribs is an important exception.

Several studies of tree shrews have included descriptions of the vertebrae and ribs. These studies have been conducted on *Ptilocercus* (Le Gros Clark, 1926), *Dendrogale* (Davis, 1938), and *Anathana* (Verma, 1965), but they all have lacked a functional-adaptive perspective. Jenkins (1974), however, did perform a functional analysis of the thoracic and lumbar vertebrae of *Tupaia glis* after he observed pronounced flexion and extension (in the sagittal plane) of the trunk during locomotion (especially during the bounding run, when speed is maximized). His study revealed several adaptations in thoracic (T) vertebra 11 through lumbar (L) vertebra 1 for extreme vertebral mobility in the region of these four vertebrae. This finding was significant because Jenkins (1974) observed little flexion of the lumbar vertebrae (they remained rigid even during extreme spinal flexion), which are typically considered to be more mobile than thoracic vertebrae (Rockwell *et al.*, 1938; Cartmill and Milton, 1977).

However, in a more detailed cineradiographic study of *T. glis* conducted by Schilling and Fischer (1999), it was found that the area of maximal mobility included the lumbar region (T11-L6) and that spinal flexion and extension contribute greatly to body propulsion during in-phase gaits (galloping in their study, because bounding was not observed).

Jenkins (1974) recognized that a flexible vertebral column in cursorial mammals increases stride length (see also Howell, 1944; Slijper, 1946; Smith and Savage, 1956; Hildebrand, 1959; Gambaryan, 1974; English, 1980; Hurov, 1987; Pridmore, 1992; Fischer, 1994), and he argued that this flexibility performs the same function in the leap and arboreal bounding run of *T. glis*. Jenkins may have, however, underestimated the significance of vertebral flexibility in increasing stride length during terrestrial running in *T. glis*, particularly considering Schilling and Fischer's (1999) conclusion that this flexibility contributes significantly to body propulsion during galloping. *T. glis*, while it could never be classified as cursorial in the sense applied to extant carnivorans and ungulates, has been shown to be much more terrestrial than was previously believed (Vandenbergh, 1963; Kaufmann, 1965; Lim, 1969; Kawamichi and Kawamichi, 1979; Langham, 1982), and increased stride length due to vertebral flexibility may be most significant in relation to the fact that *T. glis* seems to escape predators on the ground (Ridley, 1895; Le Gros Clark, 1927; Lekagul and McNeely, 1977; Langham, 1982). Hence, certain features may be difficult to interpret functionally when a scansorial (semi-terrestrial) or terrestrial species such as *T. glis* is the only species being examined.

In this analysis, both *Ptilocercus* and Tupaiinae were represented, and both arboreal (*Ptilocercus* and *T. minor*) and terrestrial (particularly *Urogale* and *T. tana*) tupaiids were examined. It should be pointed out, however, that arboreal and terrestrial differences in the tupaiid postcranium are often split down the subfamilial line because *Ptilocercus*, on the one hand, is arboreal, and most tupaiines, with the exception of *T. minor* and possibly *T. nicobarica*, are more terrestrial (Table 1.2). Also, the ancestral tupaiine was probably terrestrial (see below). Comparisons were also made to other archontans because any derived similarities shared by these taxa may represent retentions from an archontan ancestor.

MATERIALS AND METHODS SPECIFIC TO THIS CHAPTER

Using a Minolta RD-175 digital camera, I collected images of articulated rib cages and vertebral columns of tupaiid skeletal specimens. Digital images were viewed and saved in Adobe Photoshop, and qualitative comparisons were made to other archontan mammals. These included the specialized slow climbing lorisines (*Nycticebus coucang* and *Perodicticus potto*), a less specialized and small-bodied cheirogaleid (*Microcebus murinus*), a dermopteran (*Cynocephalus volans*), a chiropteran (*Pteropus* sp.), and a plesiadapiform (the atlas of *Plesiadapis gidleyi*; AMNH 17379).

RESULTS AND DISCUSSION

The results of this analysis are summarized in Tables 4.1 and 4.2. Several differences in mobility of the vertebral column were found between *Ptilocercus* and tupaiines (Table 4.1), and several similarities in the axial skeleton were discovered between *Ptilocercus* and other archontans (Table 4.2).

Ribs

The ribs of *Ptilocercus* are cranio-caudally expanded relative to those of tupaiines (Fig. 4.1). All of the species of *Tupaia*, *Dendrogale*, and *Urogale* have cranio-caudally

Table 4.1. Distribution of tupaiid axial skeletal features discussed in the text.

	Ptilocercus	Tupaiinae[a]	*Dendrogale*	*Tupaia glis*	*T. minor*	*T. tana*	*Urogale*	*Anathana*[b]
Ribs[c]	wide	narrow	narrow	narrow	narrow	narrow	narrow	narrow
Atlas[c]	wide	narrow	narrow	narrow	narrow	narrow	narrow	?
Axis spinous process	projects cranially	projects caudally	projects caudally	projects caudally	projects caudally	projects caudally	projects caudally	projects caudally
Thoracic spinous processes[c]	short and wide	long and narrow	long and narrow	long and narrow	long and narrow	long and narrow	long and narrow	long
Lumbar spinous processes	very short	long	intermediate	very long	long	very long	very long	long?
Lumbar transverse processes	short, face laterally	long, face ventrally	short, face ventrally	long, face ventrally	long, face ventrally	long, face ventrally	long, face ventrally	long, face ventrally

[a] This column summarizes the most common character states found among the species included in this subfamily.

[b] This taxon could not be examined due to a lack of postcranial specimens in American, European, and Indian museums. The features for this taxon were noted (when possible) from the figures and descriptions of Verma (1965).

[c] Width here refers to cranio-caudal width.

Table 4.2. Distribution of archontan axial skeletal features discussed in the text.

Taxon	Tupaiinae[a]	*Ptilocercus*	*Cynocephalus*	*Pteropus*	*Microcebus*[b]
Order	Scandentia	Scandentia	Dermoptera	Chiroptera	Primates
Ribs[c]	narrow	wide	wide	wide	intermediate
Atlas[c]	narrow	wide	wide	wide	narrow
Axis spinous process	projects caudally	projects cranially	projects cranially	projects cranially	projects cranially
Thoracic spinous processes[c]	long and narrow	short and wide	short and wide	short and wide	intermediate
Lumbar spinous processes	long	very short	short	short	long
Lumbar transverse processes	long, face ventrally	short, face laterally	short, face laterally	short, face laterally	intermediate, face ventrally

[a] This column summarizes the most common character states found among the species included in this subfamily.

[b] This strepsirhine was chosen to represent Primates because of its small body size (which is comparable to that of tupaiids) and its relatively less specialized type of locomotion (compared to that of other strepsirhines). While *Microcebus* frequently leaps, it is not as derived as other small-bodied strepsirhines such as galagines and lorisines, which are specialized for leaping and slow climbing, respectively. Other postcranially less specialized strepsirhines, *e.g.*, lemurids, are much larger than tupaiids.

[c] Width here refers to cranio-caudal width.

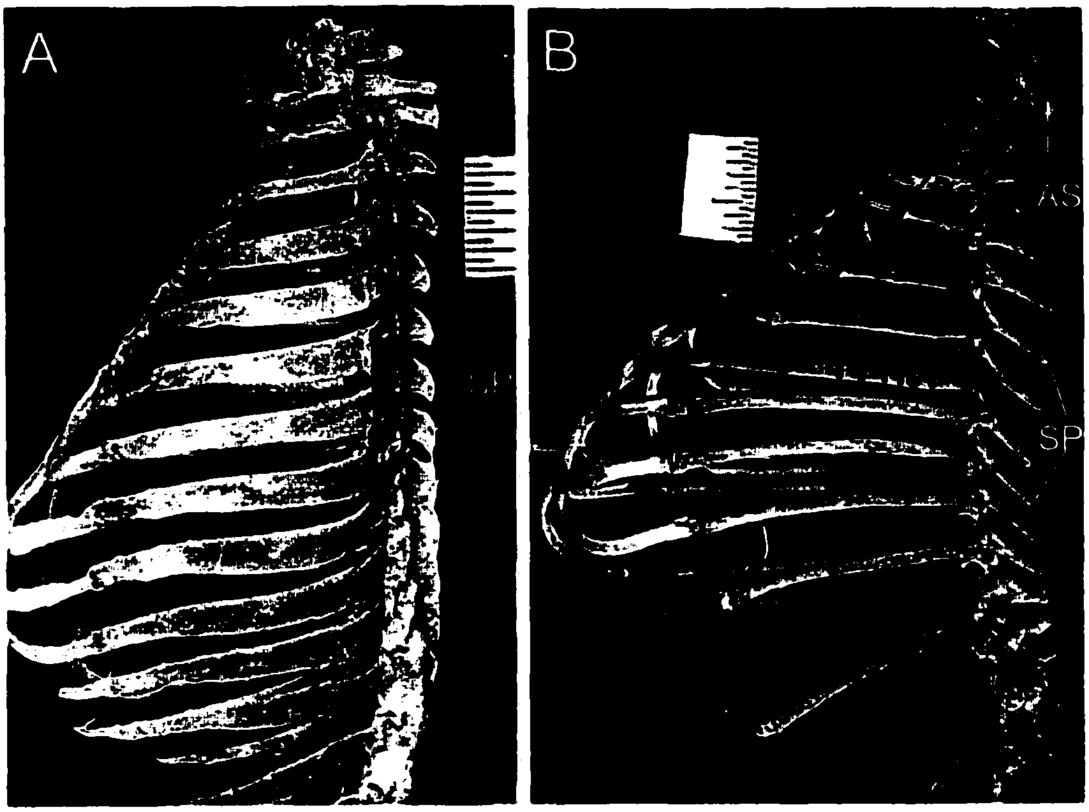


Figure 4.1. Lateral view of thorax of *Ptilocercus lowii* (A) and *Tupaia tana* (B). SP: spinous process, AS: axis spinous process. Subdivisions on scale are 0.5 mm. Note the cranio-caudally expanded ribs of *Ptilocercus* and the caudally oriented axis spinous process of *T. tana*. Also note the short, cranio-caudally wide thoracic spinous processes of *Ptilocercus*.

narrow ribs, and it appears from Verma's (1965) figure of *Anathana*'s ribs that they are not cranio-caudally expanded either (though this is difficult to determine due to the poor quality of the drawing). Jenkins (1970) discussed how expanded ribs may facilitate slow climbing and bridging (movements in which a gap between two supports is crossed by body stretching; Gebo, 1992) in lorisines by increasing "the stability of the thorax, which, in turn, increases the stability of the vertebral column" (p. 288). While *Ptilocercus* is not a slow climber, it may require this increased stability to "bridge" gaps between branches. Both dermopterans and chiropterans (see Vaughan, 1970) have cranio-caudally wide ribs as well, and this feature has been considered to be a synapomorphy uniting these two groups in the superorder Volitantia (Wible and Novacek, 1988; Szalay and Lucas, 1993, 1996; Simmons and Quinn, 1994; Simmons, 1995; Shoshani and McKenna, 1998). However, the fact that *Ptilocercus* also possesses this feature may mean that cranio-caudally expanded ribs represent an archontan feature that first evolved in a *Ptilocercus*-like ancestral archontan and has since been retained in these three groups because of its current utility. The expanded ribs of lorisines, on the other hand, are clearly derived within the primates and evolved independently from those of other archontans. This will be discussed further below.

Rib morphology is significant to the tupaiid fossil record because the only fossil tupaiid postcranial specimen ever reported was a rib cage from the Siwaliks of India that was said to possibly represent *Tupaia* (Dutta, 1975). Unfortunately, this specimen was never described or figured, but if it is indeed a tupaiid, it could be placed within the Tupaiinae if it lacks expanded ribs.

Numbers of Vertebrae

Gregory (1913), Lyon (1913), and Le Gros Clark (1926) reported that *Ptilocercus* has 7 cervical (C), 14 thoracic (T), 5 lumbar (L), 3 sacral (S) and 31-33 caudal vertebrae (thoracic vertebrae are defined here as rib-bearing vertebrae, rather than defined by reference to the anticlinal vertebra). Schultz (1961), on the other hand, determined that the average number of vertebrae for *Tupaia* is 7C, 13T, 6L, 3S, and 24 caudal vertebrae (see Lyon, 1913, as well). The same number of precaudal vertebrae is also found in *Dendrogale* (Davis, 1938) and *Anathana* (Verma, 1965). I have confirmed these precaudal counts for *Ptilocercus*, *Tupaia*, and *Dendrogale*, as well as counted the number of precaudal vertebrae in *Urogale* which, like the other tupaiines, has 7C, 13T, 6L, and 3S. Hence, *Ptilocercus* has one more thoracic and one fewer lumbar vertebrae than tupaiines. Because the lumbar region is more flexible than the thoracic region (Rockwell *et al.*, 1938; Cartmill and Milton, 1977), a reduction in lumbar vertebrae increases stability and decreases mobility (Slijper, 1946; Erickson, 1963; Ankel, 1972; Cartmill and Milton, 1977; Ward, 1993; Sanders and Bodenbender, 1994; Shapiro, 1995; Johnson and Shapiro, 1998). Therefore, the vertebral column of tupaiines may be more flexible than that of *Ptilocercus*. However, it is possible that the lumbar region of *Ptilocercus*, despite having one fewer vertebra, is just as long as that of tupaiines because region length is determined by both number of vertebrae and vertebral body length (Schultz, 1961; Erickson, 1963; Benton, 1967; Ankel, 1972; Shapiro, 1993, 1995; Ward, 1993; Johnson and Shapiro, 1998). While this seems unlikely based on comparisons of vertebral body length in the similarly sized *Ptilocercus* and *Dendrogale*, it can neither be confirmed nor denied without measurements of this region. A reduced lumbar region has been proposed as an adaptation for upright posture (Slijper, 1946; Rose, 1975; Sanders and Bodenbender, 1994; Shapiro *et al.*, 1994; Shapiro, 1995), brachiation (Erickson, 1963), bridging behavior (Cartmill and Milton, 1977), forelimb suspension (Ward, 1993; Sanders and Bodenbender, 1994), and to reduce bending loads in some or all of these activities (Johnson and Shapiro, 1998). A shortened lumbar region has been observed in the suspensory atelines and hominoids (Slijper, 1946; Schultz, 1961; Erickson, 1963; Benton, 1967; Ankel, 1972; Rose, 1975; Shapiro, 1993, 1995; Ward, 1993; Sanders and Bodenbender, 1994; Shapiro *et al.*, 1994; Johnson and Shapiro, 1998), as well as in the slow climbing sloths (Slijper, 1946). The slow climbing lorisines do not have an absolutely shortened lumbar region, but this region is relatively short when compared to the elongated thoracic region in this group (Cartmill and Milton, 1977). It is doubtful that *Ptilocercus* engages in upright posture or forelimb suspension, but it is possible that they need a more rigid spine to bridge gaps between branches. Johnson and Shapiro (1998) have argued that this is the case for the ateline *Alouatta* and that bridging "is likely to place bending stress on the spine, best resisted by a reduction in length" (p. 351).

A more elongated lumbar region in tupaiines, on the other hand, would allow more flexion and extension of the vertebral column, which has been shown to increase stride length during galloping (Howell, 1944; Slijper, 1946; Smith and Savage, 1956; Hildebrand, 1959; Gambaryan, 1974; English, 1980; Hurov, 1987; Pridmore, 1992; Fischer, 1994). An increased stride length in these predominantly terrestrial small mammals would allow them to increase their speed, which would be particularly advantageous when trying to escape predators.

The increased number of caudal vertebrae in *Ptilocercus* likely results in a longer external tail. Martin (1984, 1990) has discussed how, relative to terrestrial tupaiids, arboreal tupaiids such as *Ptilocercus* have longer tails, which allow them to better balance on branches.

Morphology of Vertebrae

The two most striking differences in the cervical vertebrae of tupaiids are found in the atlas and axis. The atlas of *Ptilocercus* is cranio-caudally expanded on the dorsal side (Fig. 4.2a), while it is quite short in tupaiines (Figs. 4.2b-c). In fact, the atlas of *Ptilocercus* is about the same length or longer than that of *Tupaia tana* (Fig. 4.2c), which is about 4.5 times larger than *Ptilocercus* in body size (Table 1.1), while it is much longer than that of *Dendrogale* (Fig. 4.2b), which is similar in body size to *Ptilocercus* (see Table 1.1). It appears that the cranio-caudally long atlas would restrict extension of the neck in *Ptilocercus*, while the short atlas of tupaiines would allow greater mobility. In addition, the cervical vertebrae of *Ptilocercus* (Fig. 4.2a) articulate tightly, restricting mobility, while those of tupaiines (see Fig. 4.2b for *Dendrogale*) exhibit more intervertebral space, allowing greater mobility. Unfortunately, the biological role of these features is not clear. The atlas of dermopterans and chiropterans (see Fenton and Crerar, 1984) is also cranio-caudally long, so this character may be primitive for Archonta even though the atlas of plesiadapiforms and euprimates is short.

The spinous process of the axis (viewed from the lateral side) is oriented cranially in *Ptilocercus* (Fig. 4.2d), in contrast to its caudal orientation in tupaiines (Figs. 4.1b, 4.2e). Evans (1939) has discussed how extension of the neck is limited by the contact of the spinous process of the axis with the atlas, which would occur in *Ptilocercus* due to

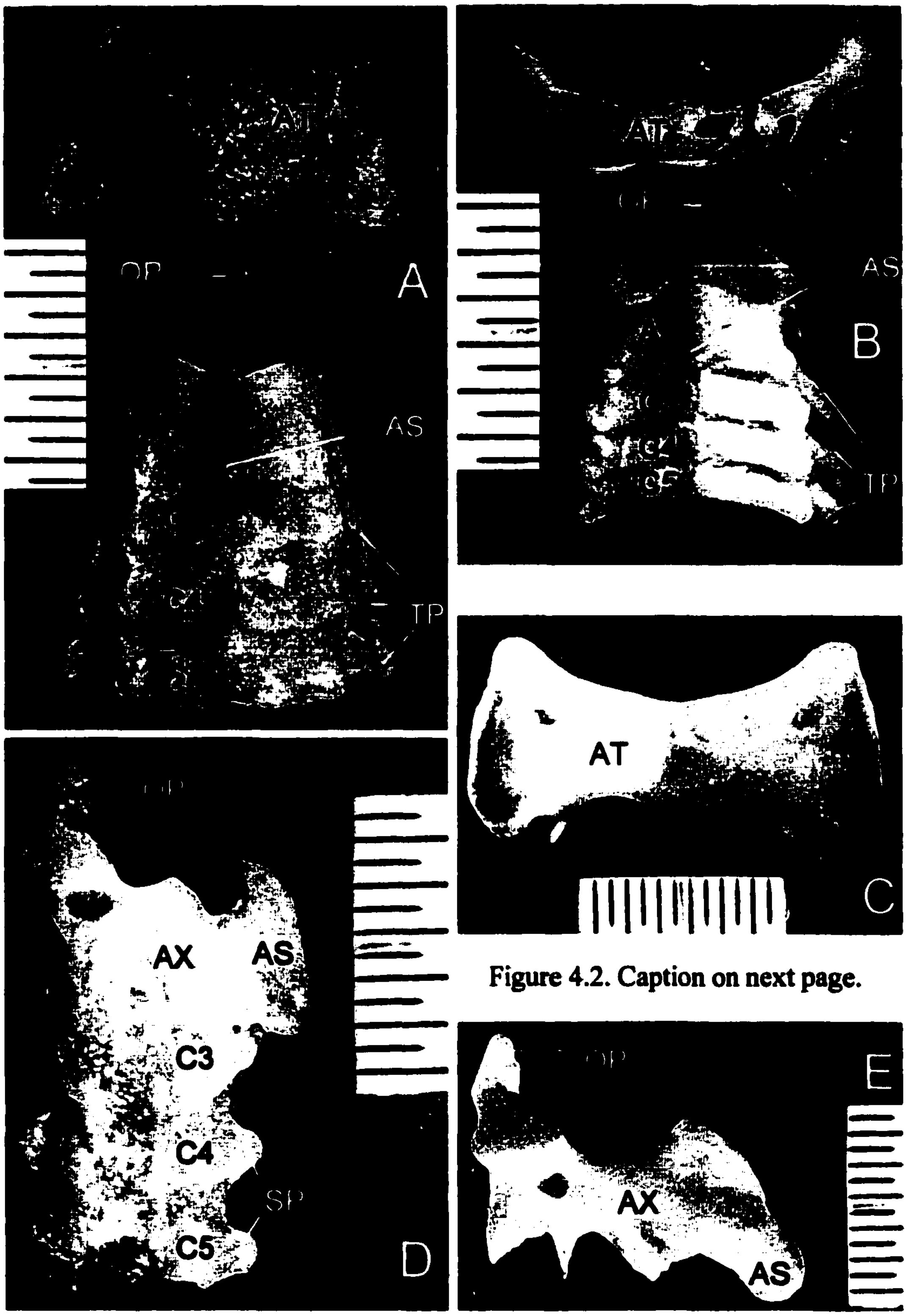


Figure 4.2. Caption on next page.

Figure 4.2. on previous page. Dorsal view of C1-C5 of *Ptilocercus lowii* (A) and *Dendrogale melanura* (B). Atlas of *Tupaia tana* (C). Lateral view of C2-C5 of *Ptilocercus lowii* (D). Lateral view of axis of *Tupaia tana* (E). AS: axis spinous process, AT: atlas, AX: axis, OP: odontoid process (dens), SP: spinous process, TP: transverse process. Subdivisions on scale are 0.5 mm. Note the cranio-caudally expanded atlas and cranially oriented axis spinous process of *Ptilocercus*. Also note the short cervical spinous processes and tightly articulating cervical vertebrae of *Ptilocercus*.

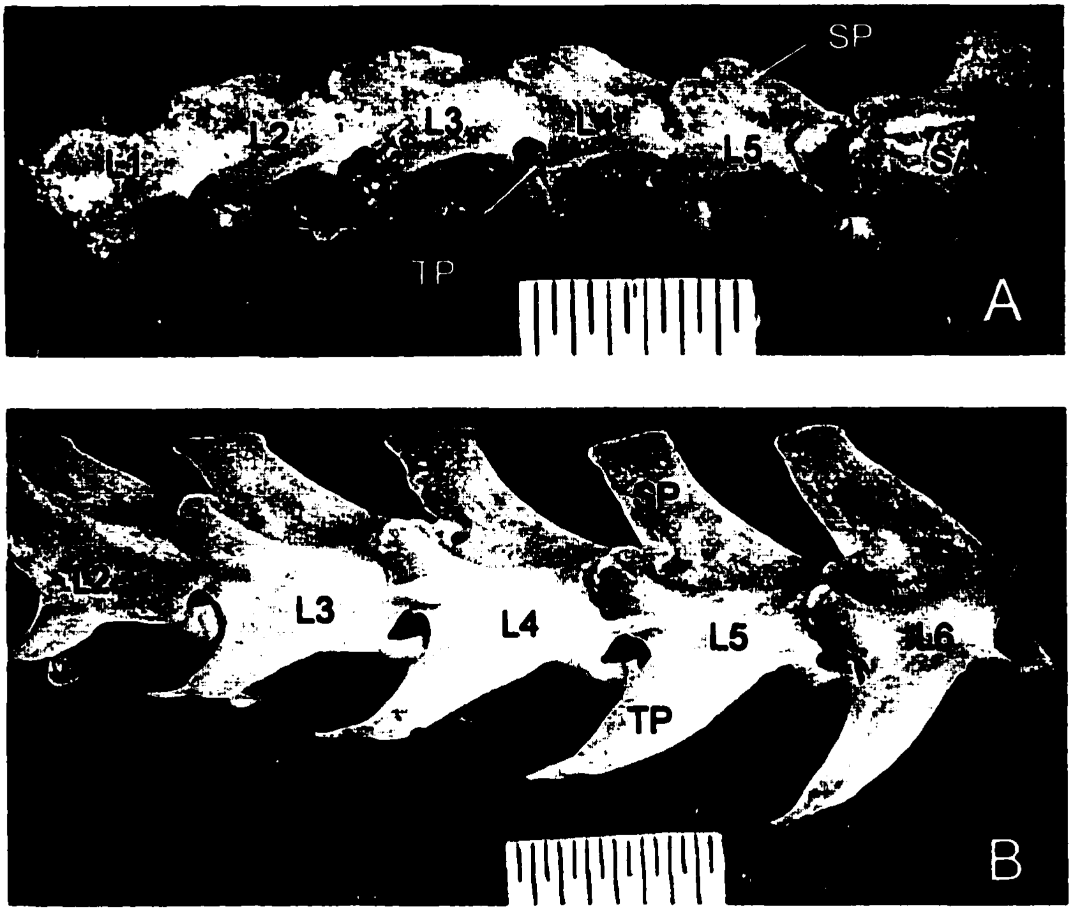


Figure 4.3. Lateral view of L1-L5 and sacrum of *Ptilocercus lowii* (A). Lateral view of L2-L6 of *Tupaia tana* (B). SA: sacrum, SP: spinous process, TP: transverse process. Subdivisions on scale are 0.5 mm. Note the short spinous processes and laterally oriented transverse processes of *Ptilocercus*. The lateral orientation of the transverse processes of *Ptilocercus* makes them difficult to see from this lateral view.

the cranial orientation of the spinous process of the axis. Again, this would restrict mobility in the neck, while the condition found in tupaiines would allow greater mobility. The condition found in *Ptilocercus* may be primitive for archontans, as it is also found in dermopterans, chiropterans, and *Microcebus*. In fact, a cranially oriented spinous process of the axis may be primitive for therians in general, as Evans (1939, figs. 12-13) has shown this condition in carnivorans, as well as in *Didelphis*. The change in orientation in tupaiines is difficult to interpret adaptively, but may be related to their terrestrial ancestry. Martin (1984, 1990) has discussed the elongation of the snout of the most terrestrial tupaiines (*T. tana* and *Urogale*) in relation to rooting in leaf litter, and Hatt (1932) has pointed out that changes in skull length, weight, and balance must affect the cervical vertebrae. If the origin of tupaiines coincided with increased terrestriality, there may have been an initial elongation of the skull (though not to the degree seen in *T. tana* or *Urogale*). Both the ligamentum nuchae, which supports and restricts the flexion of the skull, and the rectus capitis posterior major muscle, which extends the skull, attach to the spinous process of the axis (Evans, 1939), and the caudal orientation of this process may increase the mechanical advantage of this ligament and muscle. The fact that the attachment for this ligament and muscle has effectively been moved further from the skull may give them some advantage in anchoring the (elongated) skull. More definitive conclusions concerning the function of this feature would likely be reached in a study of neck myology or cranial morphology.

Wible and Novacek (1988) considered the "weak" or absent spinous processes on C3-C7 in dermopterans and chiropterans to be a synapomorphy of Volitantia (see also Simmons and Quinn, 1994; Simmons, 1995). However, the cervical spinous processes of

Ptilocercus (see Fig. 4.2d for C3-C5) are also short (Le Gros Clark, 1926) when compared to those of tupaiines. Short cervical spinous processes, therefore, may represent an archontan feature rather than a volitantian one (see below).

The spinous processes of the thoracic vertebrae of *Ptilocercus* are short (ventro-dorsally) and wide (cranio-caudally), while they are long and narrow in tupaiines (Fig. 4.1). The lumbar spinous processes are also short in *Ptilocercus*, compared to the long lumbar spinous processes of tupaiines (Fig. 4.3). Gebo (1989) stated that long (ventro-dorsally) spinous processes restrict mobility in galagines. However, Gambaryan (1974) has demonstrated in his comparisons of ungulates, which have stable vertebral columns, and carnivorans, which have mobile vertebral columns, that it is actually cranio-caudally wide spinous processes that restrict vertebral mobility. The mobility of the vertebral column of ungulates is restricted because they have little intervertebral space between their relatively wide spinous processes. On the other hand, carnivorans have greater spinal mobility because they have more intervertebral space between their relatively narrow spinous processes (Gambaryan, 1974). The short, wide spinous processes of *Ptilocercus*, therefore, may restrict spinal mobility by decreasing intervertebral space, while the long, narrow spinous processes of tupaiines may allow greater spinal mobility by increasing intervertebral space. Again, the restricted mobility in the vertebral column of *Ptilocercus* may be an adaptation for bridging, while the greater mobility in the vertebral column of tupaiines contributes to increased stride length. It is interesting that for this feature *Ptilocercus* is convergent with the slow climbing lorisines, while tupaiines are convergent with the leaping galagines. Lorisines have stable vertebral columns for slow climbing and bridging (Cartmill and Milton, 1977) and exhibit more lateral flexion of the spine (Curtis, 1995; Shapiro and Demes, 1996), while galagines have mobile vertebral columns and exhibit more sagittal flexion and extension of the spine to increase the length of their leaps (as opposed to increasing stride length during running).

Straus and Wislocki (1932) noted that the spinous processes of the lower thoracic and lumbar vertebrae of sloths are similar to those of lorisines in being short and wide, and that this similarity is likely to be convergent in these two taxa due to their shared slow climbing locomotion. *Palaeopropithecus*, a large, almost certainly slow climbing and suspensory (based on a wide range of data) subfossil lemur is, like sloths, convergent with lorisines in that its lumbar spinous processes are short (Shapiro *et al.*, 1994). Finally, among non-primate archontans, the thoracic spinous processes of dermopterans and chiropterans (see Vaughan, 1970) are short and wide, and the lumbar spinous processes are short as in *Ptilocercus*. Here again, these characters may have evolved in a *Ptilocercus*-like ancestral archontan and may, therefore, represent primitive retentions in the dermopterans and chiropterans (see below).

The length of the thoracic and lumbar spinous processes is also significant in that they act as bony levers for the vertebral extensor muscles, multifidus and semispinalis dorsi (Le Gros Clark, 1924a, 1926; Shapiro, 1993, 1995). The increased length of these processes in tupaiines gives the extensor muscles a greater mechanical advantage for powerful extension during terrestrial running, for which a great deal of vertebral flexion and extension is important to increase stride length. It is also significant that Le Gros Clark (1926) refers to the multifidus muscle in *Ptilocercus* as "not very prominently developed" (p. 1288), while in a tupaiine of similar size he describes this muscle as being "large" and the semispinalis dorsi as being "well-defined" (Le Gros Clark, 1924a, p. 489).

The lumbar transverse processes vary interspecifically in both length and orientation. In *Ptilocercus*, they are relatively short and are oriented more laterally, while they are longer and oriented more ventrally in tupaiines (Figs. 4.3-4.4). Therefore, the tips of the transverse processes in *Ptilocercus* are more closely in line with the axis of extension, allowing the erector spinae muscles (longissimus and iliocostalis, which attach to the dorsal sides of the transverse processes) to better stabilize the thorax by resisting ventral flexion of the spine (Shapiro, 1993, 1995; Johnson and Shapiro, 1998). This increases the stability of the vertebral column in *Ptilocercus* and may again be related to bridging locomotion (see Johnson and Shapiro, 1998, on *Alouatta*). In this feature, *Ptilocercus* is again convergent with the slow climbing lorisines (see Curtis, 1995; Shapiro, 1995) and the suspensory atelines and hominoids (see Benton, 1967; Ankel, 1972; Ward, 1993; Shapiro, 1993, 1995; Sanders and Bodenbender, 1994; Johnson and Shapiro, 1998), as well as with sloths (see Ward, 1993). This feature is also shared with dermopterans and chiropterans among the Archonta (see discussion below). On the other hand, the transverse processes of tupaiines extend far more ventrally, both because they are oriented in this direction and because they are longer than in *Ptilocercus*. The ventral position of the tupaiine lumbar transverse processes allows powerful flexion of the vertebral column by psoas major and quadratus lumborum, which attach to the ventral sides of the transverse processes (Shapiro, 1995). The ventral deflection of the lumbar transverse processes in tupaiines also increases the size of the compartment for enlarged erector spinae muscles, which powerfully extend the vertebral column (Benton, 1967;

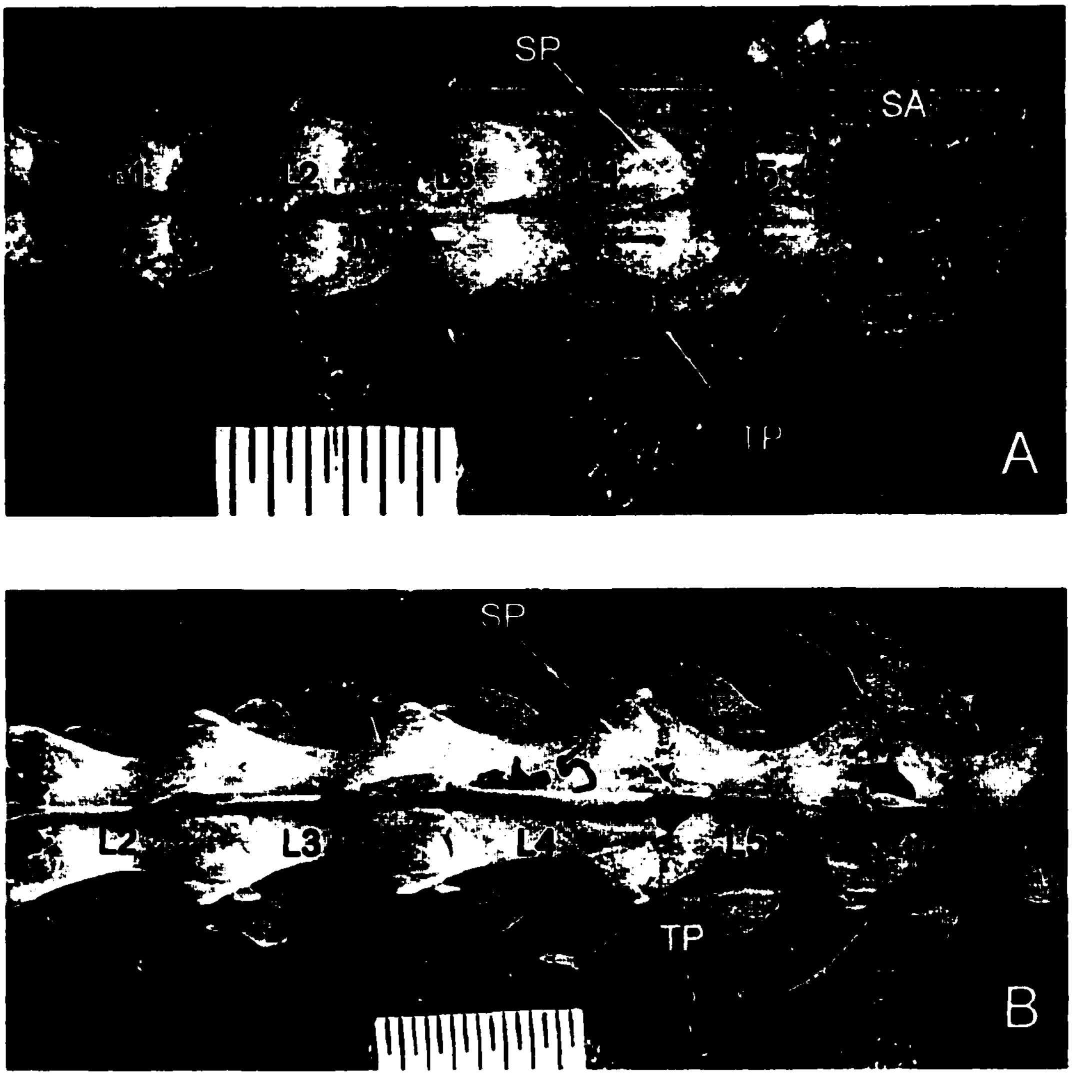


Figure 4.4. Dorsal view of L1-L5 and sacrum of *Ptilocercus lowii* (A). Dorsal view of L2-L6 of *Tupaia tana* (B). SA: sacrum, SP: spinous process, TP: transverse process. Subdivisions on scale are 0.5 mm. Note the short transverse processes of *Ptilocercus*.

Sanders and Bodenbender, 1994; Shapiro, 1995). Powerful spinal flexion and extension in tupaiines is important for terrestrial running because it increases the length of the stride during galloping and bounding (see above).

Le Gros Clark (1926) noted that in *Ptilocercus* two sacral vertebrae articulate with the ilia. Alternatively, Davis (1938) stated that in *Dendrogale* only one sacral vertebra articulates with the ilia as in *Tupaia*. The articulation of two sacral vertebrae with the ilia in *Ptilocercus* may again increase stability, while the tupaiine condition allows greater mobility.

Evolution of the Axial Skeleton in Scandentia

Many authors have stated that *Ptilocercus* is likely to exhibit primitive features for tupaiids, and that the ancestral tupaiid was probably arboreal and more similar to *Ptilocercus* in its morphology than to tupaiines (Le Gros Clark, 1926; Szalay, 1969; Campbell, 1974; Gould, 1978; Butler, 1980; Szalay and Drawhorn, 1980; Martin, 1990; Szalay and Lucas, 1993, 1996). It also seems likely that the origin of tupaiines coincided with a shift to more terrestrial locomotion and that the ancestral tupaiine was terrestrial (see also chapters 5 and 6). Hence, the features discussed above for *Ptilocercus* are probably ancestral for tupaiids, and the features discussed for tupaiines are most likely derived within Tupaiidae. The increased vertebral mobility of tupaiines is likely advantageous for terrestrial locomotion because it results in increased stride length, which would have allowed the ancestral tupaiine to move more efficiently on the ground and, perhaps more importantly, to increase its speed when escaping predators on the ground. The condition of the ribs and vertebrae of *Ptilocercus* provide stability in the thorax, which may facilitate arboreal bridging locomotion.

Evolution of the Axial Skeleton in Archonta

I have shown above that both dermopterans and chiropterans share many rib and vertebral features with *Ptilocercus*, but not with tupaiines (see Table 4.2). While these features may have evolved independently in these three lineages, it seems more probable that they represent shared derived (relative to the likely terrestrial ancestral eutherian; see Szalay, 1984, 1994; Szalay and Sargis, submitted) characters of the Archonta for the following reason. *Ptilocercus*, probably resembling the ancestral scandentian (see above), is more likely to exhibit primitive traits for Archonta than is any living dermopteran (likely derived in relation to gliding), chiropteran (likely derived in relation to flying), or euprimate (primitively derived in relation to graspleaping; see Szalay and Dagosto, 1980, 1988; Dagosto, 1988; Szalay and Lucas, 1996). If these factors are taken into account, then the adaptations for vertebral stability seen in *Ptilocercus* would have also existed in the ancestral archontan. Such adaptations for a stable thorax would have been retained in the more dermopteran-like volitantian ancestor, as well as in the dermopteran lineage, for stability during gliding, slow climbing or bridging locomotion, suspensory (hanging) behavior (see Szalay and Lucas, 1993, 1996; Simmons and Quinn, 1994; Simmons, 1995), or a combination of some or all of these behaviors. A stable thorax would also have been advantageous in the first chiropterans for hanging (see Szalay and Lucas, 1993, 1996; Simmons and Quinn, 1994; Simmons, 1995) and/or for stability of the thorax during flight (see Slijper, 1946), so the adaptations for a stable thorax were therefore retained in chiropterans as well. Finally, the graspleaping ancestral euprimate would most likely have evolved a more flexible vertebral column capable of significant flexion and extension of the spine that would have resulted in an increase in the length of its leaps. This hypothesis, as well as the one above concerning tupaiids, could be further tested with quantitative analyses of the vertebral morphology of these mammals, as well as myological comparisons of their epaxial musculature.

CHAPTER 5: FORELIMB

INTRODUCTION

The forelimb myology of tupaiids has been well described by Le Gros Clark (1924a, 1926) and George (1973, 1977). Endo *et al.* (1999) recently studied the functional morphology of *Dendrogale murina*, and made several conclusions about its forelimb morphology and myology. However, there are several problems with this study.

First, they assumed that *D. murina* is arboreal. This may not be the case as *D. melanura* is probably terrestrial (see chapter 1; Emmons pers. comm.). They also made erroneous statements about muscle attachments. For example they stated that the triceps muscle is attached to the tibia (rather than the ulna) and that the flexor carpi ulnaris originates from the lateral epicondyle (rather than the medial epicondyle). Finally, they conclude that the scapula of *D. murina* is adapted for arboreality because it has a postscapular fossa (which they also refer to as the "postcranial fossa"), a small supraspinous fossa, and a protruding acromion. However, they do not explain how the postscapular fossa or the protruding acromion are advantageous for arboreal locomotion, and my comparisons of *Dendrogale* to other tupaiids have not shown that the acromion of *Dendrogale* is particularly "protruding." I agree that *Dendrogale* has a small supraspinous fossa, but I disagree with the interpretation of this feature as being an arboreal adaptation. In fact, the small supraspinous fossa contributes to the narrow width of the *Dendrogale* scapula, and Endo *et al.* (1999) do describe the scapula of *D. murina* as "slender in cranio-caudal length" (p. 401). To interpret a narrow scapula as an arboreal adaptation is contradictory to previous evidence on various mammals (see Jolly, 1967; Roberts, 1974). Narrow scapulae are seen in terrestrial tupaiids (see below), terrestrial cercopithecids (Jolly, 1967), and some other terrestrial eütherians (Smith and Savage, 1956; Roberts, 1974), as well as in some terrestrial marsupials (Argot, in press). Therefore, the combined behavioral and morphological data show that *Dendrogale* is more likely to be terrestrial than arboreal (see below), despite the conclusions of Endo *et al.* (1999).

Stafford and Thorington (1998) studied the carpus of several different mammals, including tupaiids. Their exemplary study of carpal morphology went beyond an examination of carpal patterns, in that developmental data were incorporated into the analysis. Their work makes the wrist the one well studied region of the tupaiid forelimb, and I will be able to contribute little beyond their conclusions. However, I will note when I concur with their assessment and when I disagree with it.

RESULTS AND DISCUSSION

Standard Indices

An examination of the intermembral index shows that the smallest tupaiids, *Ptilocercus* and *Dendrogale* (see Table 1.1), have longer forelimbs relative to their hindlimbs compared to larger tupaiids (Fig. 5.1, Tables 5.1, 5.25). Interestingly, *Dendrogale* is more similar to *Ptilocercus* for this index than it is to other tupaiines. *T. gracilis*, another small tupaiid (Table 1.1), has shorter forelimbs relative to its hindlimbs (Fig. 5.1, Table 5.25) and is significantly different from every other species (Table 5.1). The other small tupaiids, the arboreal *T. minor* (Table 1.1) and *T. javanica* (which is similar in size to *T. minor*; see Martin, 1984), are similar to the larger, terrestrial/scansorial tupaiids in their limb proportions (Fig. 5.1, Tables 5.1, 5.25). Hence, this index clearly does not scale with body size. However, it is also not correlated

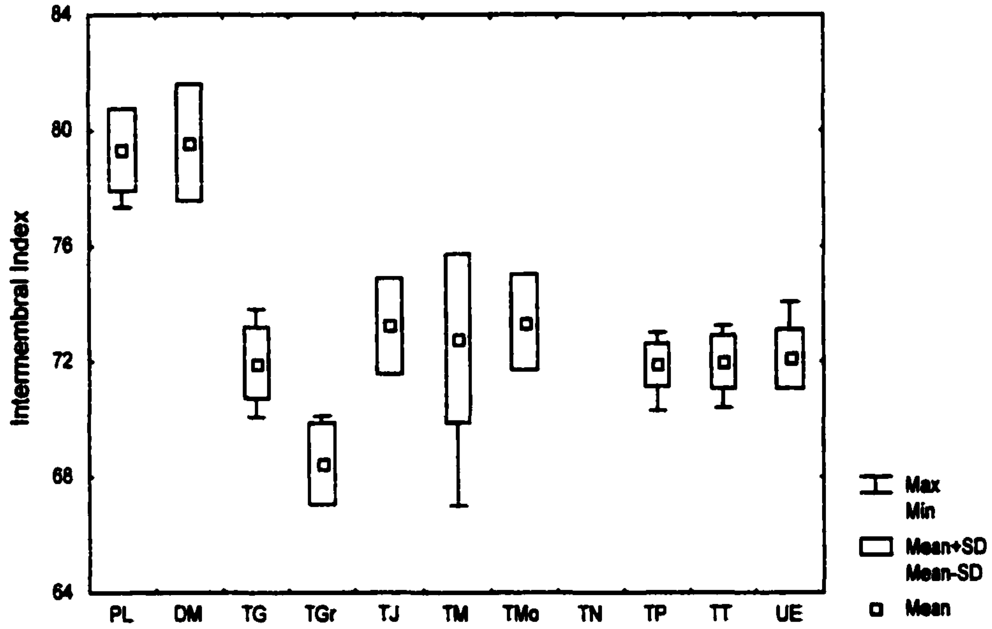


Figure 5.1. Box plot of intermembral index. Note the high indices of *Ptilocercus* and *Dendrogale*.

Table 5.1: Probabilities* from Tukey Honest Significant Difference (HSD) post hoc test of intermembral index.

	Dendrogale melanura	*Dendrogale murina*	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
D. melanura		0.9383	0.9940	**0.0001**	**0.0001**	**0.0011**	**0.0002**	**0.0014**	**0.0001**	**0.0001**	**0.0001**
D. murina	0.9383		0.9997	**0.0026**	**0.0001**	0.1483	**0.0254**	0.1702	**0.0027**	**0.0027**	**0.0043**
P. lowii	0.9940	0.9997		**0.0001**	**0.0001**	**0.0003**	**0.0001**	**0.0003**	**0.0001**	**0.0001**	**0.0001**
T. glis	**0.0001**	**0.0026**	**0.0001**		**0.0091**	0.9812	0.9790	0.9665	1.0000	1.0000	1.0000
T. gracilis	**0.0001**	**0.0001**	**0.0001**	**0.0091**		**0.0142**	**0.0019**	**0.0111**	**0.0149**	**0.0077**	**0.0060**
T. javanica	**0.0011**	0.1483	**0.0003**	0.9812	**0.0142**		1.0000	1.0000	0.9783	0.9829	0.9949
T. minor	**0.0002**	**0.0254**	**0.0001**	0.9790	**0.0019**	1.0000		1.0000	0.9769	0.9813	0.9976
T. montana	**0.0014**	0.1702	**0.0003**	0.9665	**0.0111**	1.0000	1.0000		0.9624	0.9691	0.9892
T. palawanensis	**0.0001**	**0.0027**	**0.0001**	1.0000	**0.0149**	0.9783	0.9769	0.9624		1.0000	1.0000
T. tana	**0.0001**	**0.0027**	**0.0001**	1.0000	**0.0077**	0.9829	0.9813	0.9691	1.0000		1.0000
U. everetti	**0.0001**	**0.0043**	**0.0001**	1.0000	**0.0060**	0.9949	0.9976	0.9892	1.0000	1.0000	

*probabilities in bold are significant at the p < .05 level

Table 5.2: Probabilities* from Tukey Honest Significant Difference (HSD) post hoc test of humerofemoral index.

	Dendrogale melanura	*Dendrogale murina*	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
D. melanura		0.9936	0.2414	**0.0088**	**0.0002**	0.3009	0.1661	**0.0336**	0.9999	**0.0059**	**0.0001**	**0.0001**
D. murina	0.9936		0.9779	0.3878	**0.0093**	0.9830	0.9551	0.5197	1.0000	0.2961	**0.0013**	**0.0083**
P. lowii	0.2414	0.9779		0.5602	**0.0029**	1.0000	1.0000	0.9002	0.8231	0.4002	**0.0001**	**0.0003**
T. glis	**0.0088**	0.3878	0.5602		0.0616	0.8472	0.4282	1.0000	0.1389	1.0000	**0.0001**	**0.0025**
T. gracilis	**0.0002**	**0.0093**	**0.0029**	0.0616		**0.0137**	**0.0015**	0.7031	**0.0021**	0.1903	1.0000	1.0000
T. javanica	0.3009	0.9830	1.0000	0.8472	**0.0137**		1.0000	0.9499	0.8569	0.7096	**0.0002**	**0.0044**
T. minor	0.1661	0.9551	1.0000	0.4282	**0.0015**	1.0000		0.9102	0.7376	0.2918	**0.0001**	**0.0001**
T. montana	**0.0336**	0.5197	0.9002	1.0000	0.7031	0.9499	0.9102		0.2533	1.0000	0.2935	0.7929
T. nicobarica	0.9999	1.0000	0.8231	0.1389	**0.0021**	0.8569	0.7376	0.2533		0.0980	**0.0003**	**0.0016**
T. palawanensis	**0.0059**	0.2961	0.4002	1.0000	0.1903	0.7096	0.2918	1.0000	0.0980		**0.0003**	**0.0492**
T. tana	**0.0001**	**0.0013**	**0.0001**	**0.0001**	1.0000	**0.0002**	**0.0001**	0.2935	**0.0003**	**0.0003**		0.9598
U. everetti	**0.0001**	**0.0083**	**0.0003**	**0.0025**	1.0000	**0.0044**	**0.0001**	0.7929	**0.0016**	**0.0492**	0.9598	

*probabilities in bold are significant at the p < .05 level

with substrate use, as the arboreal *Ptilocercus* is similar to the more terrestrial *Dendrogale*, and the arboreal *T. minor* is similar to terrestrial taxa, such as *T. tana* and *Urogale*.

The humerofemoral index is high in *Dendrogale* and low in *T. gracilis*, *T. tana*, and *Urogale*, which are all terrestrial (Fig. 5.2; Tables 5.2, 5.25). The values for *Dendrogale* and *T. gracilis* are not surprising in light of their intermembral indices. The relatively long forelimb of *Dendrogale* is apparently due to a relatively elongated humerus, rather than an elongation of the antebrachium. The fact that *Ptilocercus* does not have a high humerofemoral index means that its relatively long forelimb must be due to a relatively elongated antebrachium (and it should thus have a high brachial index).

The brachial index of *Ptilocercus* is, as expected, relatively high (Fig. 5.3; Tables 5.3, 5.25), but it is also high in *Urogale*. The latter is not particularly surprising when one considers *Urogale's* low humerofemoral index and average intermembral index. In other words, *Urogale* has a relatively short humerus, but not a relatively short forelimb, so it must have a relatively long antebrachium. However, it is interesting that *Ptilocercus* and *Urogale* have high values because *Ptilocercus* is the smallest (along with *Dendrogale*; see Table 1.1), most arboreal tupaiid, while *Urogale* is the largest, most terrestrial tupaiid. Hence, this index is clearly not associated with differences related to either phylogeny (these taxa are from different clades), body size, or substrate preference. The value of all such gross indices is questionable when considering relatively less specialized taxa (compared to various eutherian specialists), such as tupaiids. This, however, is not the case when considering taxa such as primates, where brachiators, such

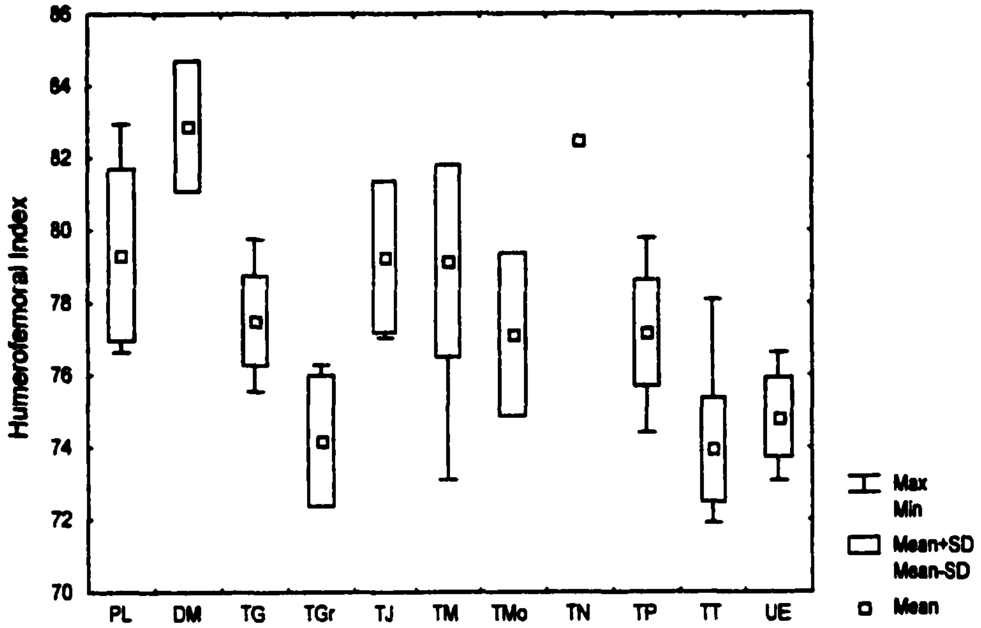


Figure 5.2. Box plot of humerofemoral index. Note the high index of *Dendrogale* and the low indices of *T. gracilis*, *T. tana*, and *Urogale*.

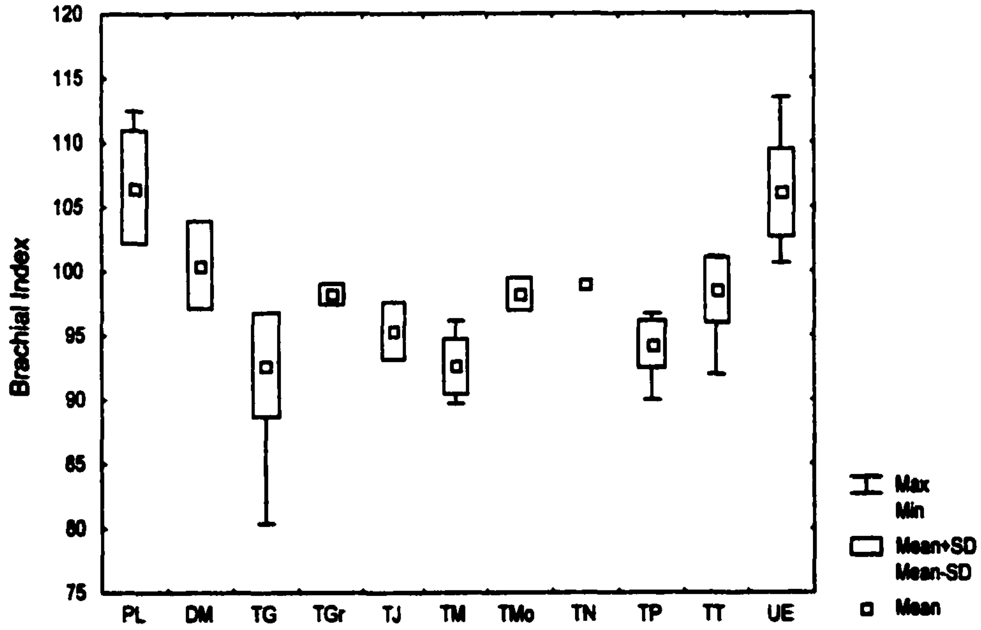


Figure 5.3. Box plot of brachial index. Note the high indices of *Ptilocercus* and *Urogale*.

Table 5.3: Probabilities* from Tukey Honest Significant Difference (HSD) post hoc test of brachial index.

	Dendrogale melanura	*Dendrogale murina*	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
D. melanura		0.9914	0.9946	0.0716	0.9698	0.6609	0.0807	0.9787	0.9988	0.2466	0.9560	0.9974
D. murina	0.9914		0.3307	0.8594	1.0000	0.9999	0.8641	1.0000	1.0000	0.9892	1.0000	0.3379
P. lowii	0.9946	0.3307		**0.0001**	**0.0195**	**0.0025**	**0.0001**	0.0676	0.5234	**0.0001**	**0.0003**	1.0000
T. glis	0.0716	0.8594	**0.0001**		0.1777	0.9907	1.0000	0.4266	0.6759	0.9776	**0.0004**	**0.0001**
T. gracilis	0.9698	1.0000	**0.0195**	0.1777		0.9957	0.2296	1.0000	1.0000	0.7137	1.0000	**0.0097**
T. javanica	0.6609	0.9999	**0.0025**	0.9907	0.9957		0.9913	0.9984	0.9972	1.0000	0.9634	**0.0013**
T. minor	0.0807	0.8641	**0.0001**	1.0000	0.2296	0.9913		0.4684	0.6878	0.9876	**0.0027**	**0.0001**
T. montana	0.9787	1.0000	0.0676	0.4266	1.0000	0.9984	0.4684		1.0000	0.8842	1.0000	0.0516
T. nicobarica	0.9988	1.0000	0.5234	0.6759	1.0000	0.9972	0.6878	1.0000		0.9380	1.0000	0.5420
T. palawanensis	0.2466	0.9892	**0.0001**	0.9776	0.7137	1.0000	0.9876	0.8842	0.9380		0.0603	**0.0001**
T. tana	0.9560	1.0000	**0.0003**	**0.0004**	1.0000	0.9634	**0.0027**	1.0000	1.0000	0.0603		**0.0001**
U. everetti	0.9974	0.3379	1.0000	**0.0001**	**0.0097**	**0.0013**	**0.0001**	0.0516	0.5420	**0.0001**	**0.0001**	

*probabilities in bold are significant at the $p < .05$ level

Table 5.4: Probabilities* from Tukey Honest Significant Difference (HSD) post hoc test of scapula shape index.

	Dendrogale melanura	*Dendrogale murina*	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
D. melanura		1.0000	**0.0003**	1.0000	1.0000	1.0000	0.9994	0.9994	0.9999	1.0000	0.9996	1.0000
D. murina	1.0000		**0.0003**	1.0000	1.0000	1.0000	0.9996	0.9996	0.9999	1.0000	0.9997	1.0000
P. lowii	**0.0003**	**0.0003**		**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0002**	**0.0044**	**0.0001**	**0.0001**	**0.0001**
T. glis	1.0000	1.0000	**0.0001**		1.0000	1.0000	0.9940	0.9996	1.0000	1.0000	0.9828	1.0000
T. gracilis	1.0000	1.0000	**0.0001**	1.0000		1.0000	0.9998	0.9999	1.0000	1.0000	0.9999	1.0000
T. javanica	1.0000	1.0000	**0.0001**	1.0000	1.0000		0.9768	0.9970	0.9999	1.0000	0.9608	1.0000
T. minor	0.9994	0.9996	**0.0001**	0.9940	0.9998	0.9768		1.0000	1.0000	0.9942	1.0000	0.9495
T. montana	0.9994	0.9996	**0.0002**	0.9996	0.9999	0.9970	1.0000		1.0000	0.9995	1.0000	0.9956
T. nicobarica	0.9999	0.9999	**0.0044**	1.0000	1.0000	0.9999	1.0000	1.0000		1.0000	1.0000	0.9998
T. palawanensis	1.0000	1.0000	**0.0001**	1.0000	1.0000	1.0000	0.9942	0.9995	1.0000		0.9880	1.0000
T. tana	0.9996	0.9997	**0.0001**	0.9828	0.9999	0.9608	1.0000	1.0000	1.0000	0.9880		0.8921
U. everetti	1.0000	1.0000	**0.0001**	1.0000	1.0000	1.0000	0.9495	0.9956	0.9998	1.0000	0.8921	

*probabilities in bold are significant at the $p < .05$ level

as hylobatids, have high intermembral indices, and leapers, such as indriids, galagids, and tarsiids, have low intermembral indices.

Scapula

The scapula of *Ptilocercus* is short and relatively broad, while the scapulae of tupaiines are longer and relatively narrower (Figs. 5.4, 5.6; Tables 5.5, 5.25). Consequently, the vertebral border of the scapula is relatively long in *Ptilocercus*, while it is relatively short in tupaiines. The scapula shape index of *Ptilocercus* is significantly different from that of all other tupaiines (Table 5.4). The supraspinous fossa of *Ptilocercus* is expanded cranially and the metacromion (attachment area for the spinodeltoideus muscle; George, 1977) is angled more cranially (Fig. 5.6). Both of these features are also found in arboreal guenons (Gebo and Sargis, 1994). The supraspinatus muscle attaches to the supraspinous fossa and the deltoid muscle (pars spinodeltoideus; George, 1977) attaches to the ventral half of the caudal lip of the scapular spine; both of these muscles are important in the elevation of the arm, and the supraspinatus is also responsible for resisting humeral displacement during arm elevation (Larson, 1993). Hence, the demands on this muscle are greater in arboreal mammals because they raise their arms above their head more frequently than terrestrial mammals. The cranial expansion of the supraspinous fossa in *Ptilocercus* is, therefore, not surprising considering this taxon is more arboreal than any tupaiine. Le Gros Clark (1926) described the supraspinatus muscle of *Ptilocercus* as "powerfully developed" (p. 1271). The more cranial orientation of the metacromion may provide better leverage for the deltoid during arm elevation (Gebo and Sargis, 1994). Finally, the longer vertebral border (relative to the length of the scapula) may increase the mechanical advantage of

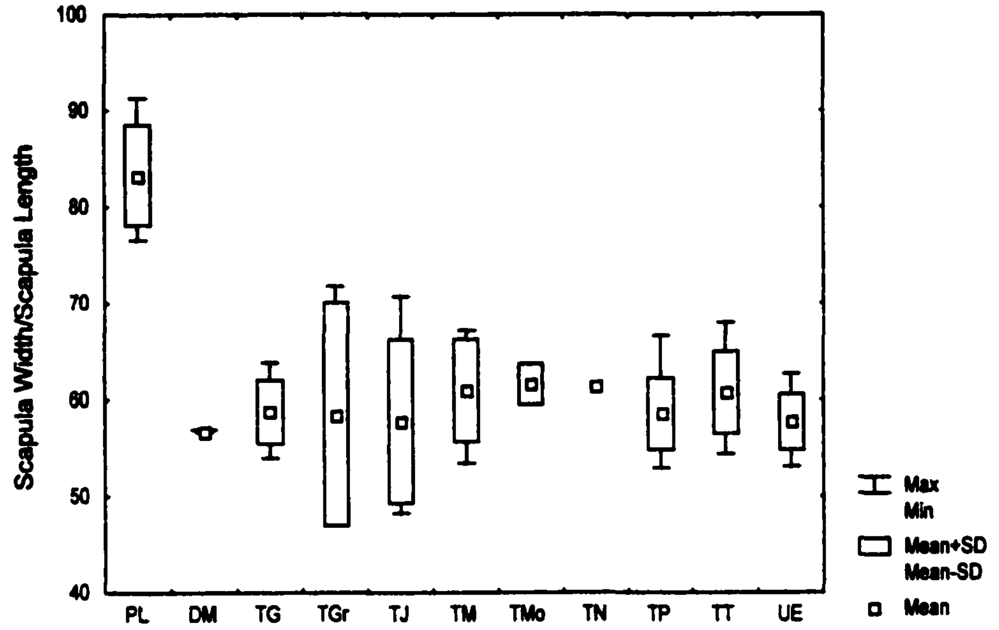


Figure 5.4. Box plot of scapula shape index. Note the high index of *Ptilocercus*.

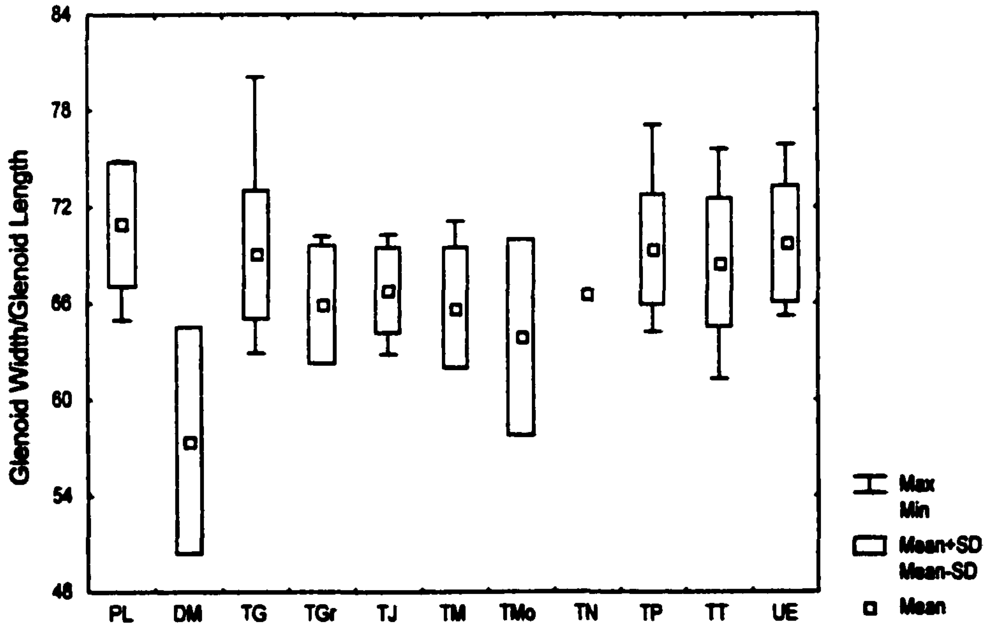


Figure 5.5. Box plot of glenoid fossa shape index. Note the low index of *Dendrogale*.

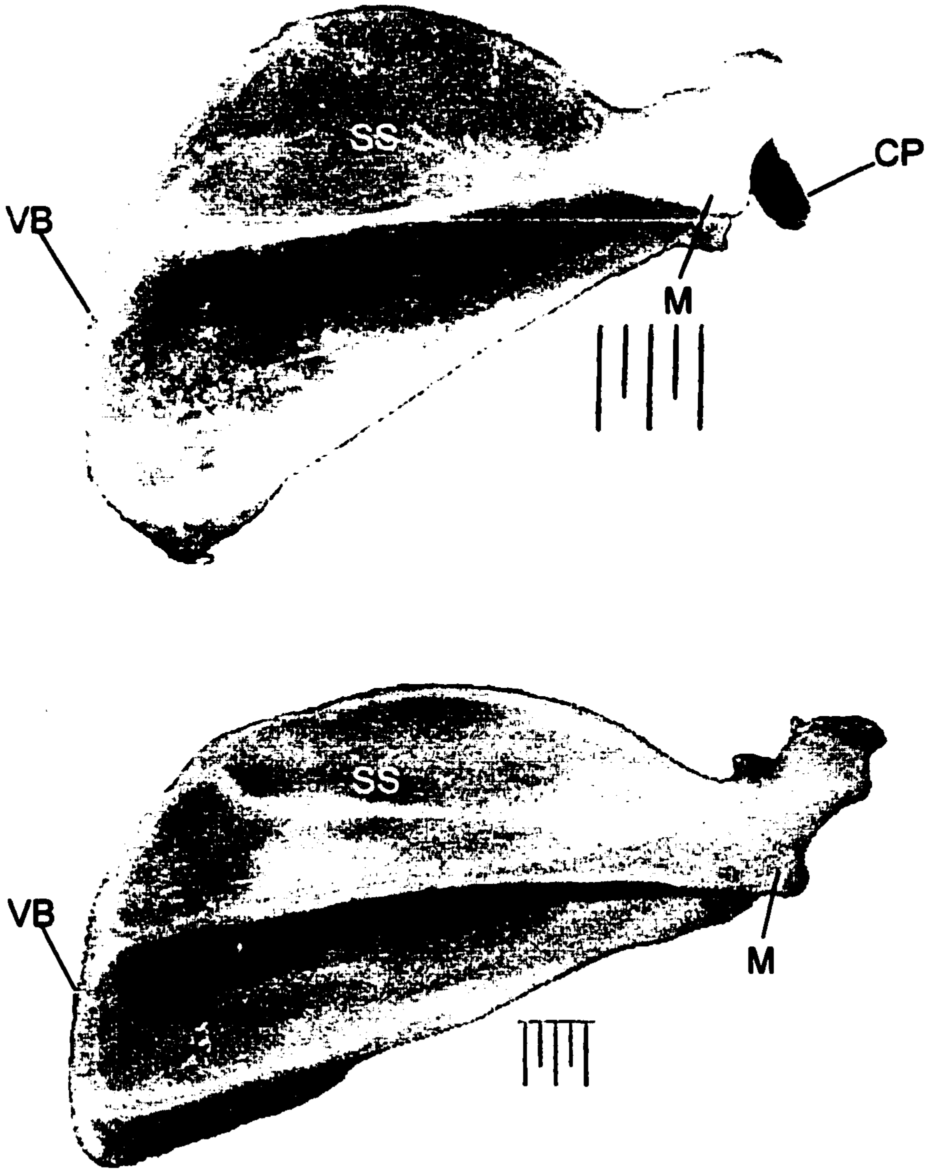


Figure 5.6. Scapulae of *Ptilocercus* (top) and *T. tana* (bottom). CP: coracoid process, M: metacromion, SS: supraspinous fossa, VB: vertebral border. Subdivisions on scale are 0.5 mm. Note the short, wide scapula and the cranial angulation of the metacromion of *Ptilocercus*. Also note the long, caudally oriented coracoid process of *Ptilocercus*.

Table 5.5. Distribution of tupaiid forelimb features discussed in the text.

Taxon	*Ptilocercus*	Tupaiinae[a]	*Dendrogale*	*Tupaia glis*	*T. minor*	*T. tana*	*Urogale*
Scapula shape	short and wide	long and narrow	long and narrow	long and narrow	long and narrow	long and narrow	long and narrow
Coracoid process	long, extends caudally	shorter, extends medially	intermediate, extends medially	short, extends medially	intermediate, extends medially	short, extends medially	short, extends medially
Lesser tuberosity	robust, strong medial protrusion	gracile, weak medial protrusion	gracile, weak medial protrusion	gracile, weak medial protrusion	gracile, weak medial protrusion	gracile, weak medial protrusion	gracile, weak medial protrusion
Capitulum shape	rounded, (separated from trochlea)	flatter (continuous with trochlea)	flatter (continuous with trochlea)	flatter (continuous with trochlea)	flatter (continuous with trochlea)	flatter (continuous with trochlea)	flatter (continuous with trochlea)
Entepicondylar foramen	present	present[b]	present	variable[c]	present	present	absent
Olecranon Process	short	longer	intermediate	long	short	long	long
Radial central fossa shape	circular	ovoid	ovoid	ovoid	ovoid	ovoid	ovoid

[a] This column summarizes the most common character states found among the species included in this subfamily.

[b] This feature is also present in *Anathana* (Verma, 1965).

[c] While this feature is not always absent in this taxon as it is in *Urogale*, it is absent on many specimens. More specifically, it is absent in *T. glis belangeri* and *T. glis longipes* specimens, but present on specimens of other *T. glis* subspecies.

the muscles that attach to the vertebral border, the serratus anterior and rhomboideus (Jolly, 1967). The serratus anterior participates in scapular rotation during arm-raising (Larson, 1993) and, along with the rhomboideus, stabilizes and resists the rotation of the scapula. These muscles, therefore, need a high mechanical advantage because they must resist the turning of the scapula during climbing (Jolly, 1967). The relatively long vertebral border in *Ptilocercus* is, therefore, likely to be an adaptation for climbing during arboreal locomotion.

A widening of the scapula is seen in several other mammals, including the arboreal didelphid *Caluromys* (Argot, in press; Szalay and Sargis, submitted), the slow climbing and bridging lorisines (Roberts and Davidson, 1975), and the climbing and suspensory atelines and hominoids (Erickson, 1963; Larson, 1993). On the other hand, long and narrow scapulae like those of tupaiines are also found in the terrestrial didelphid *Monodelphis* (Argot, in press) and terrestrial cercopithecids (Jolly, 1967; Larson, 1993), as well as some other terrestrial eutherians (Smith and Savage, 1956; Roberts, 1974). This, combined with the fact that even the most arboreal tupaiines (*i.e.*, *T. minor*) have long, narrow scapulae (Fig. 5.4; Table 5.5), suggests that the ancestral tupaiine had a long, narrow scapula and was probably terrestrial (see above). If the ancestral tupaiid was arboreal and had a *Ptilocercus*-like, short, wide scapula, then the evolution of Tupaiinae was characterized by a lengthening and narrowing of the scapula in response to a shift to terrestriality. This feature, however, is by no means perfectly correlated with substrate preference, as the terrestrial didelphid *Metachirus* has a wide scapula (Argot, in press; Szalay and Sargis, submitted) and arboreal strepsirhines like *Microcebus* have narrow scapulae (Table 5.6; see Jouffroy, 1975; Roberts and Davidson, 1975; and Simmons, 1994, fig. 3).

Just as the suspensory hominoids have a short and very wide scapula, the slow climbing and suspensory dermopterans also exhibit this feature (Table 5.6; see Simmons, 1994, fig. 3). The scapula of chiropterans is also short and is even wider than that of dermopterans (Table 5.6; see Simmons, 1994, fig. 3), which may also be related to suspensory (hanging) behavior (see Szalay and Lucas, 1993, 1996; Simmons and Quinn, 1994; Simmons, 1995) or to flying. The short, relatively wide scapula of *Ptilocercus* represents an intermediate condition between the long, narrow scapula of tupaiines and the short, very wide scapula of volitantians (Table 5.6; see Simmons, 1994, fig. 3). Assuming that *Ptilocercus* represents the primitive archontan condition (see chapter 4) for this feature, one can postulate a transformation from the condition of the scapula in *Ptilocercus* to that seen in dermopterans, and then from the dermopteran condition to that seen in chiropterans. The dermopteran condition is likely more similar to that of the ancestral volitantian than is the chiropteran condition. The transformation from the ancestral archontan to the ancestral volitantian would include a widening of the scapula in response to increased slow climbing, bridging, hanging, gliding, or a combination of some or all of these behaviors. A continued widening of the scapula during the evolution of the protochiropteran may have also been related to hanging (see Szalay and Lucas, 1993, 1996; Simmons and Quinn, 1994; Simmons, 1995) or the transition to flying.

The shape of the glenoid fossa is very similar among tupaiids (Figs. 5.5, 5.7; Tables 5.7, 5.25), although it is quite narrow in the single specimen of *D. melanura* (Table 5.7). The latter may be related to a shoulder joint that is more restricted to

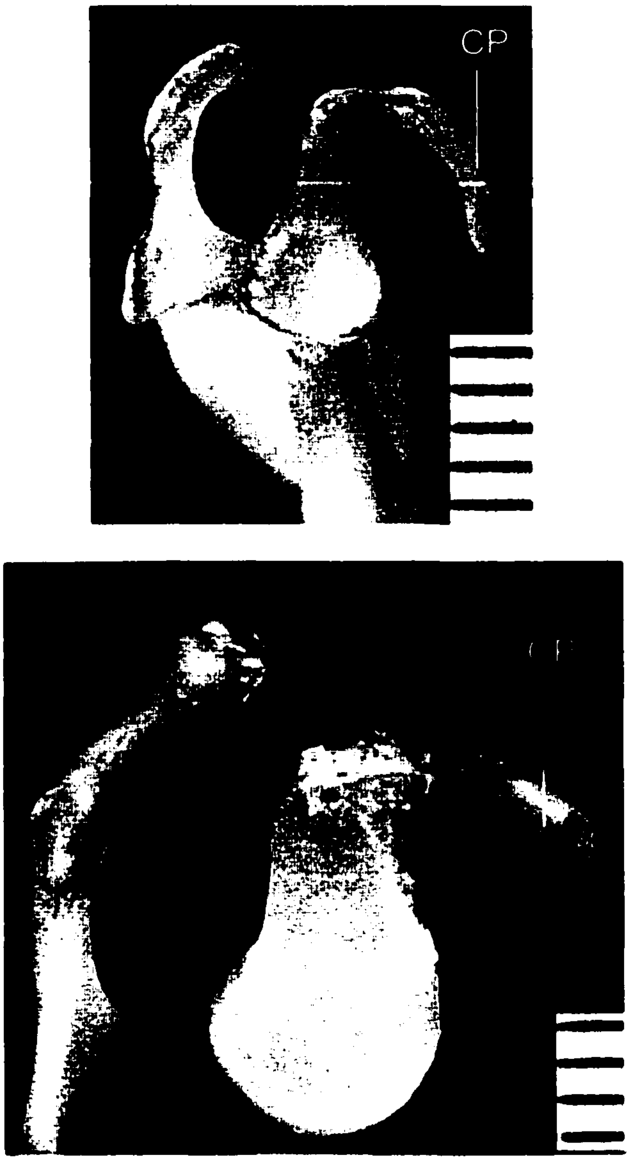


Figure 5.7. Glenoid fossae of *Ptilocercus* (above) and *T. tana* (below). CP: coracoid process. Subdivisions on scale are 0.5 mm. Note the long, caudally oriented coracoid process of *Ptilocercus*.

Table 5.6. Distribution of archontan forelimb features discussed in the text.

Taxon	Tupaiinae[a]	*Ptilocercus*	*Cynocephalus*	*Pteropus*	*Microcebus*	Plesiadapiformes
Scapula shape	long and narrow	short and wide	short and very wide	very short & very wide	long and narrow	?
Coracoid process	shorter, extends medially	long, extends caudally	long, extends caudally	long, extends caudally	long, extends caudally	?
Greater tuberosity	below head	below head	below head	below head[b]	below head	below head
Lesser tuberosity	gracile, weak medial protrusion	robust, strong medial protrusion	robust, strong medial protrusion	robust, strong medial protrusion[c]	robust, strong medial protrusion[d]	robust, strong medial protrusion
Capitulum shape	flatter (continuous with trochlea)	rounded, (separated from trochlea)	rounded	flatter	rounded	rounded
Entepicondylar foramen	present	present	present	absent	present	present
Olecranon Process	longer	short	very short	nearly absent[e]	short	intermediate
Radial central fossa shape	ovoid	circular	circular	ovoid	circular	circular

[a] This column summarizes the most common character states found among the species included in this subfamily.
[b] From Vaughan (1970; see fig. 13).
[c] This character state is not from *Pteropus* specifically, but from chiropterans in general (from Schlosser-Sturm and Schliemann, 1995). Simmons (1994) corrected Beard's (1993b) misinterpretation of an autapomorphic condition found in chiropterans for this feature.
[d] This character state is not from *Microcebus* specifically, but from euprimates in general (after Beard, 1993b).
[e] Ulnar patella present (Walton and Walton, 1970; Szalay and Lucas, 1993, 1996; Simmons, 1994).

Table 5.7: Probabilities* from Tukey Honest Significant Difference (HSD) post hoc test of glenoid fossa shape index.

	Dendrogale melanura	*Dendrogale murina*	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
D. melanura		0.778	**0.002**	**0.003**	0.108	**0.031**	0.066	0.373	0.281	**0.003**	**0.005**	**0.002**
D. murina	0.778		0.658	0.865	1.000	0.995	1.000	1.000	1.000	0.840	0.920	0.795
P. lowii	**0.002**	0.658		0.997	0.803	0.771	0.444	0.546	0.996	1.000	0.976	1.000
T. glis	**0.003**	0.865	0.997		0.974	0.972	0.704	0.808	1.000	1.000	1.000	1.000
T. gracilis	0.108	1.000	0.803	0.974		1.000	1.000	1.000	1.000	0.962	0.994	0.928
T. javanica	**0.031**	0.995	0.771	0.972	1.000		1.000	0.998	1.000	0.960	0.997	0.910
T. minor	0.066	1.000	0.444	0.704	1.000	1.000		1.000	1.000	0.698	0.880	0.573
T. montana	0.373	1.000	0.546	0.808	1.000	0.998	1.000		1.000	0.779	0.898	0.708
T. nicobarica	0.281	1.000	0.996	1.000	1.000	1.000	1.000	1.000		1.000	1.000	1.000
T. palawanensis	**0.003**	0.840	1.000	1.000	0.962	0.960	0.698	0.779	1.000		1.000	1.000
T. tana	**0.005**	0.920	0.976	1.000	0.994	0.997	0.880	0.898	1.000	1.000		0.999
U. everetti	**0.002**	0.795	1.000	1.000	0.928	0.910	0.573	0.708	1.000	1.000	0.999	

*probabilities in bold are significant at the $p < .05$ level

Table 5.8: Probabilities* from Tukey Honest Significant Difference (HSD) post hoc test of humeral head shape index.

	Dendrogale melanura	*Dendrogale murina*	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
D. melanura		1.0000	0.7306	1.0000	1.0000	0.9789	0.8735	0.9970	1.0000	1.0000	1.0000	0.9999
D. murina	1.0000		0.3114	0.9896	1.0000	0.7543	0.4619	0.9046	0.9959	1.0000	0.9998	1.0000
P. lowii	0.7306	0.3114		0.1140	0.0652	0.9989	1.0000	0.9949	0.9817	**0.0022**	**0.0143**	**0.0004**
T. glis	1.0000	0.9896	0.1140		0.9722	0.9029	0.1929	0.9969	1.0000	0.4454	0.9740	0.0632
T. gracilis	1.0000	1.0000	0.0652	0.9722		0.5353	0.1200	0.8477	0.9982	1.0000	1.0000	1.0000
T. javanica	0.9789	0.7543	0.9989	0.9029	0.5353		1.0000	1.0000	1.0000	0.1646	0.4936	**0.0427**
T. minor	0.8735	0.4619	1.0000	0.1929	0.1200	1.0000		0.9999	0.9980	**0.0025**	**0.0198**	**0.0003**
T. montana	0.9970	0.9046	0.9949	0.9969	0.8477	1.0000	0.9999		1.0000	0.5939	0.9044	0.2974
T. nicobarica	1.0000	0.9959	0.9817	1.0000	0.9982	1.0000	0.9980	1.0000		0.9925	0.9999	0.9452
T. palawanensis	1.0000	1.0000	**0.0022**	0.4454	1.0000	0.1646	**0.0025**	0.5939	0.9925		0.9891	0.9995
T. tana	1.0000	0.9998	**0.0143**	0.9740	1.0000	0.4936	**0.0198**	0.9044	0.9999	0.9891		0.6292
U. everetti	0.9999	1.0000	**0.0004**	0.0632	1.0000	**0.0427**	**0.0003**	0.2974	0.9452	0.9995	0.6292	

*probabilities in bold are significant at the $p < .05$ level

parasagittal movements during terrestrial locomotion, but little can be said about this because of the poor sample size for this taxon. The length and orientation of the coracoid process does vary between *Ptilocercus* and tupaiines (Figs. 5.6-5.7) in that it is longer and more caudally oriented in *Ptilocercus* and shorter and more medially oriented in tupaiines (Table 5.5). Both heads of the coracobrachialis muscle, an adductor of the humerus, originate from the coracoid process. The fact that this muscle has two heads in all tupaiids may be an indication of the arboreal ancestry of the group (in addition to the convincing tarsal evidence; see chapter 6 and Szalay and Drawhorn, 1980) because the arboreal *Caluromys* is the only didelphid with two heads of the coracobrachialis (Argot, in press) and terrestrial viverrids lack one of the two heads (Taylor, 1974). Grand (1983) has discussed the importance of the humeral adductor musculature in arboreal mammals, explaining that adduction of the limbs is extremely important for maintaining contact with arboreal substrates. Hence, the presence of two heads of the coracobrachialis in tupaiids may increase the adduction capabilities of this muscle (Taylor, 1974; Argot, in press). The longer coracoid process in *Ptilocercus* certainly lengthens the lever arm of the coracobrachialis muscle, which may increase its leverage and give it some advantage in adduction during arboreal locomotion in this taxon. Argot (in press) reported that the arboreal didelphid *Caluromys* also possesses a long coracoid process. Finally, it is also interesting that only in the arboreal tupaiids, *Ptilocercus* and *T. minor*, does the short head of the biceps brachii muscle originate from the coracoid process (Le Gros Clark, 1924a, 1926; George, 1977). This is also the case in the arboreal didelphid, *Caluromys* (Argot, in press). The longer coracoid process, therefore, may also provide a longer lever arm for the biceps brachii muscle, which plays an important role in pulling the body up during climbing in arboreal mammals like *Ptilocercus* and *T. minor* (see Argot, in press).

The condition of the coracoid process seen in *Ptilocercus* is more like that of dermopterans, chiropterans, and some strepsirhines like *Microcebus*, than is that of tupaiines (Table 5.6; see Jouffroy, 1975; Roberts and Davidson, 1975; Simmons, 1994, fig. 2). Hence, this feature may be primitive for Archonta. A cluster analysis of the variables included in the two scapular indices shows that *Ptilocercus* is quite different from tupaiines in its scapular morphology (Fig. 5.8).

Humerus

The shape of the humeral head is relatively similar among tupaiids (Figs. 5.9-5.10; Table 5.25), although it is wider in the arboreal *Ptilocercus* and *T. minor* than it is in *T. palawanensis* and the terrestrial *Urogale* and *T. tana* (Fig. 5.9; Table 5.8). The narrower humeral heads of the terrestrial *Urogale* and *T. tana* restrict shoulder mobility more to the parasagittal plane (Gebo and Sargis, 1994). While this same relationship was not found in arboreal and terrestrial marsupials (Szalay and Sargis, submitted), it does exist in arboreal and terrestrial guenons (Gebo and Sargis, 1994). The humeral head of all tupaiids projects above the greater and lesser tuberosities (Fig. 5.10), which allows greater mobility in the shoulder joint (Grand, 1968; Walker, 1974; Ziemer, 1978; Gebo *et al.*, 1988; Harrison, 1989; Rose, 1989; Larson, 1993; Szalay and Sargis, submitted). This condition may also provide more stability in the shoulder joint of arboreal mammals using abducted limb positions because the rotator cuff muscles, which attach to the tuberosities and stabilize the glenohumeral joint, are given a more extensive area of insertion around the humeral head (Grand, 1968; Jenkins, 1971; Fleagle and Simons,

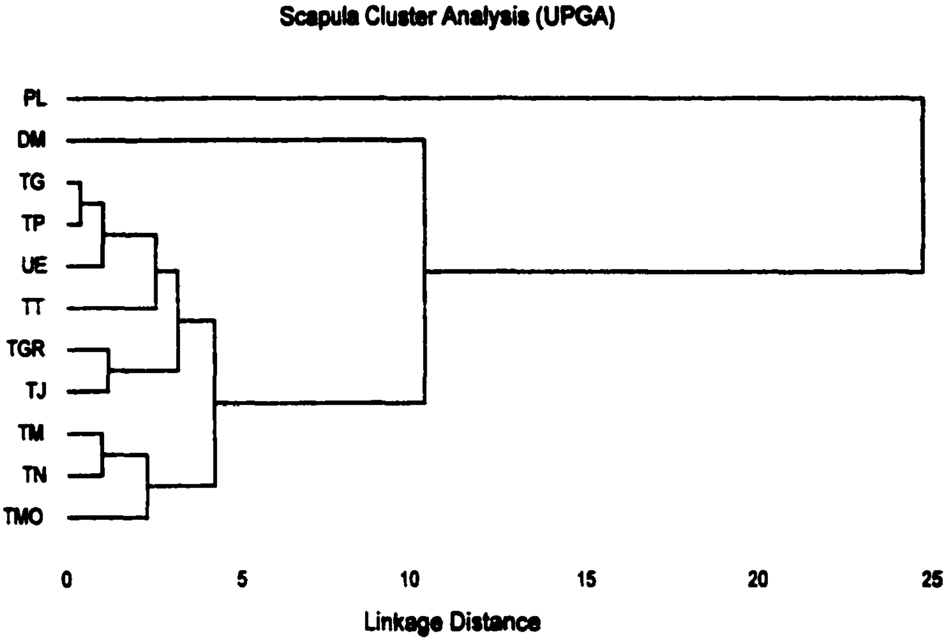


Figure 5.8. Cluster analysis of the variables included in two scapular indices. Note the difference between *Ptilocercus* and the tupaiines.

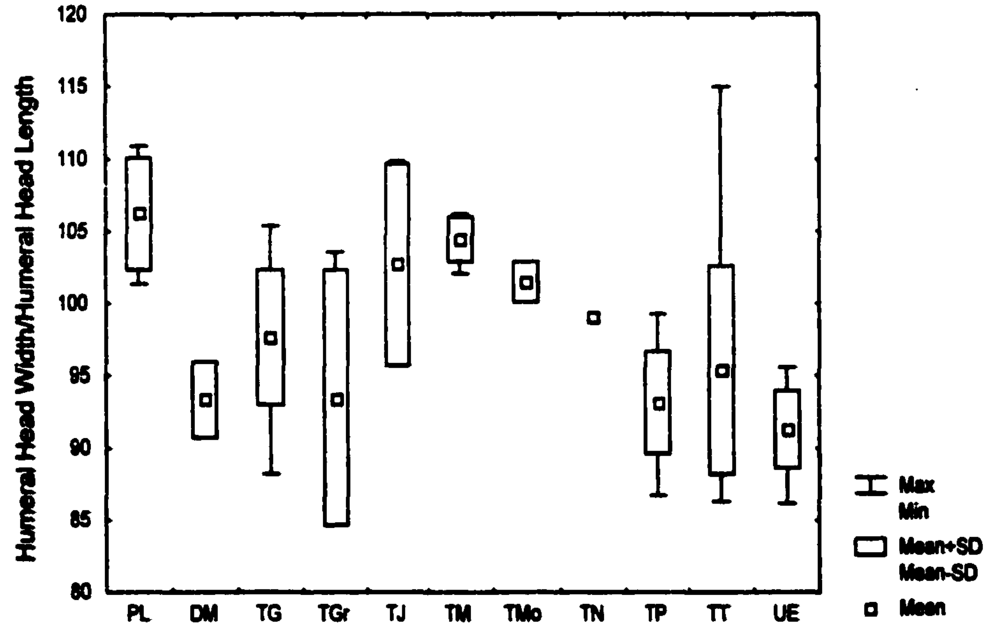


Figure 5.9. Box plot of humeral head shape index. Note the high indices of *Ptilocercus* and *T. minor*.

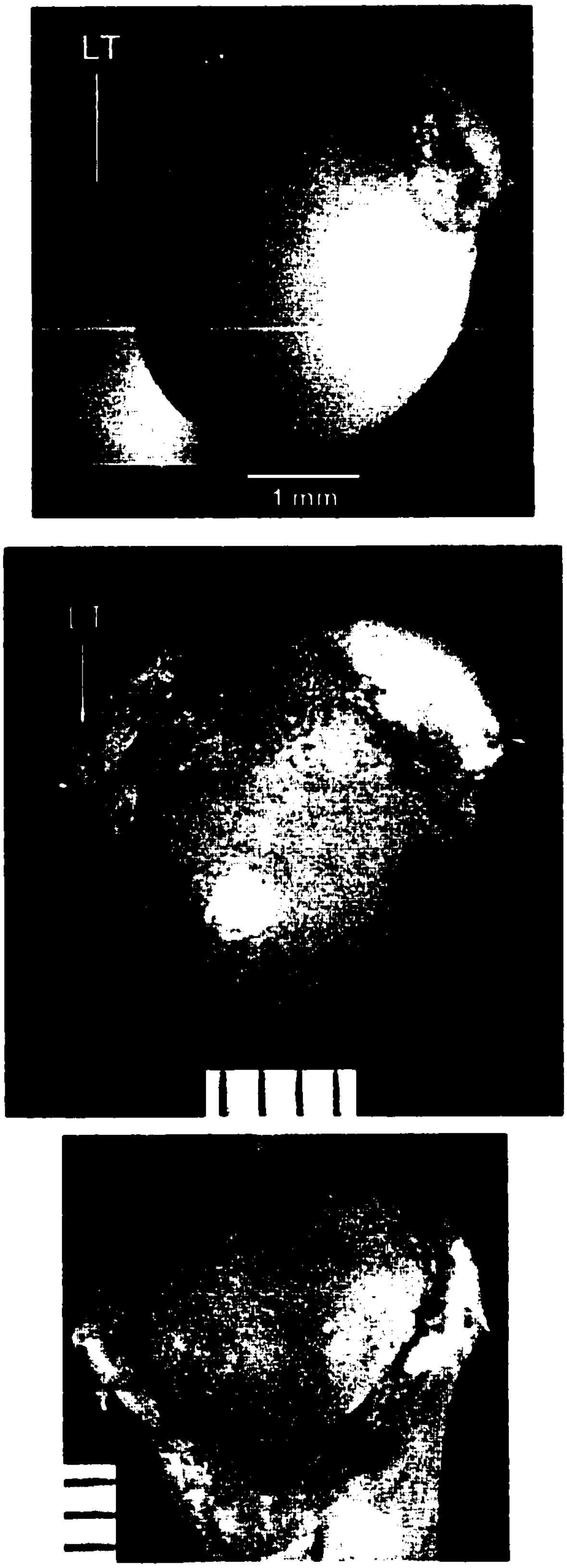


Figure 5.10. Proximal view of humeri of *Ptilocercus* (top) and *T. tana* (middle) and posterior view of proximal humerus of *Urogale* (bottom). LT: lesser tuberosity. Subdivisions on scale are 0.5 mm. Note the robust and medially protruding lesser tuberosity of *Ptilocercus*.

1982; Harrison, 1989). The tupaiid condition is contrasted with that of terrestrial cercopithecids, for instance, whose greater tuberosity projects above the humeral head, restricting mobility at the shoulder joint (Jolly, 1967; Fleagle and Simons, 1982; Gebo *et al.*, 1988; Harrison, 1989; Rose, 1989; Larson, 1993). The terrestrial marsupials *Metachirus* and *Rhyncholestes* also have higher greater tuberosities than those of the arboreal marsupials *Caluromys* and *Dromiciops* (Szalay and Sargis, submitted), as do terrestrial guenons compared to arboreal guenons (Gebo and Sargis, 1994). The fact that all tupaiids, including the most terrestrial species, exhibit a humeral head that projects above the tuberosities may represent additional evidence for the arboreal ancestry of this group. Actually, this condition may represent the primitive condition for Archonta because it is also seen in strepsirhines like *Microcebus* (Table 5.6), plesiadapiforms (see Szalay *et al.*, 1975; Beard, 1993b), dermopterans, and chiropterans (contra Beard, 1993b; see Vaughan, 1970; Simmons, 1994).

The lesser tuberosity of *Ptilocercus* is robust and protrudes far medially, whereas it is gracile and does not exhibit strong medial protrusion in tupaiines (Fig. 5.10; Table 5.5). The condition in *Ptilocercus* provides a longer lever arm for the subscapularis muscle, which is a powerful medial rotator of the humerus that is important during vertical climbing (Larson, 1988; Beard 1989). This makes sense in the case of *Ptilocercus* because it is known to spend a lot of time on vertical supports (Stafford and Thorington, 1998). The condition found in *Ptilocercus* also occurs in dermopterans, plesiadapiforms (Fig. 7.2), and primates (Beard, 1989, 1993b), as well as chiropterans (Table 5.6; contra Beard, 1993b; see Schlosser-Sturm and Schliemann, 1995). Hence, this condition may represent the primitive archontan condition. This will be discussed further in the character analysis in chapter 7.

The delto-pectoral crest is relatively similar among all tupaiids (Fig. 5.11; Tables 5.9, 5.25), although it is shorter in *T. javanica* and longer in *T. tana* (Fig. 5.11; Table 5.9). The length of the delto-pectoral crest is clearly not correlated with substrate preference in either tupaiids or marsupials (Szalay and Sargis, submitted), although it is in guenons (Gebo and Sargis, 1994). The delto-pectoral crest of tupaiids is found on the anterior surface of the humeral shaft just as it is in dermopterans and chiropterans (Beard, 1993b). This is likely the primitive condition for Archonta. Hence, the more lateral placement of the delto-pectoral crest found in primates and plesiadapiforms (Beard, 1993b) may represent a synapomorphy uniting these groups (contra Beard, 1993b; see chapter 7).

Moving to the distal humerus, an examination of the trochlea and capitulum width index shows that *Ptilocercus* is significantly different from every tupaiine species except for the single specimens of *D. melanura*, *D. murina*, and *T. nicobarica* (Table 5.10). However, *Ptilocercus* is significantly different from *Dendrogale* sp. when the two species (specimens) are considered together (Fig. 5.12; Table 5.11). It seems likely that *Ptilocercus* would also be significantly different from *T. nicobarica* for this index if larger samples were available for the latter species because the trochlea and capitulum of *T. nicobarica* are extremely similar in their morphology to those of other tupaiines (Fig. 5.12; Table 5.25). This index reflects the wider (more spindle-shaped) capitulum of tupaiines compared to the rounder (more spheroidal) capitulum of *Ptilocercus* (Figs. 5.13-5.15; Tables 5.5, 5.12, 5.25). It is also indicative of the separation of the trochlea

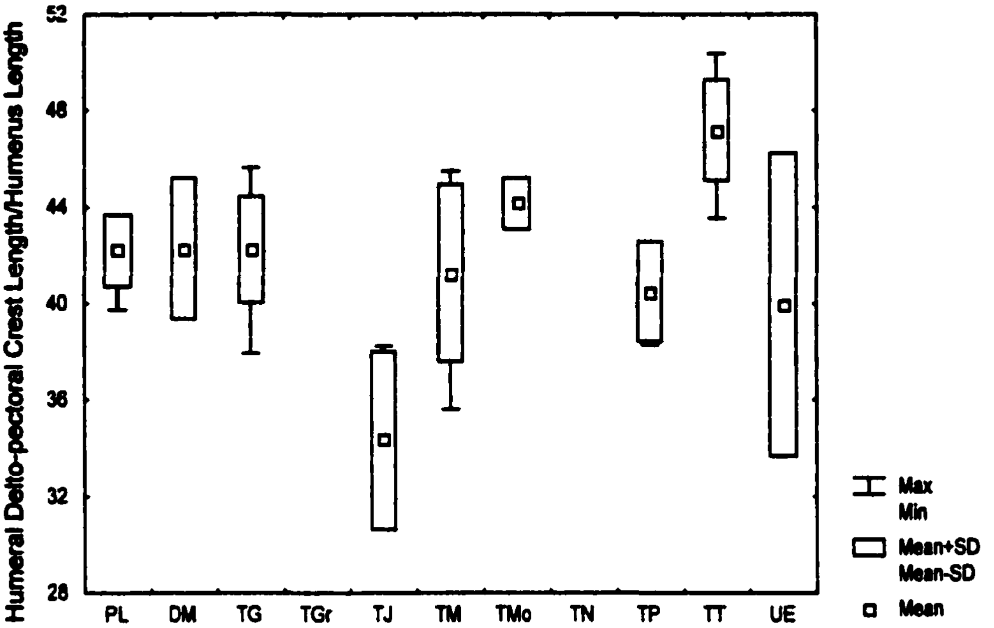


Figure 5.11. Box plot of delto-pectoral crest length index. Note the low index of *T. javanica* and the high index of *T. tana*.

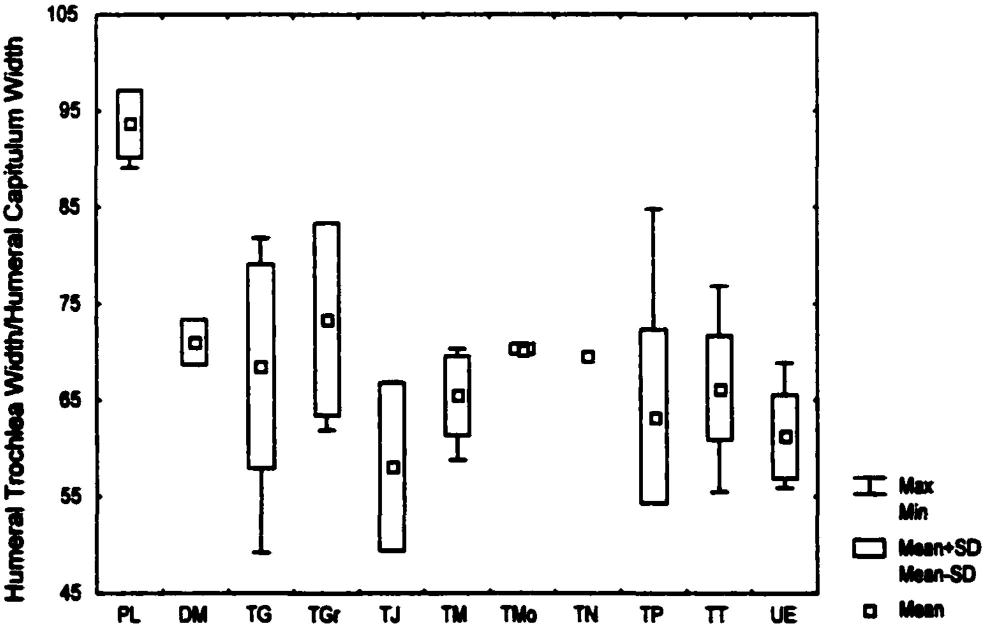


Figure 5.12. Box plot of trochlea and capitulum width index. Note the high index of *Ptilocercus*.

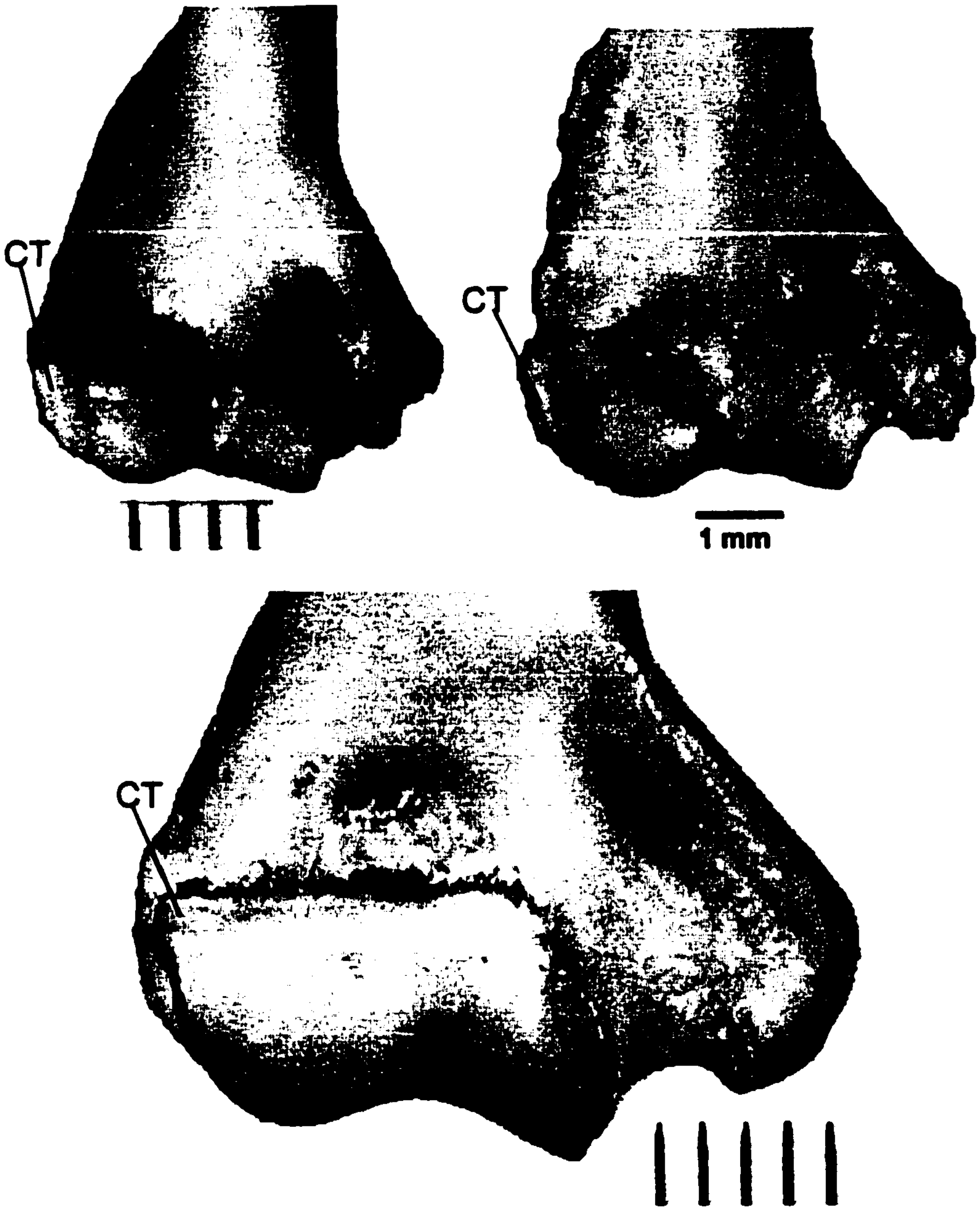


Figure 5.13. Distal humeri of *Ptilocercus* (top) and *T. tana* (bottom). CT: capitular tail. Subdivisions on scale are 0.5 mm. Note the rounded capitulum (which is separated from the trochlea) in *Ptilocercus*. See figure 5.14 for entepicondylar foramen label and figure 5.23 for medial epicondyle label.

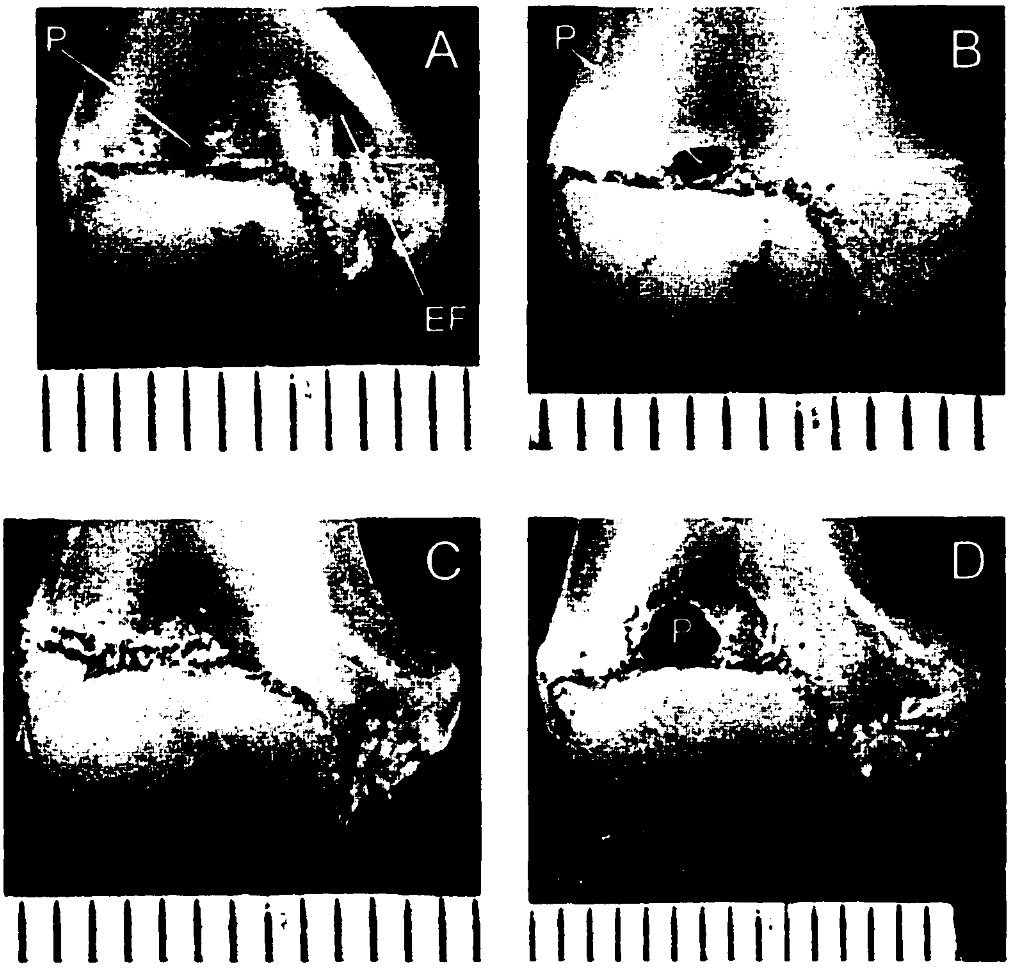


Figure 5.14. Distal humeri of *T. glis wilkinsoni* (A), *T. glis belangeri* (B), *T. glis longipes* (C), and *Urogale* (D). EF: entepicondylar foramen, P: perforation of olecranon fossa. Subdivisions on scale are 0.5 mm. Note the absence of the entepicondylar foramen in *T. glis belangeri* (B), *T. glis longipes* (C), and *Urogale* (D). Also note the large perforation of the olecranon fossa in *Urogale* (D). See figure 5.13 for capitular tail label and figure 5.23 for medial epicondyle label.

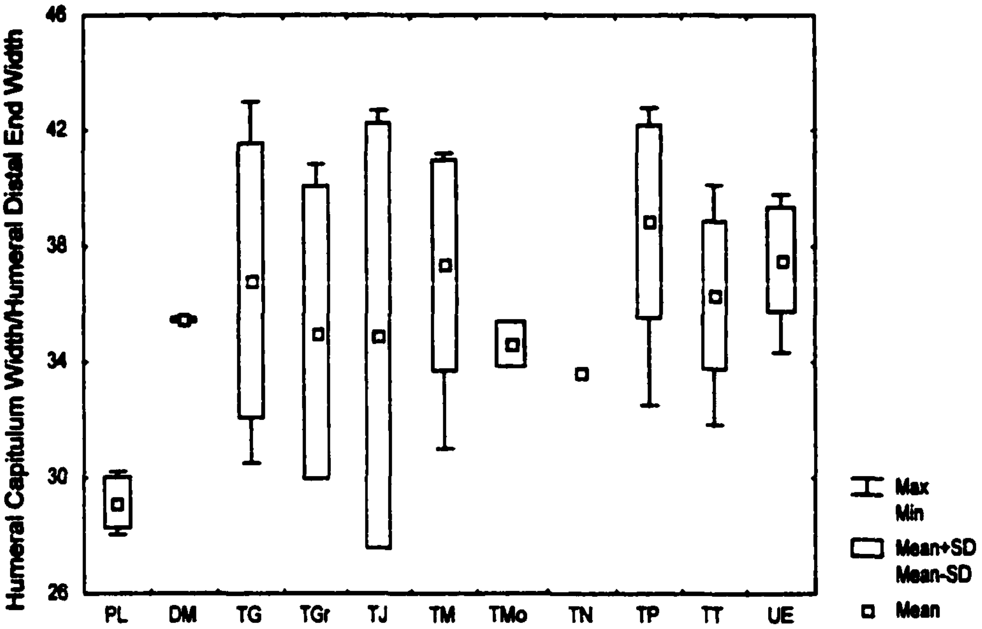


Figure 5.15. Box plot of capitulum width index. Note the low index of *Ptilocercus*.

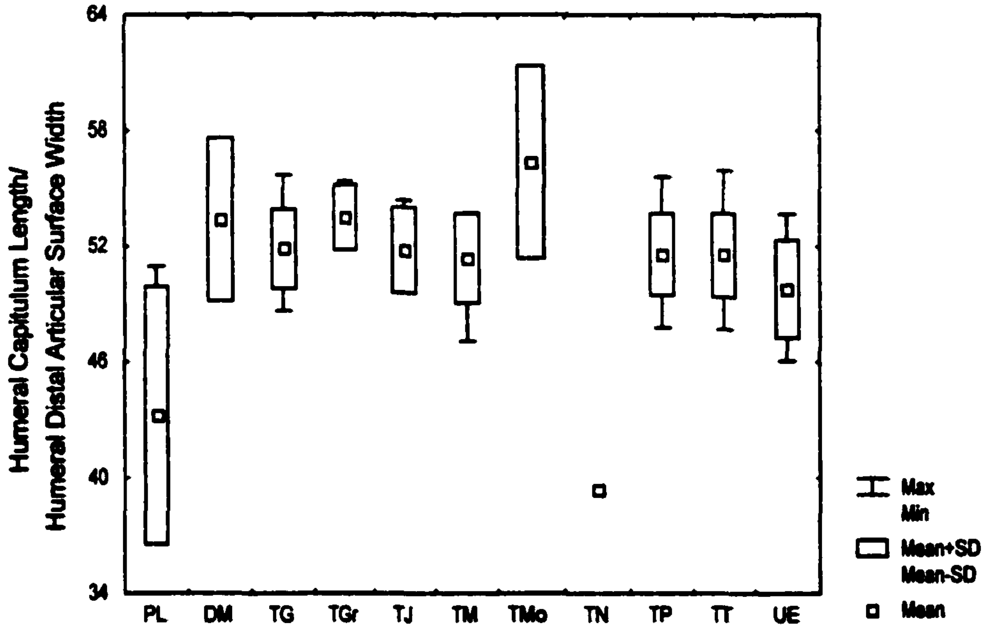


Figure 5.16. Box plot of capitulum length index. Note the low indices of *Ptilocercus* and *T. nicobarica*.

Table 5.9: Probabilities* from Tukey Honest Significant Difference (HSD) post hoc test of delto-pectoral crest length index with *Dendrogale* species combined.

	Dendrogale sp.	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
Dendrogale **sp.**		1.0000	1.0000	0.0580	1.0000	0.9996	0.9994	0.3522	0.9976
P. lowii	1.0000		1.0000	**0.0071**	0.9999	0.9978	0.9971	**0.0338**	0.9918
T. glis	1.0000	1.0000		**0.0015**	0.9996	0.9959	0.9913	**0.0019**	0.9825
T. javanica	0.0580	**0.0071**	**0.0015**		**0.0277**	**0.0074**	0.1586	**0.0002**	0.4070
T. minor	1.0000	0.9999	0.9996	**0.0277**		0.9549	1.0000	**0.0052**	0.9999
T. montana	0.9996	0.9978	0.9959	**0.0074**	0.9549		0.8900	0.9029	0.8605
T. palawanensis	0.9994	0.9971	0.9913	0.1586	1.0000	0.8900		**0.0114**	1.0000
T. tana	0.3522	**0.0338**	**0.0019**	**0.0002**	**0.0052**	0.9029	**0.0114**		**0.0286**
U. everetti	0.9976	0.9918	0.9825	0.4070	0.9999	0.8605	1.0000	**0.0286**	

*probabilities in bold are significant at the $p < .05$ level

Table 5.10: Probabilities* from Tukey Honest Significant Difference (HSD) post hoc test of trochlea & capitulum width index.

	Dendrogale melanura	*Dendrogale murina*	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
D. melanura		1.0000	0.3802	1.0000	1.0000	0.8802	0.9990	1.0000	1.0000	0.9877	0.9995	0.9482
D. murina	1.0000		0.1784	1.0000	1.0000	0.9799	1.0000	1.0000	1.0000	0.9998	1.0000	0.9966
P. lowii	0.3802	0.1784		**0.0001**	**0.0362**	**0.0001**	**0.0001**	**0.0311**	0.1902	**0.0001**	**0.0001**	**0.0001**
T. glis	1.0000	1.0000	**0.0001**		0.9969	0.5559	0.9982	1.0000	1.0000	0.7877	0.9987	0.3257
T. gracilis	1.0000	1.0000	**0.0362**	0.9969		0.3921	0.9284	1.0000	1.0000	0.6659	0.9365	0.3871
T. javanica	0.8802	0.9799	**0.0001**	0.5559	0.3921		0.9550	0.8420	0.9762	0.9966	0.8667	1.0000
T. minor	0.9990	1.0000	**0.0001**	0.9982	0.9284	0.9550		0.9997	1.0000	1.0000	1.0000	0.9860
T. montana	1.0000	1.0000	**0.0311**	1.0000	1.0000	0.8420	0.9997		1.0000	0.9872	0.9999	0.9203
T. nicobarica	1.0000	1.0000	0.1902	1.0000	1.0000	0.9762	1.0000	1.0000		0.9997	1.0000	0.9955
T. palawanensis	0.9877	0.9998	**0.0001**	0.7877	0.6659	0.9966	1.0000	0.9872	0.9997		0.9970	1.0000
T. tana	0.9995	1.0000	**0.0001**	0.9987	0.9365	0.8667	1.0000	0.9999	1.0000	0.9970		0.8600
U. everetti	0.9482	0.9966	**0.0001**	0.3257	0.3871	1.0000	0.9860	0.9203	0.9955	1.0000	0.8600	

*probabilities in bold are significant at the $p < .05$ level

Table 5.11: Probabilities* from Tukey Honest Significant Difference (HSD) post hoc test of trochlea & capitulum width index with *Dendrogale* species combined.

	Dendrogale sp.	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
Dendrogale **sp.**		**0.0349**	1.0000	1.0000	0.7365	0.9974	1.0000	1.0000	0.9578	0.9987	0.8334
P. lowii	**0.0349**		**0.0002**	**0.0291**	**0.0002**	**0.0002**	**0.0249**	0.1614	**0.0002**	**0.0002**	**0.0002**
T. glis	1.0000	**0.0002**		0.9944	0.5035	0.9964	1.0000	1.0000	0.7423	0.9973	0.2839
T. gracilis	1.0000	**0.0291**	0.9944		0.3457	0.9028	1.0000	1.0000	0.6141	0.9128	0.3411
T. javanica	0.7365	**0.0002**	0.5035	0.3457		0.9359	0.8022	0.9640	0.9938	0.8302	0.9999
T. minor	0.9974	**0.0002**	0.9964	0.9028	0.9359		0.9993	1.0000	0.9999	1.0000	0.9777
T. montana	1.0000	**0.0249**	1.0000	1.0000	0.8022	0.9993		1.0000	0.9795	0.9997	0.8930
T. nicobarica	1.0000	0.1614	1.0000	1.0000	0.9640	1.0000	1.0000		0.9992	1.0000	0.9921
T. palawanensis	0.9578	**0.0002**	0.7423	0.6141	0.9938	0.9999	0.9795	0.9992		0.9945	0.9999
T. tana	0.9987	**0.0002**	0.9973	0.9128	0.8302	1.0000	0.9997	1.0000	0.9945		0.8225
U. everetti	0.8334	**0.0002**	0.2839	0.3411	0.9999	0.9777	0.8930	0.9921	0.9999	0.8225	

*probabilities in bold are significant at the p < .05 level

Table 5.12: Probabilities* from Tukey Honest Significant Difference (HSD) post hoc test of capitulum width index.

	Dendrogale melanura	*Dendrogale murina*	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
D. melanura		1.0000	0.9182	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	0.9989	1.0000	1.0000
D. murina	1.0000		0.9078	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	0.9992	1.0000	1.0000
P. lowii	0.9182	0.9078		**0.0119**	0.6063	0.6363	**0.0194**	0.8390	0.9925	**0.0011**	**0.0288**	**0.0084**
T. glis	1.0000	1.0000	**0.0119**		0.9996	0.9992	1.0000	0.9995	0.9994	0.9437	1.0000	1.0000
T. gracilis	1.0000	1.0000	0.6063	0.9996		1.0000	0.9981	1.0000	1.0000	0.8896	1.0000	0.9946
T. javanica	1.0000	1.0000	0.6363	0.9992	1.0000		0.9970	1.0000	1.0000	0.8680	1.0000	0.9920
T. minor	1.0000	1.0000	**0.0194**	1.0000	0.9981	0.9970		0.9981	0.9981	0.9990	0.9999	1.0000
T. montana	1.0000	1.0000	0.8390	0.9995	1.0000	1.0000	0.9981		1.0000	0.9272	1.0000	0.9954
T. nicobarica	1.0000	1.0000	0.9925	0.9994	1.0000	1.0000	0.9981	1.0000		0.9652	0.9999	0.9965
T. palawanensis	0.9989	0.9992	**0.0011**	0.9437	0.8896	0.8680	0.9990	0.9272	0.9652		0.8087	0.9994
T. tana	1.0000	1.0000	**0.0288**	1.0000	1.0000	1.0000	0.9999	1.0000	0.9999	0.8087		0.9992
U. everetti	1.0000	1.0000	**0.0084**	1.0000	0.9946	0.9920	1.0000	0.9954	0.9965	0.9994	0.9992	

*probabilities in bold are significant at the p < .05 level

from the capitulum in *Ptilocercus* and the continuity between these structures in tupaiines (Figs. 5.13-5.14; Table 5.5). The gap between the two structures in *Ptilocercus* was not included in the width measurement of the capitulum (see Table 2.3), whereas the zona conoidea of tupaiines was included in the width measurement of the capitulum because the radius articulates with this region in eutherians (see Szalay and Dagosto, 1980; Rose, 1988, 1993). The latter is not the case for metatherians (Szalay and Trofimov, 1996; Szalay and Sargis, submitted). Finally, a relatively wider trochlea in *Ptilocercus* may reflect greater loads incurred on the trochlea (see Szalay and Dagosto, 1980; Rose, 1988) in the highly flexed and abducted forelimb postures used during arboreal locomotion (see below).

The rounded, globular (more spherical) capitulum of *Ptilocercus* (Figs. 5.13-5.14; Table 5.5) provides more mobility in the elbow joint by allowing the radius to rotate more freely (see Szalay and Dagosto, 1980; Rose, 1988; Harrison, 1989; Gebo and Sargis, 1994). The distinct separation of the capitulum from the trochlea in *Ptilocercus* allows both the radius and ulna greater freedom of movement (see Gebo and Sargis, 1994). On the other hand, the continuity between the trochlea and capitulum of tupaiines keeps the ulna and radius tightly packed together, restricting both their range of motion and the general mobility of the elbow joint. This, in combination with the flatter (more spindle-shaped) capitulum (Figs. 5.13-5.14; Table 5.5), provides more stability by restricting radial rotation, while allowing flexion and extension in the parasagittal plane (Gebo and Sargis, 1994). In the humeroradial articulation of *Ptilocercus*, stability is sacrificed for mobility (see Szalay and Dagosto, 1980), but some additional stability may be provided by the "stops" medial and lateral to the capitulum. The medial stop is the gutter separating the capitulum from the trochlea, which is absent in tupaiines because they have a continuous articular zona conoidea between the trochlea and capitulum (Figs. 5.13-5.14). The lateral stop is the capitular tail (the proximolateral extension of the capitulum that articulates with the rim around the central fossa on the proximal surface of the radial head; Rose, 1993), which is more prominent in *Ptilocercus* than in most tupaiines (Figs. 5.13-5.14). These features ensure stability, particularly during forearm flexion (Rose, 1993), and the medial gutter would seem to be especially important in this role during the flexed, abducted forelimb postures that are habitually employed during arboreal locomotion.

These differences were not found in arboreal and terrestrial marsupials (Argot, in press; Szalay and Sargis, submitted), but they do, however, exist in arboreal and terrestrial guenons, albeit in a somewhat different form (Gebo and Sargis, 1994). Arboreal guenons, like *Ptilocercus*, exhibit a separation between their trochlea and capitulum, but, unlike in *Ptilocercus*, these structures are separated by a ridge rather than a gutter (Gebo and Sargis, 1994). In general, the terrestrially adapted cercopithecids have a flattened capitulum (Rose, 1988; Harrison, 1989), a condition that is also present in tupaiines, and, more specifically, terrestrial guenons also exhibit this feature (Gebo and Sargis, 1994). Here again, the condition in *Ptilocercus* probably represents the primitive condition for tupaiids, and the tupaiine condition likely evolved in response to increased terrestriality. Greater stability in the humeroradial joint restricts movements more to the parasagittal plane, which is advantageous for efficient terrestrial locomotion. The tupaiine capitulum probably evolved from a *Ptilocercus*-like condition by flattening and widening medially into the region of the central gutter and laterally into the region of the capitular tail. Even the most arboreal tupaiines like *T. minor* are constrained by their terrestrial heritage in that they exhibit the same capitular condition as all other tupaiines (Table 5.5).

As Szalay and Dagosto (1980) pointed out, the spherical capitulum of *Ptilocercus* is similar to that of plesiadapiforms, early euprimates, and dermopterans (Table 5.6), and hence this condition is likely primitive for Archonta (Szalay and Lucas, 1993, 1996; contra Beard, 1993b). This will be discussed further in the character analysis in chapter 7.

The capitulum of *Ptilocercus* and *T. nicobarica* is relatively short compared to that of other tupaiids (Fig. 5.16; Table 5.25). For the capitulum length index, these two taxa are significantly different from every other species except for the single specimen of *D. murina* (Table 5.13), and they are significantly different from *Dendrogale* sp. when the two *Dendrogale* species (specimens) are considered together (Table 5.14). In *Ptilocercus*, this, in addition to a wider trochlea, may be another indication that it is the trochlea, rather than the capitulum, that is incurring the greatest loads at the elbow joint (see above; see Szalay and Dagosto, 1980; Rose, 1988). In other words, the transmission of compressive forces from weight bearing through the elbow joint of *Ptilocercus* has been shifted from the humeroradial articulation to the humeroulnar articulation (see below; see Szalay and Dagosto, 1980; Rose, 1988). The fact that the values for this index are similar in *T. nicobarica* and *Ptilocercus* may help support the claim that *T. nicobarica* is indeed arboreal (Kloss, 1903; Prashanth and Veenakumari, 1996; but see Martin, 1984), but this must be considered cautiously because this species is represented by only a single specimen. Neither *T. nicobarica* nor *Ptilocercus* are significantly

Table 5.13: Probabilities* from Tukey Honest Significant Difference (HSD) post hoc test of capitulum length index.

	Dendrogale melanura	*Dendrogale murina*	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
D. melanura		0.8632	**0.0015**	0.8313	0.9973	0.9102	0.7635	1.0000	**0.0006**	0.7925	0.7695	0.3429
D. murina	0.8632		0.3832	1.0000	0.9947	1.0000	1.0000	0.7175	0.1052	1.0000	1.0000	1.0000
P. lowii	**0.0015**	0.3832		**0.0001**	**0.0004**	**0.0046**	**0.0007**	**0.0001**	0.9720	**0.0003**	**0.0002**	**0.0083**
T. glis	0.8313	1.0000	**0.0001**		0.9956	1.0000	1.0000	0.3980	**0.0006**	1.0000	1.0000	0.5659
T. gracilis	0.9973	0.9947	**0.0004**	0.9956		0.9996	0.9824	0.9809	**0.0005**	0.9894	0.9835	0.5015
T. javanica	0.9102	1.0000	**0.0046**	1.0000	0.9996		1.0000	0.6919	**0.0033**	1.0000	1.0000	0.9828
T. minor	0.7635	1.0000	**0.0007**	1.0000	0.9824	1.0000		0.3395	**0.0016**	1.0000	1.0000	0.9652
T. montana	1.0000	0.7175	**0.0001**	0.3980	0.9809	0.6919	0.3395		**0.0001**	0.3606	0.3099	**0.0441**
T. nicobarica	**0.0006**	0.1052	0.9720	**0.0006**	**0.0005**	**0.0033**	**0.0016**	**0.0001**		**0.0010**	**0.0008**	**0.0092**
T. palawanensis	0.7925	1.0000	**0.0003**	1.0000	0.9894	1.0000	1.0000	0.3606	**0.0010**		1.0000	0.8675
T. tana	0.7695	1.0000	**0.0002**	1.0000	0.9835	1.0000	1.0000	0.3099	**0.0008**	1.0000		0.7973
U. everetti	0.3429	1.0000	**0.0083**	0.5659	0.5015	0.9828	0.9652	**0.0441**	**0.0092**	0.8675	0.7973	

*probabilities in bold are significant at the $p < .05$ level

Table 5.14: Probabilities* from Tukey Honest Significant Difference (HSD) post hoc test of capitulum length index with *Dendrogale* species combined.

	Dendrogale sp.	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
***Dendrogale* sp.**		**0.0021**	0.9992	1.0000	0.9998	0.9952	0.9822	**0.0014**	0.9975	0.9964	0.7495
P. lowii	**0.0021**		**0.0002**	**0.0004**	**0.0046**	**0.0007**	**0.0002**	0.9634	**0.0003**	**0.0003**	**0.0083**
T. glis	0.9992	**0.0002**		0.9933	1.0000	1.0000	0.3805	**0.0006**	1.0000	1.0000	0.5431
T. gracilis	1.0000	**0.0004**	0.9933		0.9992	0.9762	0.9743	**0.0006**	0.9850	0.9775	0.4804
T. javanica	0.9998	**0.0046**	1.0000	0.9992		1.0000	0.6676	**0.0033**	1.0000	1.0000	0.9766
T. minor	0.9952	**0.0007**	1.0000	0.9762	1.0000		0.3245	**0.0017**	1.0000	1.0000	0.9555
T. montana	0.9822	**0.0002**	0.3805	0.9743	0.6676	0.3245		**0.0002**	0.3446	0.2962	**0.0429**
T. nicobarica	**0.0014**	0.9634	**0.0006**	**0.0006**	**0.0033**	**0.0017**	**0.0002**		**0.0011**	**0.0009**	**0.0092**
T. palawanensis	0.9975	**0.0003**	1.0000	0.9850	1.0000	1.0000	0.3446	**0.0011**		1.0000	0.8476
T. tana	0.9964	**0.0003**	1.0000	0.9775	1.0000	1.0000	0.2962	**0.0009**	1.0000		0.7742
U. everetti	0.7495	**0.0083**	0.5431	0.4804	0.9766	0.9555	**0.0429**	**0.0092**	0.8476	0.7742	

*probabilities in bold are significant at the $p < .05$ level

different from other tupaiids for the capitulum shape index (Fig. 5.17; Table 5.25). This index is not very informative, and only *Urogale* is significantly different from *T. glis* and *T. gracilis*. The trochlea and capitulum length index is not very informative either, although for this index *T. nicobarica* is more similar to terrestrial taxa like *T. tana* and *Urogale* rather than the arboreal *T. minor* (Fig. 5.18; Tables 5.15, 5.25).

The trochlea of the arboreal *Ptilocercus* and *T. minor* is shorter than in more terrestrial taxa, such as *T. palawanensis*, *T. montana*, and *T. tana* (Figs. 5.13, 5.19; Tables 5.16, 5.25). *Ptilocercus* is also significantly different from the more terrestrial *T. glis* and *Urogale* (Table 5.16). The increased length of the trochlea in the terrestrial tupaiines is found not in the body of the trochlea, but in the medial trochlear keel (Fig. 5.13). A more pronounced version of this feature is found in several cursorial mammals (Jenkins, 1973), as well as in terrestrial cercopithecines (Rose, 1988; Harrison, 1989). The longer (proximodistally) medial trochlear keel of terrestrial tupaiines better resists the torques produced in semi-flexed and flexed pronated postures, and hence increases stability in the elbow joint (see Jenkins, 1973; Rose, 1988; Harrison, 1989). It also restricts movements more to the parasagittal plane during terrestrial quadrupedal walking and running (see Jenkins, 1973; Harrison, 1989), thereby increasing the efficiency of terrestrial locomotion.

The fact that the trochlea shape index of *Ptilocercus* is high (Fig. 5.20; Tables 5.17, 5.25) is the result of two factors discussed above. The trochlea of *Ptilocercus* is both relatively wide and short (see above). *Ptilocercus* is significantly different from every tupaiine species except for the single specimens of *D. melanura* and *T. nicobarica* (Table 5.17). Also, *Ptilocercus* is significantly different from *Dendrogale* sp. when both

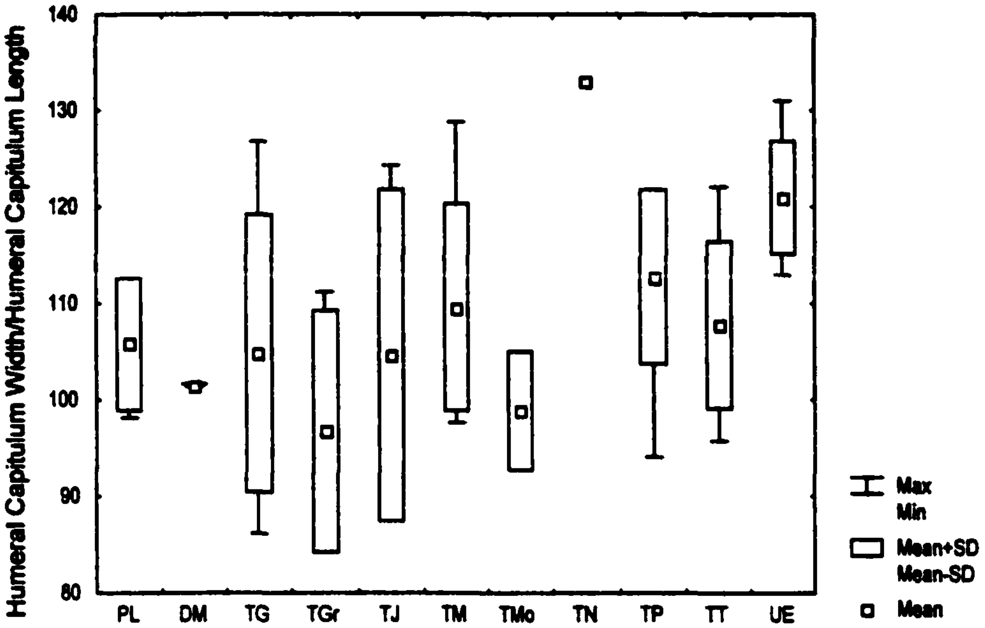


Figure 5.17. Box plot of capitulum shape index.

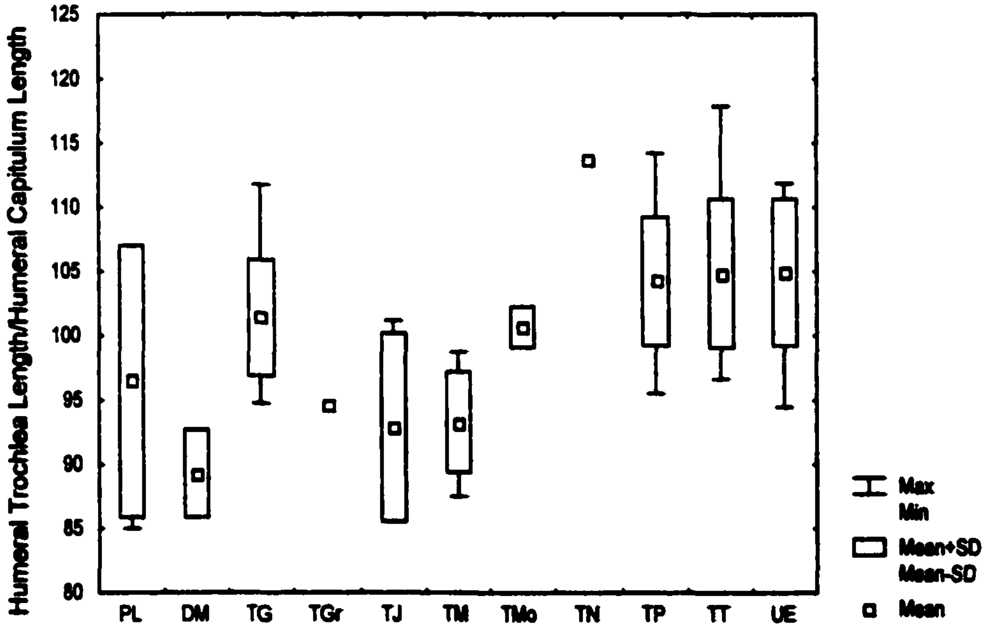


Figure 5.18. Box plot of trochlea and capitulum length index.

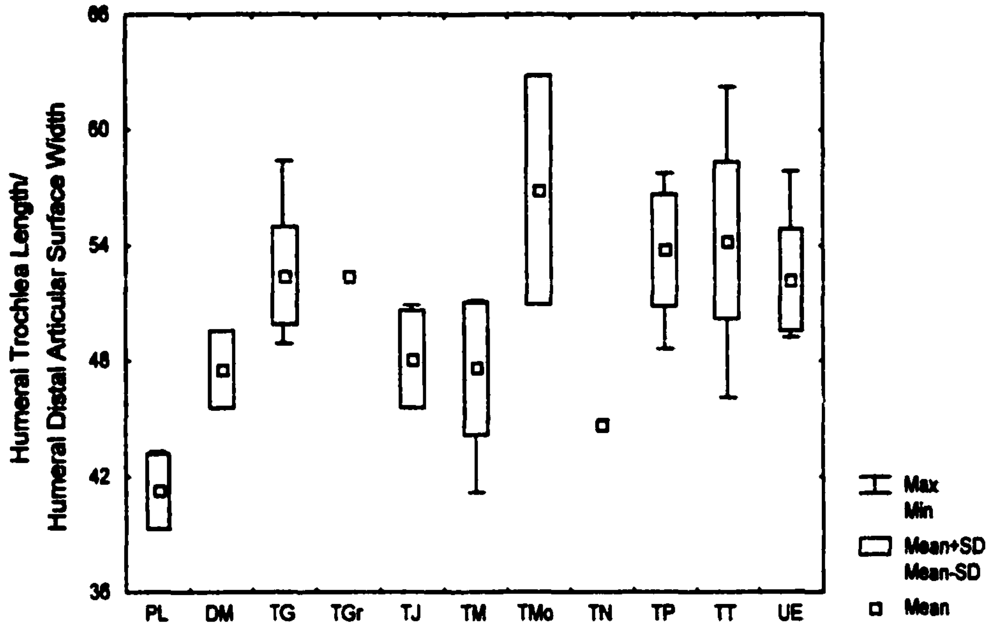


Figure 5.19. Box plot of trochlea length index. Note the low index of *Ptilocercus*.

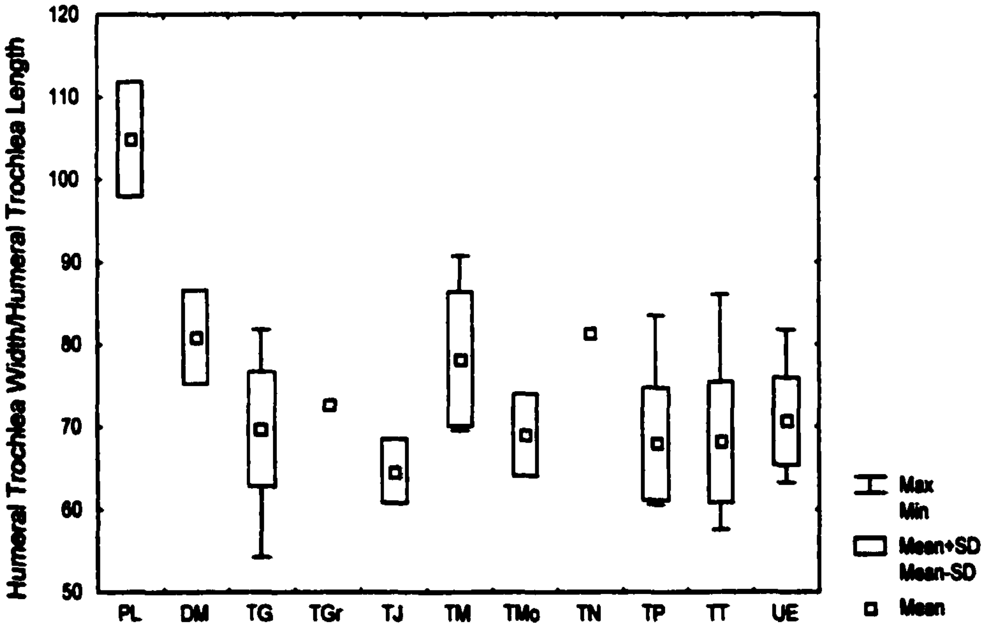


Figure 5.20. Box plot of trochlea shape index. Note the high index of *Ptilocercus*.

Table 5.15: Probabilities* from Tukey Honest Significant Difference (HSD) post hoc test of trochlea & capitulum length index

	Dendrogale melanura	*Dendrogale murina*	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
D. melanura		1.0000	0.9271	0.2952	0.9967	0.9979	0.9938	0.6404	**0.0393**	0.1151	0.0811	0.0851
D. murina	1.0000		0.9998	0.8340	1.0000	1.0000	1.0000	0.9670	0.1800	0.5409	0.4495	0.4560
P. lowii	0.9271	0.9998		0.9414	1.0000	0.9997	0.9993	0.9993	0.2312	0.5522	0.3892	0.4174
T. glis	0.2952	0.8340	0.9414		0.9861	0.3503	0.0505	1.0000	0.5662	0.9691	0.8119	0.8662
T. gracilis	0.9967	1.0000	1.0000	0.9861		1.0000	1.0000	0.9989	0.3789	0.8679	0.8038	0.8058
T. javanica	0.9979	1.0000	0.9997	0.3503	1.0000		1.0000	0.9154	0.0639	0.0829	**0.0405**	**0.0494**
T. minor	0.9938	1.0000	0.9993	0.0505	1.0000	1.0000		0.8573	**0.0364**	**0.0048**	**0.0010**	**0.0020**
T. montana	0.6404	0.9670	0.9993	1.0000	0.9989	0.9154	0.8573		0.7248	0.9993	0.9966	0.9965
T. nicobarica	**0.0393**	0.1800	0.2312	0.5662	0.3789	0.0639	**0.0364**	0.7248		0.8806	0.9151	0.9261
T. palawanensis	0.1151	0.5409	0.5522	0.9691	0.8679	0.0829	**0.0048**	0.9993	0.8806		1.0000	1.0000
T. tana	0.0811	0.4495	0.3892	0.8119	0.8038	**0.0405**	**0.0010**	0.9966	0.9151	1.0000		1.0000
U. everetti	0.0851	0.4560	0.4174	0.8662	0.8058	**0.0494**	**0.0020**	0.9965	0.9261	1.0000	1.0000	

*probabilities in bold are significant at the p < .05 level

Table 5.16: Probabilities* from Tukey Honest Significant Difference (HSD) post hoc test of trochlea length index.

	Dendrogale melanura	*Dendrogale murina*	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
D. melanura		1.0000	0.6133	0.9964	0.9998	1.0000	1.0000	0.6857	0.9982	0.9536	0.9057	0.9982
D. murina	1.0000		0.9698	0.7554	0.9609	1.0000	1.0000	0.2325	1.0000	0.4995	0.3854	0.8082
P. lowii	0.6133	0.9698		**0.0001**	0.1199	0.2843	0.1618	**0.0002**	0.9982	**0.0001**	**0.0001**	**0.0002**
T. glis	0.9964	0.7554	**0.0001**		1.0000	0.5799	0.0572	0.7645	0.4612	0.9919	0.8705	1.0000
T. gracilis	0.9998	0.9609	0.1199	1.0000		0.9884	0.9572	0.9919	0.8559	1.0000	1.0000	1.0000
T. javanica	1.0000	1.0000	0.2843	0.5799	0.9884		1.0000	0.1284	0.9988	0.2328	0.1153	0.7079
T. minor	1.0000	1.0000	0.1618	0.0572	0.9572	1.0000		**0.0278**	0.9993	**0.0093**	**0.0016**	0.1494
T. montana	0.6857	0.2325	**0.0002**	0.7645	0.9919	0.1284	**0.0278**		0.1035	0.9808	0.9943	0.7488
T. nicobarica	0.9982	1.0000	0.9982	0.4612	0.8559	0.9988	0.9993	0.1035		0.2432	0.1681	0.5284
T. palawanensis	0.9536	0.4995	**0.0001**	0.9919	1.0000	0.2328	**0.0093**	0.9808	0.2432		1.0000	0.9897
T. tana	0.9057	0.3854	**0.0001**	0.8705	1.0000	0.1153	**0.0016**	0.9943	0.1681	1.0000		0.8870
U. everetti	0.9982	0.8082	**0.0002**	1.0000	1.0000	0.7079	0.1494	0.7488	0.5284	0.9897	0.8870	

*probabilities in bold are significant at the p < .05 level

Table 5.17: Probabilities* from Tukey Honest Significant Difference (HSD) post hoc test of trochlea shape index.

	Dendrogale melanura	*Dendrogale murina*	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
D. melanura		0.9994	0.3300	0.5798	0.9792	0.3128	0.9987	0.7483	1.0000	0.4308	0.4328	0.6857
D. murina	0.9994		**0.0303**	0.9970	1.0000	0.9193	1.0000	0.9984	1.0000	0.9824	0.9841	0.9992
P. lowii	0.3300	**0.0303**		**0.0001**	**0.0061**	**0.0001**	**0.0001**	**0.0001**	0.1375	**0.0001**	**0.0001**	**0.0001**
T. glis	0.5798	0.9970	**0.0001**		1.0000	0.9861	0.2110	1.0000	0.8726	0.9999	0.9999	1.0000
T. gracilis	0.9792	1.0000	**0.0061**	1.0000		0.9967	0.9998	1.0000	0.9987	0.9999	1.0000	1.0000
T. javanica	0.3128	0.9193	**0.0001**	0.9861	0.9967		0.1688	0.9999	0.5944	0.9998	0.9996	0.9679
T. minor	0.9987	1.0000	**0.0001**	0.2110	0.9998	0.1688		0.8650	1.0000	0.1006	0.0771	0.4831
T. montana	0.7483	0.9984	**0.0001**	1.0000	1.0000	0.9999	0.8650		0.9354	1.0000	1.0000	1.0000
T. nicobarica	1.0000	1.0000	0.1375	0.8726	0.9987	0.5944	1.0000	0.9354		0.7527	0.7578	0.9273
T. palawanensis	0.4308	0.9824	**0.0001**	0.9999	0.9999	0.9998	0.1006	1.0000	0.7527		1.0000	0.9986
T. tana	0.4328	0.9841	**0.0001**	0.9999	1.0000	0.9996	0.0771	1.0000	0.7578	1.0000		0.9988
U. everetti	0.6857	0.9992	**0.0001**	1.0000	1.0000	0.9679	0.4831	1.0000	0.9273	0.9986	0.9988	

*probabilities in bold are significant at the p < .05 level

Table 5.18: Probabilities* from Tukey Honest Significant Difference (HSD) post hoc test of trochlea shape index with *Dendrogale* species combined.

	Dendrogale sp.	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
***Dendrogale* sp.**		**0.0105**	0.5183	0.9954	0.2611	1.0000	0.8037	1.0000	0.3388	0.3324	0.6751
P. lowii	**0.0105**		**0.0002**	**0.0050**	**0.0002**	**0.0002**	**0.0002**	0.1186	**0.0002**	**0.0002**	**0.0002**
T. glis	0.5183	**0.0002**		1.0000	0.9786	0.1844	1.0000	0.8405	0.9998	0.9998	1.0000
T. gracilis	0.9954	**0.0050**	1.0000		0.9942	0.9995	1.0000	0.9975	0.9999	0.9999	1.0000
T. javanica	0.2611	**0.0002**	0.9786	0.9942		0.1465	0.9998	0.5481	0.9996	0.9990	0.9542
T. minor	1.0000	**0.0002**	0.1844	0.9995	0.1465		0.8319	1.0000	0.0860	0.0656	0.4389
T. montana	0.8037	**0.0002**	1.0000	1.0000	0.9998	0.8319		0.9137	1.0000	1.0000	1.0000
T. nicobarica	1.0000	0.1186	0.8405	0.9975	0.5481	1.0000	0.9137		0.7101	0.7154	0.9040
T. palawanensis	0.3388	**0.0002**	0.9998	0.9999	0.9996	0.0860	1.0000	0.7101		1.0000	0.9974
T. tana	0.3324	**0.0002**	0.9998	0.9999	0.9990	0.0656	1.0000	0.7154	1.0000		0.9976
U. everetti	0.6751	**0.0002**	1.0000	1.0000	0.9542	0.4389	1.0000	0.9040	0.9974	0.9976	

*probabilities in bold are significant at the p < .05 level

Dendrogale species (specimens) are considered together (Table 5.18). As mentioned above, the wider trochlea of *Ptilocercus* may be indicative of greater compressive forces being transmitted through the trochlea (Szalay and Dagosto, 1980; Rose, 1988) during the flexed and abducted forelimb postures utilized on arboreal substrates. This may be in response to the increased mobility and decreased stability at the humeroradial articulation (Szalay and Dagosto, 1980). In other words, in a species like *Ptilocercus* that has a spherical capitulum (and rounded radial head; see below) and a great deal of mobility at the humeroradial articulation, the trochlea may assume a larger load-bearing role at the elbow joint (Szalay and Dagosto, 1980). Hence, the trochlea, rather than the capitulum, may be incurring greater loads produced during the flexed arm positions employed in arboreal locomotion (Szalay and Dagosto, 1980). This shift in load-bearing from the capitulum to the trochlea may have transpired early in archontan evolution because it appears to have occurred in plesiadapiforms (Szalay and Dagosto, 1980). The fact that *Ptilocercus* and plesiadapiforms both exhibit this shift may indicate that the transfer had taken place in the ancestral archontan (Szalay and Dagosto, 1980), but a shift back to greater capitulum load-bearing must have occurred in the lineage leading to volitantians because they are characterized by a reduced trochlea that is taken to an extreme in chiropterans (Szalay and Lucas, 1993, 1996).

Unfortunately, the humeral trochlea depth (HTD) measurement was incorporated into this study quite late, so the sample sizes for this measurement are very low (Tables 5.25-5.26). Despite this, the trochlea of *Ptilocercus* does appear to be more shallow than that of tupaiines (Figs. 5.21, 5.23; Table 5.25). With the current sample sizes, however, *Ptilocercus* is only significantly different from *T. javanica*, *T. minor*, *T. tana*, and

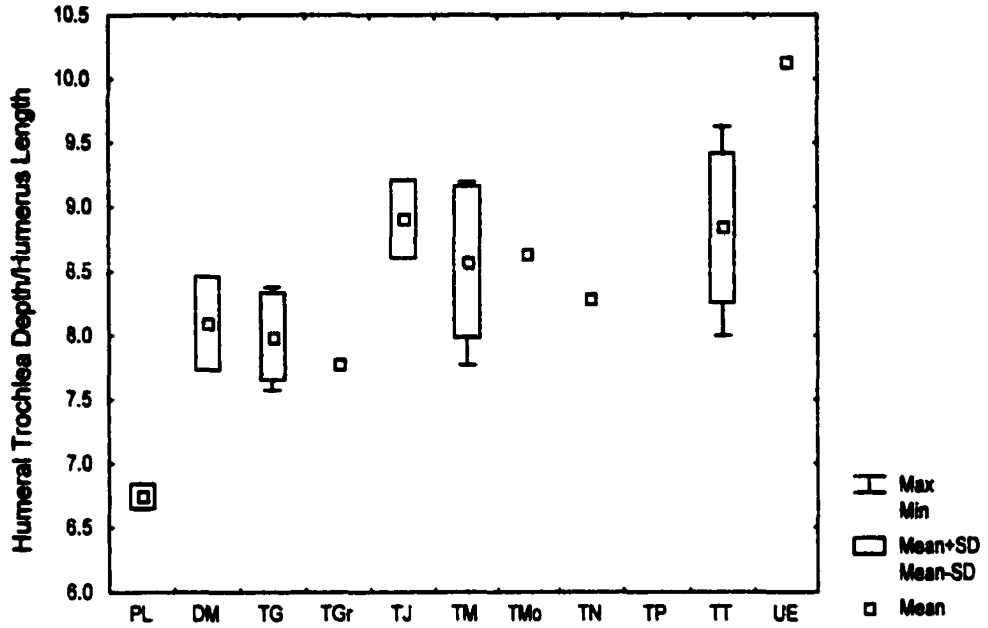


Figure 5.21. Box plot of trochlea depth index. Note the low index of *Ptilocercus*.

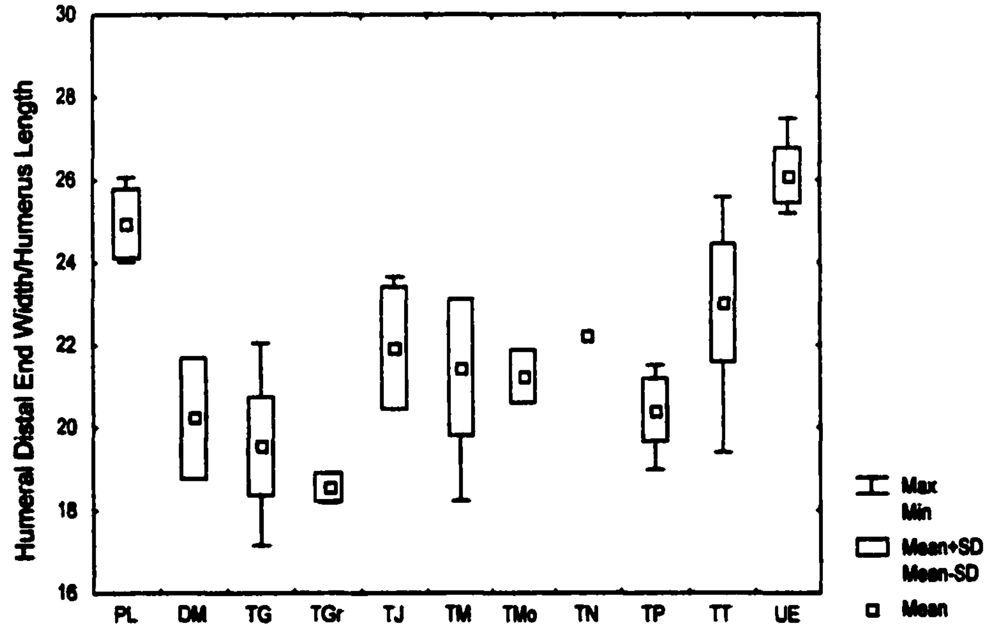


Figure 5.22. Box plot of humeral distal end width index. Note the high indices of *Ptilocercus* and *Urogale*.

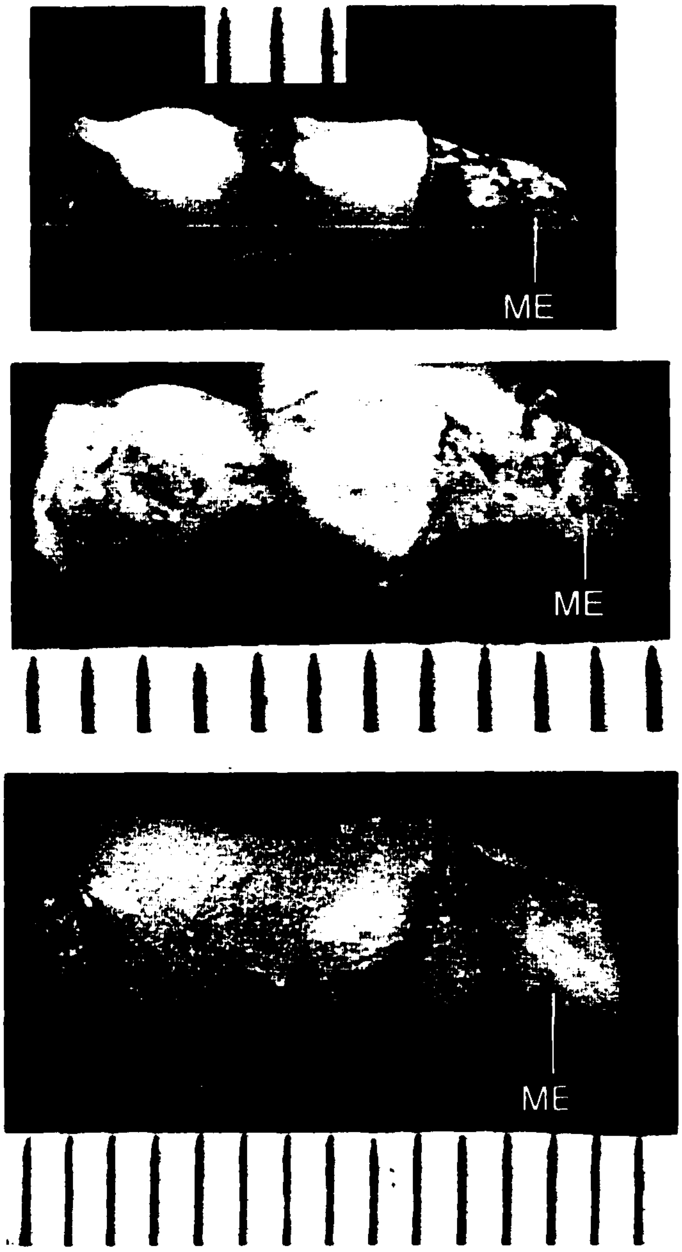


Figure 5.23. Distal view of humeri of *Ptilocercus* (top, middle) and *T. tana* (bottom). ME: medial epicondyle. Subdivisions on scale are 0.5 mm. Note the shallow trochlea of *Ptilocercus*.

Urogale (Table 5.19). The deeper, more wedge-shaped trochlea of tupaiines provides stability by creating greater articular contact between the trochlea and the trochlear notch of the ulna at the humeroulnar joint. This is especially important in close-packed positions of the joint, and is probably related to repetitive loading of the elbow joint produced by rapid terrestrial running (Szalay and Sargis, submitted). Like tupaiines, the terrestrially adapted cercopithecids also possess a deep trochlea (Rose, 1988). While this feature does not differentiate arboreal and terrestrial guenons (Gebo and Sargis, submitted), it does differentiate arboreal and terrestrial marsupials (Argot, in press; Szalay and Sargis, submitted). The trochlea of the terrestrial *Metachirus* and *Rhyncholestes* is deep, while the trochlea of the arboreal *Caluromys* and *Dromiciops* is shallow (Szalay and Sargis, submitted; see also Argot, in press). The more shallow trochlea of *Ptilocercus* provides more mobility at the humeroulnar articulation, depending on how open (including length and depth) the trochlear notch of the ulna is (see below). Obviously, increased sampling is required among tupaiids before anything more definitive can be stated about this index.

The humeral distal end width index shows that *Urogale* and *Ptilocercus* both have relatively wide distal ends (Fig. 5.22; Tables 5.20, 5.25). *Urogale* is significantly different from every taxon except *Ptilocercus* and the single specimen of *T. nicobarica*, while *Ptilocercus* is significantly different from every taxon except *Urogale*, *T. tana*, and the single specimen of *T. nicobarica* (as well as *D. melanura*, but it is significantly different from *Dendrogale* sp.; Table 5.21). This index reflects the longer medial epicondyle of *Ptilocercus* and *Urogale* (Figs. 5.13-5.14, 5.23). It is interesting that *Ptilocercus*, the smallest and most arboreal tupaiid, and *Urogale*, the largest and most

Table 5.19: Probabilities* from Tukey Honest Significant Difference (HSD) post hoc test of trochlea depth index.

	Dendrogale melanura	*Dendrogale murina*	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia tana*	*Urogale everetti*
D. melanura		0.9997	0.2155	0.9998	0.9991	0.9973	1.0000	1.0000	1.0000	0.9970	0.3361
D. murina	0.9997		0.6977	1.0000	1.0000	0.7930	0.9601	0.9866	0.9999	0.7098	0.0954
P. lowii	0.2155	0.6977		0.0529	0.7613	**0.0039**	**0.0036**	0.0888	0.2613	**0.0003**	**0.0005**
T. glis	0.9998	1.0000	0.0529		1.0000	0.4796	0.7637	0.9786	1.0000	0.0977	**0.0213**
T. gracilis	0.9991	1.0000	0.7613	1.0000		0.7358	0.9330	0.9767	0.9997	0.6368	0.0803
T. javanica	0.9973	0.7930	**0.0039**	0.4796	0.7358		0.9992	1.0000	0.9931	1.0000	0.6464
T. minor	1.0000	0.9601	**0.0036**	0.7637	0.9330	0.9992		1.0000	1.0000	0.9977	0.2148
T. montana	1.0000	0.9866	0.0888	0.9786	0.9767	1.0000	1.0000		1.0000	1.0000	0.5640
T. nicobarica	1.0000	0.9999	0.2613	1.0000	0.9997	0.9931	1.0000	1.0000		0.9915	0.2906
T. tana	0.9970	0.7098	**0.0003**	0.0977	0.6368	1.0000	0.9977	1.0000	0.9915		0.3690
U. everetti	0.3361	0.0954	**0.0005**	**0.0213**	0.0803	0.6464	0.2148	0.5640	0.2906	0.3690	

*probabilities in bold are significant at the p < .05 level

Table 5.20: Probabilities* from Tukey Honest Significant Difference (HSD) post hoc test of humeral distal end width index.

	Dendrogale melanura	*Dendrogale murina*	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
D. melanura		0.9834	0.2040	0.9538	0.7043	1.0000	1.0000	1.0000	1.0000	0.9999	0.9519	**0.0099**
D. murina	0.9834		**0.0025**	1.0000	1.0000	0.6792	0.8130	0.9572	0.7994	0.9977	0.0931	**0.0001**
P. lowii	0.2040	**0.0025**		**0.0001**	**0.0001**	0.0558	**0.0005**	**0.0241**	0.6507	**0.0001**	0.1404	0.8680
T. glis	0.9538	1.0000	**0.0001**		0.9731	0.0650	**0.0135**	0.7332	0.5344	0.7315	**0.0001**	**0.0001**
T. gracilis	0.7043	1.0000	**0.0001**	0.9731		**0.0356**	**0.0270**	0.3715	0.2516	0.4267	**0.0001**	**0.0001**
T. javanica	1.0000	0.6792	0.0558	0.0650	**0.0356**		1.0000	0.9999	1.0000	0.6881	0.9509	**0.0002**
T. minor	1.0000	0.8130	**0.0005**	**0.0135**	**0.0270**	1.0000		1.0000	1.0000	0.7552	0.1053	**0.0001**
T. montana	1.0000	0.9572	**0.0241**	0.7332	0.3715	0.9999	1.0000		0.9999	0.9988	0.6839	**0.0002**
T. nicobarica	1.0000	0.7994	0.6507	0.5344	0.2516	1.0000	1.0000	0.9999		0.9390	1.0000	0.0915
T. palawanensis	0.9999	0.9977	**0.0001**	0.7315	0.4267	0.6881	0.7552	0.9988	0.9390		**0.0001**	**0.0001**
T. tana	0.9519	0.0931	0.1404	**0.0001**	**0.0001**	0.9509	0.1053	0.6839	1.0000	**0.0001**		**0.0001**
U. everetti	**0.0099**	**0.0001**	0.8680	**0.0001**	**0.0001**	**0.0002**	**0.0001**	**0.0002**	0.0915	**0.0001**	**0.0001**	

*probabilities in bold are significant at the p < .05 level

Table 5.21: Probabilities* from Tukey Honest Significant Difference (HSD) post hoc test of humeral distal end width index with *Dendrogale* species combined.

	Dendrogale sp.	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
Dendrogale sp.		**0.0010**	0.9994	0.9016	0.8828	0.9663	0.9988	0.9484	1.0000	0.0816	**0.0002**
P. lowii	**0.0010**		**0.0002**	**0.0002**	**0.0498**	**0.0005**	**0.0214**	0.6131	**0.0002**	0.1264	0.8403
T. glis	0.9994	**0.0002**		0.9625	0.0580	**0.0120**	0.6971	0.4979	0.6953	**0.0002**	**0.0002**
T. gracilis	0.9016	**0.0002**	0.9625		**0.0317**	**0.0240**	0.3412	0.2287	0.3937	**0.0002**	**0.0002**
T. javanica	0.8828	**0.0498**	0.0580	**0.0317**		0.9999	0.9999	1.0000	0.6510	0.9350	**0.0002**
T. minor	0.9663	**0.0005**	**0.0120**	**0.0240**	0.9999		1.0000	0.9999	0.7199	0.0945	**0.0002**
T. montana	0.9988	**0.0214**	0.6971	0.3412	0.9999	1.0000		0.9998	0.9977	0.6467	**0.0002**
T. nicobarica	0.9484	0.6131	0.4979	0.2287	1.0000	0.9999	0.9998		0.9209	0.9999	0.0820
T. palawanensis	1.0000	**0.0002**	0.6953	0.3937	0.6510	0.7199	0.9977	0.9209		**0.0002**	**0.0002**
T. tana	0.0816	0.1264	**0.0002**	**0.0002**	0.9350	0.0945	0.6467	0.9999	**0.0002**		**0.0002**
U. everetti	**0.0002**	0.8403	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	0.0820	**0.0002**	**0.0002**	

*probabilities in bold are significant at the p < .05 level

Table 5.22: Probabilities* from Tukey Honest Significant Difference (HSD) post hoc test of olecranon process length index.

	Dendrogale melanura	*Dendrogale murina*	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
D. melanura		1.0000	0.9832	0.9871	1.0000	1.0000	0.9998	1.0000	0.9998	0.5144	0.8059	**0.0174**
D. murina	1.0000		0.9982	0.9282	1.0000	0.9999	1.0000	1.0000	1.0000	0.3142	0.6013	**0.0066**
P. lowii	0.9832	0.9982		**0.0051**	0.5125	0.6335	0.9993	0.9899	1.0000	**0.0001**	**0.0003**	**0.0001**
T. glis	0.9871	0.9282	**0.0051**		0.9770	0.9968	**0.0046**	0.6039	0.5324	0.2368	0.8640	**0.0001**
T. gracilis	1.0000	1.0000	0.5125	0.9770		1.0000	0.8345	0.9993	0.9769	0.1456	0.4927	**0.0002**
T. javanica	1.0000	0.9999	0.6335	0.9968	1.0000		0.9060	0.9994	0.9804	0.3917	0.7822	**0.0018**
T. minor	0.9998	1.0000	0.9993	**0.0046**	0.8345	0.9060		1.0000	1.0000	**0.0001**	**0.0002**	**0.0001**
T. montana	1.0000	1.0000	0.9899	0.6039	0.9993	0.9994	1.0000		1.0000	**0.0350**	0.1432	**0.0001**
T. nicobarica	0.9998	1.0000	1.0000	0.5324	0.9769	0.9804	1.0000	1.0000		0.0685	0.1878	**0.0007**
T. palawanensis	0.5144	0.3142	**0.0001**	0.2368	0.1456	0.3917	**0.0001**	**0.0350**	0.0685		0.9839	**0.0276**
T. tana	0.8059	0.6013	**0.0003**	0.8640	0.4927	0.7822	**0.0002**	0.1432	0.1878	0.9839		**0.0002**
U. everetti	**0.0174**	**0.0066**	**0.0001**	**0.0001**	**0.0002**	**0.0018**	**0.0001**	**0.0001**	**0.0007**	**0.0276**	**0.0002**	

*probabilities in bold are significant at the p < .05 level

terrestrial tupaiid (see Tables 1.1-1.2), share this feature, especially considering the fact that they represent two different clades. They clearly possess this feature in relation to very different biological roles. The medial epicondyle is the site of origin for the wrist and digital flexors (*e.g.*, the flexor digitorum profundus muscle; George, 1977; Argot, in press). Hence, a long medial epicondyle provides a larger area of attachment for an enlarged flexor muscle mass. These muscles are particularly important to arboreal mammals for flexion of the digits during grasping of branches. This makes sense in the case of *Ptilocercus* because it is capable of grasping (see chapter 3; A. Zitzmann, pers. comm.), and Le Gros Clark (1926) refers to the flexor digitorum profundus muscle of *Ptilocercus* as a large muscle. A large medial epicondyle is also found in arboreal marsupials, while this feature is reduced in terrestrial marsupials (Argot, in press; Szalay and Sargis, submitted). A shorter medial epicondyle is common in many cursorial mammals (Jenkins, 1973), and is also found in terrestrial cercopithecines (Jolly, 1967; Harrison, 1989). The reduction of the medial epicondyle in terrestrial mammals is related to a relative reduction in the size of the flexor musculature (Jolly, 1967; Jenkins, 1973; Harrison, 1989; Argot, in press). The reduced length of the medial epicondyle in terrestrial cercopithecines is also related to its more posterior orientation in these taxa (Jolly, 1967; Harrison, 1989). While this may also contribute to the narrower distal ends of many tupaiines (see Fig. 5.23), the posterior deflection of the medial epicondyle seen in tupaiines is not close to the degree of posterior deflection seen in terrestrial cercopithecines (see Harrison, 1989).

So, if terrestrial mammals often have shorter medial epicondyles, then why does *Urogale* have an elongated medial epicondyle? Wharton (1950) reported that *Urogale* nests in burrows and was observed rooting and digging. This explains the large medial epicondyle of *Urogale* because powerful flexion of the digits and the wrist by the flexor musculature that originates at the medial epicondyle is important in scratch-digging (see Taylor, 1974; Hildebrand, 1985), which involves the use of the claws of the manus for digging (Hildebrand, 1985). *Urogale* also exhibits rooting and digging adaptations in its skull (Martin, 1984, 1990) and claws (see below; Fig. 5.45; Martin, 1984).

Urogale is unique among tupaiids in two other features of the distal humerus, both of which may be related to its scratch digging behavior. First, *Urogale* is the only taxon in which the entepicondylar foramen is always absent (Figs. 5.13-5.14; Table 5.5). This absence (solid bone medially) may strengthen and buttress the medial epicondyle, which anchors the flexor musculature that powerfully flexes the wrist and digits during scratch-digging (see above; Hildebrand, 1985). The entepicondylar foramen is present in all other tupaiids except for *T. glis*, in which it is variable (Table 5.5). More specifically, it is absent in *T. glis longipes* and *T. glis belangeri*, but is present in other subspecies of *T. glis*, including *T. glis chinensis*. This is interesting because *T. longipes* and *T. belangeri* are commonly recognized as species distinct from *T. glis* (Martin, 1984; Wilson, 1993), but this is the only postcranial feature examined in this study that would provide additional evidence for this taxonomic separation (see chapter 7). Presence of the entepicondylar foramen is clearly primitive for therians, as well as for both Archonta and Scandentia, and Simmons (1994) has proposed that the absence of this feature in all chiropterans is a synapomorphy that unites megachiropterans and microchiropterans. However, as Simmons (1994) pointed out, this is clearly a very plastic character that may have little phylogenetic value, and the data reported here show that the entepicondylar foramen has been lost independently at least three times within Archonta (in chiropterans, in catarrhines, and in *Urogale*).

The other feature that is almost completely unique to *Urogale* among tupaiids is the consistent (and large) perforation of the olecranon fossa (Fig. 5.14). The only other tupaiid that exhibits this feature, albeit variably, is *T. glis* (Fig. 5.14). This may be related to increased extension during terrestrial locomotion because other terrestrial mammals also exhibit this feature (Taylor, 1974). In *Urogale*, however, it is more likely related to digging because this behavior includes repeated and powerful extension of the antebrachium (see Hildebrand, 1985).

A cluster analysis was performed (see chapter 2) on the variables included in nine of the eleven humeral indices, so that all eleven taxa could be included in the analysis. This analysis shows that *Ptilocercus* is quite different from tupaiines in its humeral morphology (Fig. 5.24). The addition of the variables included in a tenth index resulted in the exclusion of one taxon, but *Ptilocercus* was still separated from the tupaiines (Fig. 5.25). Finally, the addition of the variables included in the eleventh index resulted in the exclusion of two taxa, but *Ptilocercus* remained distant from the tupaiines (Fig. 5.26).

Ulna

The olecranon process of *Urogale* is relatively long, while that of the arboreal *Ptilocercus* and *T. minor* is relatively short (Figs. 5.27-5.28; Tables 5.5, 5.22, 5.25). These differences could be interpreted as relating to substrate preference because arboreal and terrestrial didelphids also exhibit these differences (Argot, in press; Szalay and Sargis, submitted). The olecranon process is the insertion site for the triceps brachii muscle, an extensor of the antebrachium, so the longer olecranon process of *Urogale*

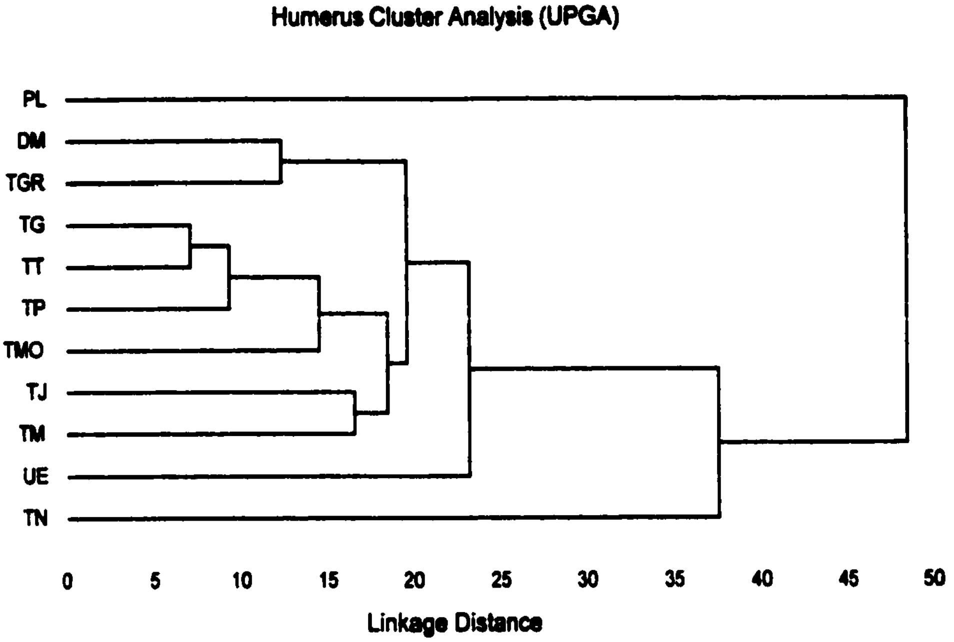


Figure 5.24. Cluster analysis of the variables included in nine humeral indices (does not include trochlea depth index or delto-pectoral crest length index). Note the difference between *Ptilocercus* and the tupaiines.

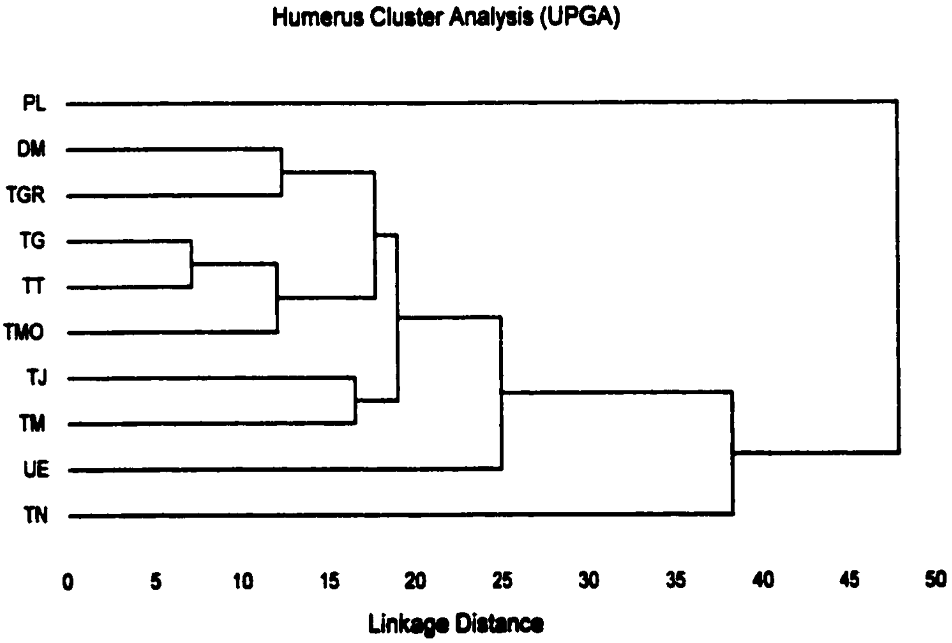


Figure 5.25. Cluster analysis of the variables included in ten humeral indices (does not include delto-pectoral crest length index). Note the difference between *Ptilocercus* and the tupaiines.

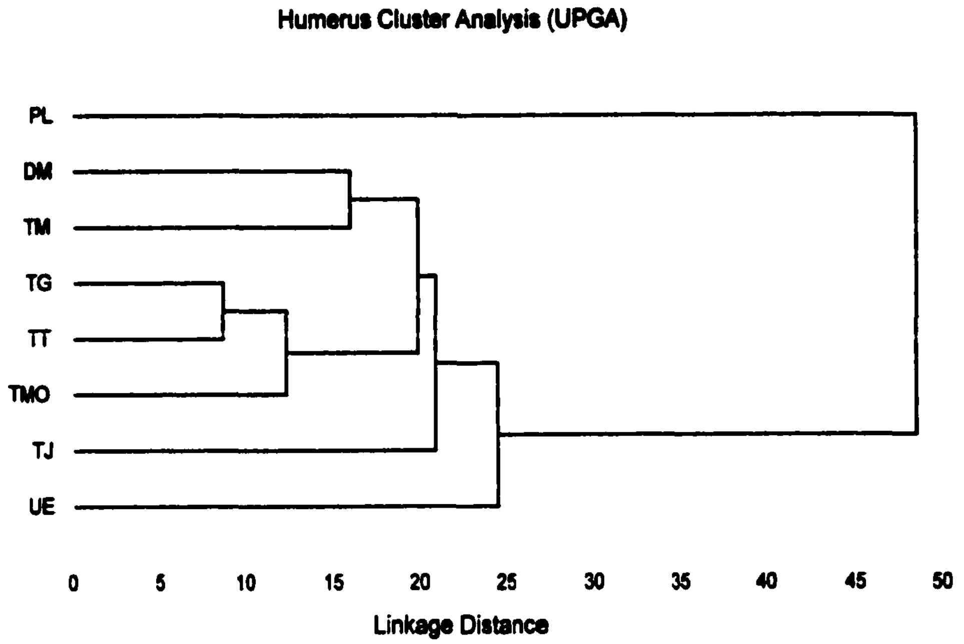


Figure 5.26. Cluster analysis of the variables included in eleven humeral indices. Note the difference between *Ptilocercus* and the tupaiines.

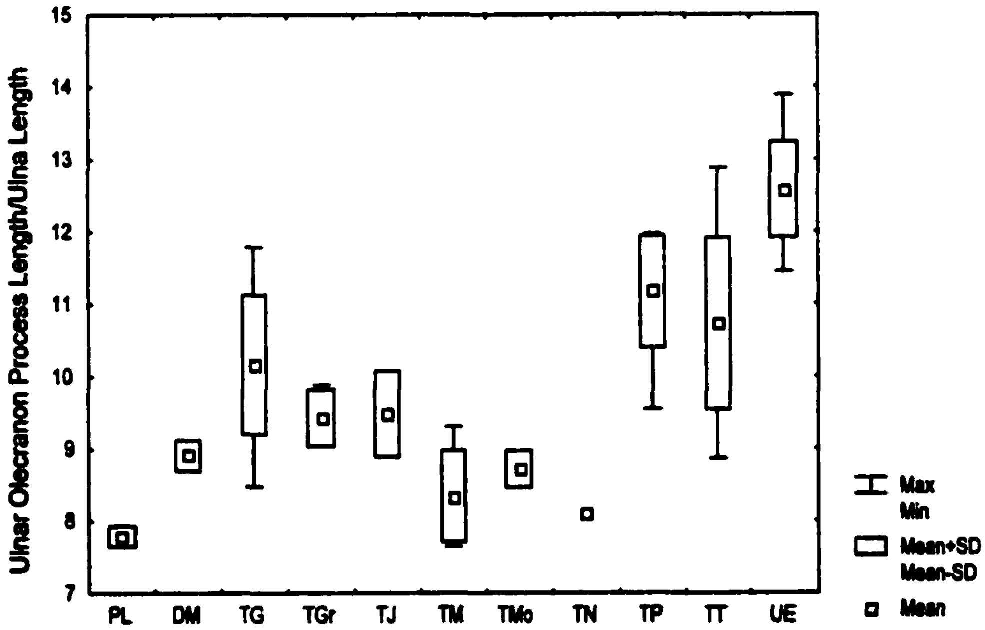


Figure 5.27. Box plot of olecranon process length index. Note the low indices of *Ptilocercus* and *T. minor*, as well as the high index of *Urogale*.

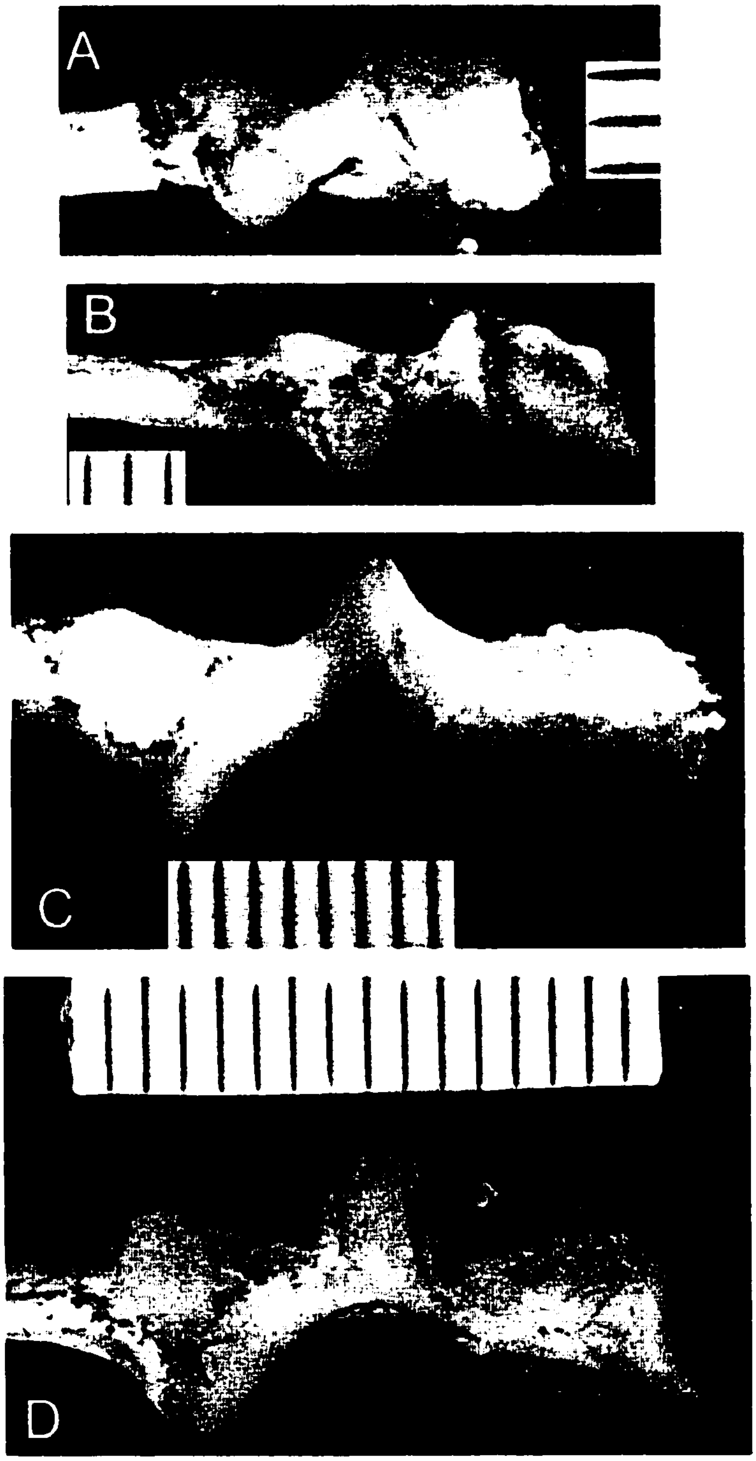


Figure 5.28. **Proximal ulnae of *Ptilocercus* (A, B), *Urogale* (C), and *T. tana* (D). Subdivisions on scale are 0.5 mm. Note the short olecranon process of *Ptilocercus*.**

provides a longer lever arm and larger attachment area for the triceps muscle. Hence, the long olecranon process of *Urogale* might be related to powerful extension of the forearm by the triceps brachii muscle for propulsion during terrestrial locomotion (see Argot, in press). However, it is more likely related to *Urogale's* digging habits (see above; Wharton, 1950) because digging requires very powerful extension of the antebrachium and scratch diggers are characterized by a long olecranon process (Hildebrand, 1985). The shorter olecranon process of the arboreal *Ptilocercus* and *T. minor* is probably related to the fact that these arboreal taxa do not require powerful extension of the forearm in arboreal locomotion (see Argot, in press) because they typically employ flexed arm postures in an attempt to keep their center of gravity close to the branch they are moving on (see Napier, 1967; Cartmill, 1985).

The condition found in *Ptilocercus* may represent the primitive condition for tupaiids. This condition may also be primitive for Archonta because the olecranon process is nearly absent in chiropterans (although the ulnar patella is present; Walton and Walton, 1970; Szalay and Lucas, 1993, 1996; Simmons, 1994), very short in dermopterans (Szalay and Lucas, 1993, 1996), and short in *Microcebus* (Table 5.6).

Neither the shape nor the orientation of the radial facet on the ulna is correlated with substrate preference in tupaiids (Figs. 5.28-5.29, 5.31; Table 5.25). In fact, there are no significant differences between any tupaiid species for the ulnar radial facet shape index. This is surprising because this feature is related to substrate preference in both marsupials (Szalay and Sargis, submitted) and guenons (Gebo and Sargis, 1994). There is also no relationship between substrate preference and the shape of the trochlear notch in tupaiids (Figs. 5.30, 5.32; Table 5.25). Here again, there are no significant differences

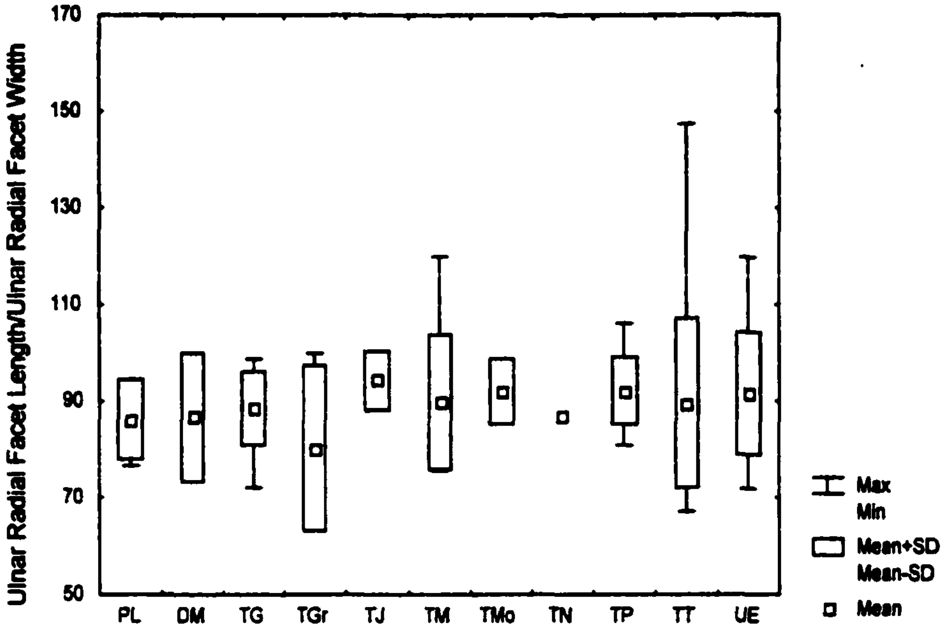


Figure 5.29. Box plot of ulnar radial facet shape index.

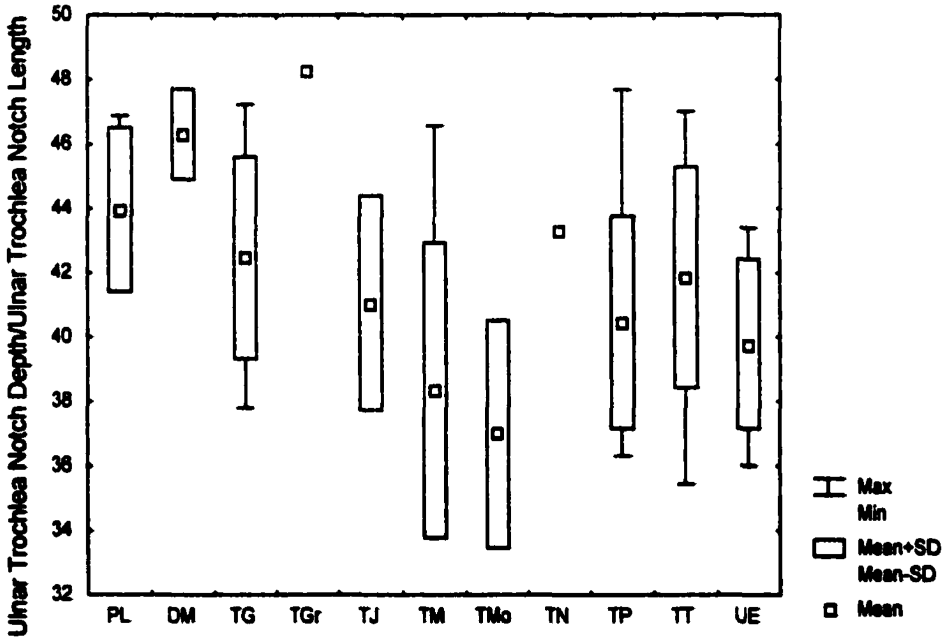


Figure 5.30. Box plot of ulnar trochlear notch shape index.

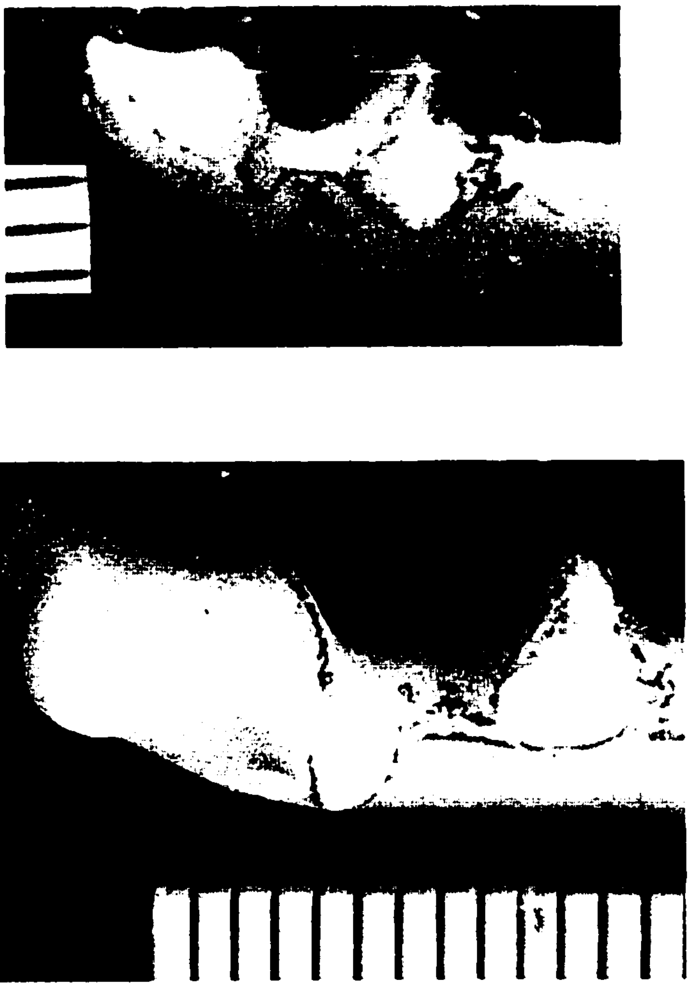


Figure 5.31. Proximal ulnae (lateral view) of *Ptilocercus* (top) and *T. tana* (bottom). Subdivisions on scale are 0.5 mm.

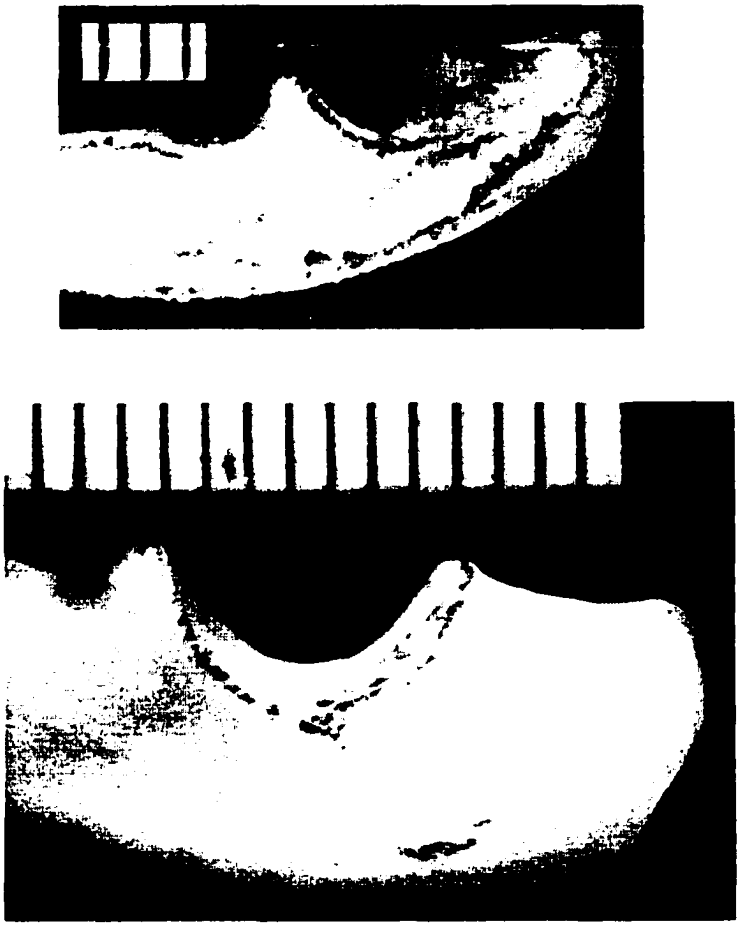


Figure 5.32. Proximal ulnae (medial view) of *Ptilocercus* (top) and *T. tana* (bottom). Subdivisions on scale are 0.5 mm.

between any tupaiid species for the ulnar trochlear notch shape index, which appears to be quite variable in tupaiids (Fig. 5.30). Unlike the lack of differentiation in tupaiids, arboreal marsupials like *Caluromys* and *Dromiciops* have a long, shallow (open) trochlear notch that provides more mobility, while terrestrial marsupials like *Metachirus* and *Rhyncholestes* have a short, deep (restricted) trochlear notch that provides stability (Szalay and Sargis, submitted; see also Argot, in press). The fact that the trochlear notch of *Ptilocercus* is as open as that of tupaiines (Fig. 5.30), yet its trochlea is more shallow (see above; Figs. 5.21, 5.23) may allow some additional mobility at the humeroulnar articulation like that of arboreal marsupials.

The proximal ulna (and olecranon process) of all tupaiids is curved anteriorly (Fig. 5.31), but it may be slightly more curved in *Ptilocercus* (Fig. 5.32). Even the most terrestrial tupaiines do not exhibit the retroflexed olecranon process seen in terrestrial cercopithecines (see Jolly, 1967; Harrison, 1989; Rose, 1993). In fact, terrestrial tupaiines do not even converge on terrestrial marsupials, which have a straighter (less anteriorly curved) proximal ulna (Argot, in press; Szalay and Sargis, submitted). This may represent another indication of the arboreal ancestry of tupaiids because the anterior curvature of the olecranon process restricts extension and gives the triceps muscle a mechanical advantage when the forearm is flexed, whereas a straighter (and especially a retroflexed) olecranon process allows more extension and gives the triceps muscle a mechanical advantage in more extended forearm postures (Jolly, 1967, Harrison, 1989). In other words, the former condition is preferable for the triceps to extend a flexed forearm for propulsion on uneven, discontinuous arboreal supports, while the latter condition is preferable for the triceps to extend a less flexed forearm for propulsion on the ground, a substrate that is more even and continuous than arboreal supports (Harrison, 1989). An anteriorly curved olecranon process is certainly primitive for Scandentia, but it may be primitive for Archonta as well (Szalay and Lucas, 1993, 1996).

Radius

The radial head and central fossa of *Ptilocercus* are more circular, while the radial head of tupaiines is more rectangular and the central fossa is more ovoid (Figs. 5.33, 5.35; Tables 5.5, 5.23, 5.25). For the radial head shape index, *Ptilocercus* is significantly different from every tupaiine species except for the single specimen of *D. murina* (Table 5.23), but it is significantly different from *Dendrogale* sp. when the two *Dendrogale* species (specimens) are considered together (Table 5.24). The shape of the radial head and central fossa are directly correlated with that of the capitulum, which was discussed above. As with a more rounded capitulum, a more circular radial head, like that of *Ptilocercus*, provides more mobility in the elbow joint by allowing the radius to rotate more freely (Szalay and Dagosto, 1980; Rose, 1988; Harrison, 1989; MacLeod and Rose, 1993; Gebo and Sargis, 1994). The more rectangular radial head of tupaiines provides more stability at the humeroradial articulation by restricting radial rotation, which is advantageous for movements in the parasagittal plane (Szalay and Dagosto, 1980; Harrison, 1989). As discussed above, based on the morphology of the trochlea and capitulum, it appears likely that the transmission of loads through the elbow joint is different in *Ptilocercus* and tupaiines. The shape of the radial head further supports this proposal, as the wide, rectangular head of tupaiines (which has a broad articular contact with the capitulum) is better adapted to incur loads at the humeroradial articulation than is the narrow, round head of *Ptilocercus* (Fig. 5.35). As discussed above, a transfer in

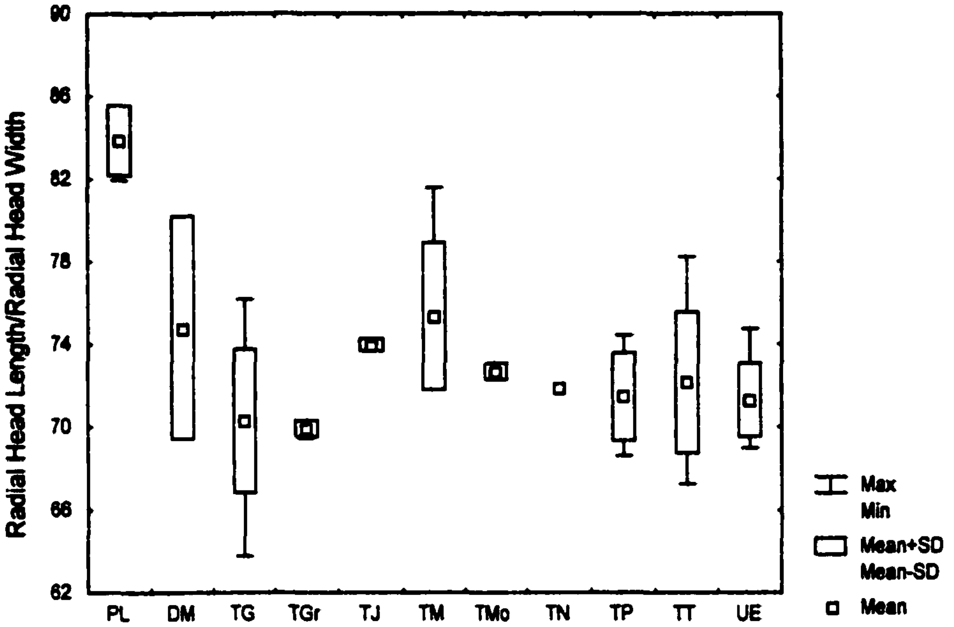


Figure 5.33. Box plot of radial head shape index. Note the high index of *Ptilocercus*.

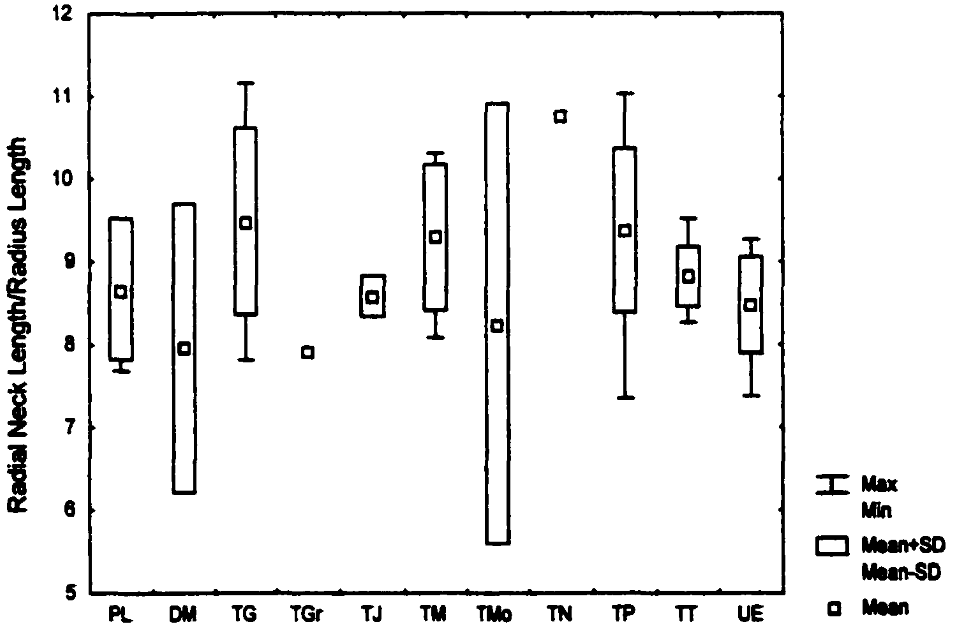


Figure 5.34. Box plot of radial neck length index.

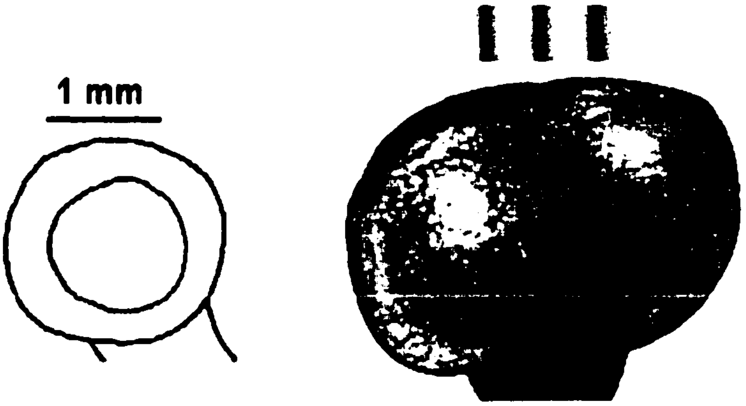


Figure 5.35. Radial head (proximal view) and central fossa of *Ptilocercus* (drawing on left) and *T. tana* (photo on right). Subdivisions on scale are 0.5 mm. Note the circular radial head and central fossa of *Ptilocercus*.

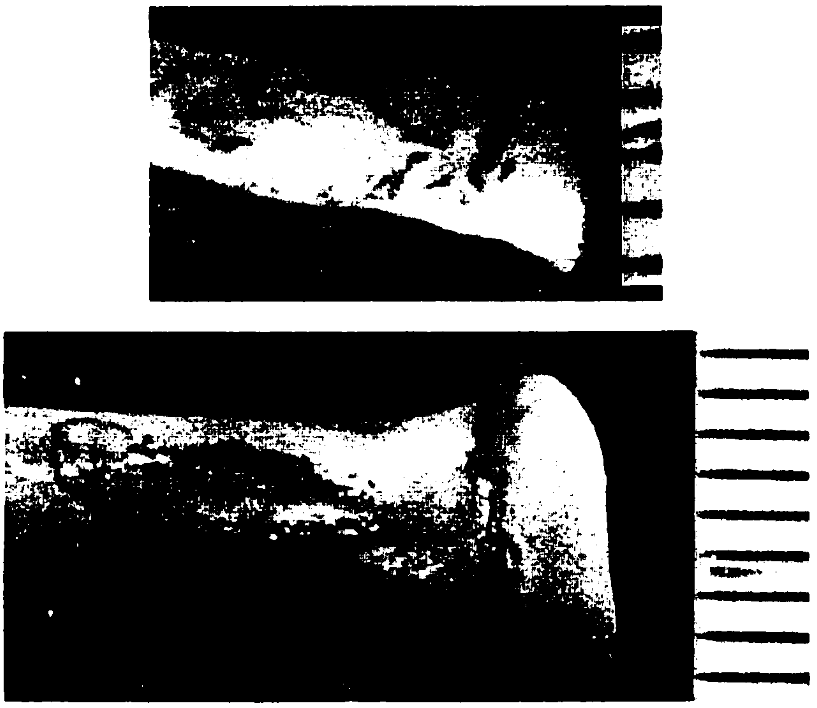


Figure 5.36. Proximal radii of *Ptilocercus* (top) and *T. tana* (bottom). Subdivisions on scale are 0.5 mm.

Table 5.23: Probabilities* from Tukey Honest Significant Difference (HSD) post hoc test of radial head shape index.

	Dendrogale melanura	*Dendrogale murina*	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
D. melanura		0.7816	**0.0142**	1.0000	1.0000	0.9994	0.9596	1.0000	1.0000	1.0000	1.0000	1.0000
D. murina	0.7816		0.9121	0.2160	0.3021	0.9760	0.9955	0.8747	0.8905	0.4559	0.5865	0.4201
P. lowii	**0.0142**	0.9121		**0.0001**	**0.0001**	**0.0196**	**0.0039**	**0.0043**	**0.0312**	**0.0001**	**0.0001**	**0.0001**
T. glis	1.0000	0.2160	**0.0001**		1.0000	0.8645	**0.0148**	0.9941	1.0000	0.9974	0.8057	0.9989
T. gracilis	1.0000	0.3021	**0.0001**	1.0000		0.9213	0.2427	0.9957	1.0000	0.9995	0.9831	0.9998
T. javanica	0.9994	0.9760	**0.0196**	0.8645	0.9213		1.0000	1.0000	1.0000	0.9925	0.9994	0.9877
T. minor	0.9596	0.9955	**0.0039**	**0.0148**	0.2427	1.0000		0.9912	0.9935	0.2472	0.4121	0.1825
T. montana	1.0000	0.8747	**0.0043**	0.9941	0.9957	1.0000	0.9912		1.0000	1.0000	1.0000	1.0000
T. nicobarica	1.0000	0.8905	**0.0312**	1.0000	1.0000	1.0000	0.9935	1.0000		1.0000	1.0000	1.0000
T. palawanensis	1.0000	0.4559	**0.0001**	0.9974	0.9995	0.9925	0.2472	1.0000	1.0000		1.0000	1.0000
T. tana	1.0000	0.5865	**0.0001**	0.8057	0.9831	0.9994	0.4121	1.0000	1.0000	1.0000		0.9998
U. everetti	1.0000	0.4201	**0.0001**	0.9989	0.9998	0.9877	0.1825	1.0000	1.0000	1.0000	0.9998	

*probabilities in bold are significant at the $p < .05$ level

Table 5.24: Probabilities* from Tukey Honest Significant Difference (HSD) post hoc test of radial head shape index with *Dendrogale* species combined.

	Dendrogale sp.	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
Dendrogale sp.		**0.0476**	0.6301	0.7648	1.0000	1.0000	0.9997	0.9993	0.9277	0.9812	0.9040
P. lowii	**0.0476**		**0.0002**	**0.0002**	**0.0205**	**0.0042**	**0.0047**	**0.0323**	**0.0002**	**0.0002**	**0.0002**
T. glis	0.6301	**0.0002**		1.0000	0.8491	**0.0157**	0.9916	1.0000	0.9960	0.7890	0.9982
T. gracilis	0.7648	**0.0002**	1.0000		0.9089	0.2392	0.9938	1.0000	0.9992	0.9780	0.9996
T. javanica	1.0000	**0.0205**	0.8491	0.9089		1.0000	1.0000	1.0000	0.9895	0.9990	0.9835
T. minor	1.0000	**0.0042**	**0.0157**	0.2392	1.0000		0.9879	0.9908	0.2436	0.4027	0.1810
T. montana	0.9997	**0.0047**	0.9916	0.9938	1.0000	0.9879		1.0000	1.0000	1.0000	0.9999
T. nicobarica	0.9993	**0.0323**	1.0000	1.0000	1.0000	0.9908	1.0000		1.0000	1.0000	1.0000
T. palawanensis	0.9277	**0.0002**	0.9960	0.9992	0.9895	0.2436	1.0000	1.0000		1.0000	1.0000
T. tana	0.9812	**0.0002**	0.7890	0.9780	0.9990	0.4027	1.0000	1.0000	1.0000		0.9997
U. everetti	0.9040	**0.0002**	0.9982	0.9996	0.9835	0.1810	0.9999	1.0000	1.0000	0.9997	

*probabilities in bold are significant at the $p < .05$ level

load-bearing from the humeroradial articulation to the humeroulnar articulation appears to have occurred in *Ptilocercus*.

These differences were not found in arboreal and terrestrial didelphids (Argot, in press; Szalay and Sargis, submitted), but they were found in the arboreal *Dromiciops* and the terrestrial *Caenolestes* (Szalay and Sargis, submitted). As with the shape of the capitulum, the condition of the radial head in *Ptilocercus* probably represents the primitive condition for tupaiids, and the tupaiine condition likely evolved in response to increased terrestriality (see discussion concerning capitulum above). Like the capitulum, the tupaiine radial head probably evolved from a *Ptilocercus*-like condition by widening medially and laterally. Even the most arboreal tupaiines, such as *T. minor*, exhibit the same radial head condition as all other tupaiines (Table 5.5), which is likely an expression of their terrestrial ancestry.

In conjunction with a more rounded capitulum, the circular condition of the radial central fossa found in *Ptilocercus* may be primitive for Archonta (Szalay and Lucas, 1993, 1996; contra Beard, 1993b), as it is also present in *Microcebus*, plesiadapiforms, and dermopterans (Table 5.6). This will be discussed further in the character analysis in chapter 7.

The length of the radial neck is not related to substrate preference in tupaiids (Figs. 5.34, 5.36; Table 5.25), and there are no significant differences between any tupaiid species for the radial neck length index. As in tupaiids, no differences in radial neck length were found between arboreal and terrestrial marsupials (Argot, in press; Szalay and Sargis, submitted), although terrestrial cercopithecids do exhibit a short radial neck (Harrison, 1989). As expected, based on the ulnar radial facet data (see above), there is no relationship between the length of the rim of the radial head and substrate preference in tupaiids (Figs. 5.36-5.37; Table 5.25). Here again, there are no significant differences between any tupaiid species for the radial head rim length index.

A cluster analysis on the variables included in the six ulnar and radial indices shows that *Ptilocercus* is distinct from tupaiines in its ulnar and radial morphology (Fig. 5.38). A cluster analysis was also performed on the variables included in eighteen of the twenty forelimb indices, so that all eleven taxa could be included in the analysis. This analysis shows that *Ptilocercus* is very different from tupaiines in its forelimb morphology (Fig. 5.39). The addition of the variables included in a nineteenth index resulted in the exclusion of one taxon, but *Ptilocercus* was still separated from the tupaiines (Fig. 5.40). Finally, the addition of the variables included in the twentieth index resulted in the exclusion of two taxa, but *Ptilocercus* remained distant from the tupaiines (Fig. 5.41). It is interesting that while *Ptilocercus* is separated from the tupaiines, *Dendrogale*, *Urogale*, and *T. tana* (formerly *Lyonogale*) are nested among species of *Tupaia* (Figs. 5.39-5.40; see chapter 7).

Manus

As stated above, Stafford and Thorington's (1998) detailed study of archontan wrist morphology provided a great deal of data on the carpus of tupaiids and little can be added here. My major disagreement with their conclusions stems from their discussion of the nature of fusion of the scaphoid and lunate in tupaiids. First, I should say that Stafford and Thorington (1998) have cleared up much of the confusion that has existed regarding this topic in tupaiid carpal morphology. For instance, Verma (1965) claimed that in *Anathana* the scaphoid and lunate are fused, the trapezium and trapezoid are

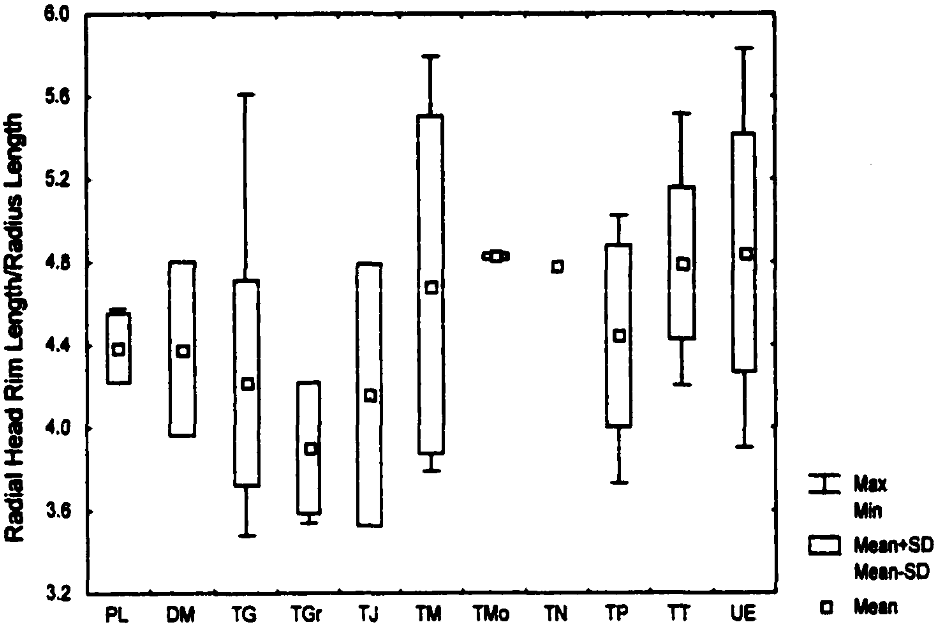


Figure 5.37. Box plot of radial head rim length index.

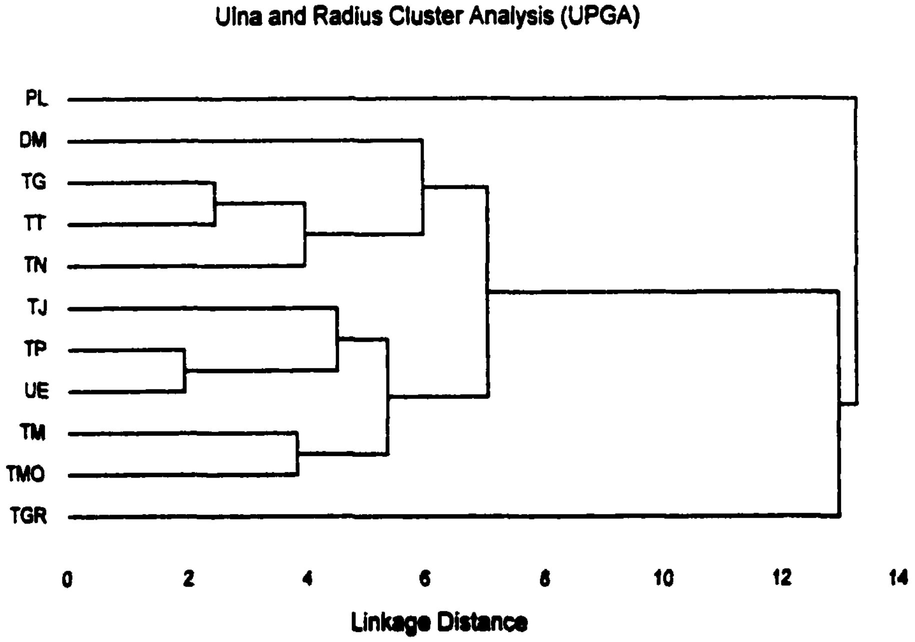


Figure 5.38. Cluster analysis of the variables included in six ulnar and radial indices. Note the difference between *Ptilocercus* and the tupaiines.

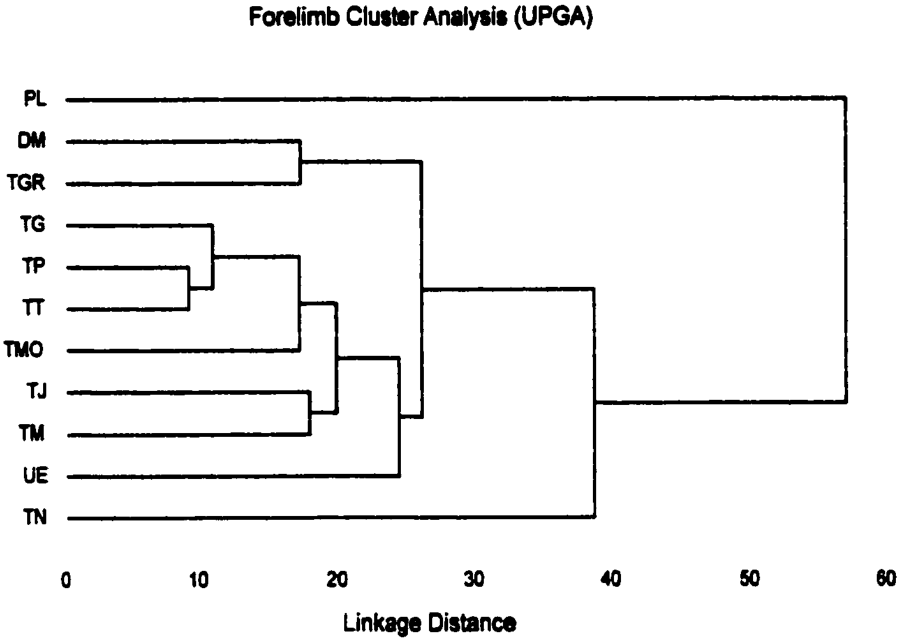


Figure 5.39. Cluster analysis of the variables included in 18 forelimb indices (does not include trochlea depth index or delto-pectoral crest length index). Note the difference between *Ptilocercus* and the tupaiines.

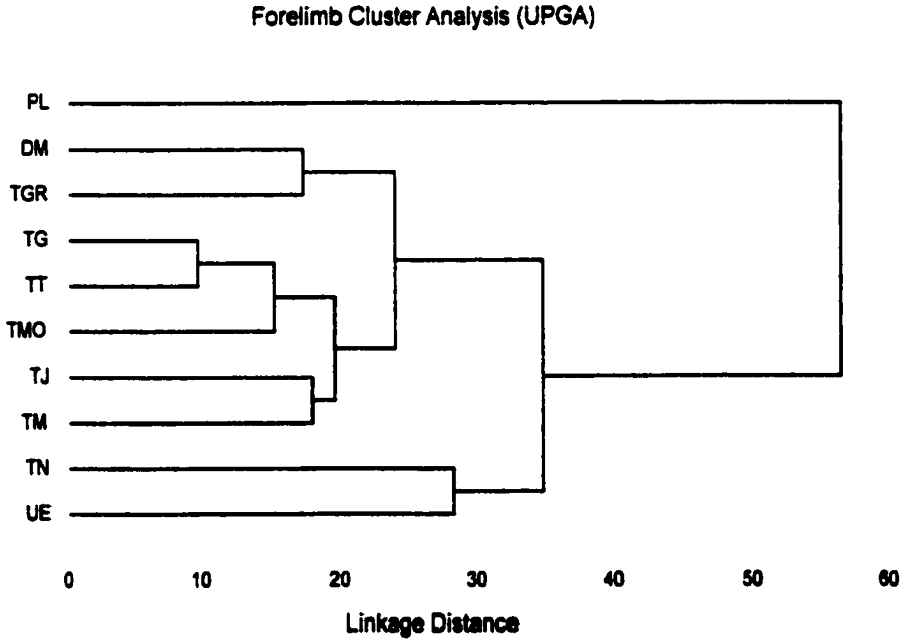


Figure 5.40. Cluster analysis of the variables included in 19 forelimb indices (does not include delto-pectoral crest length index). Note the difference between *Ptilocercus* and the tupaiines.

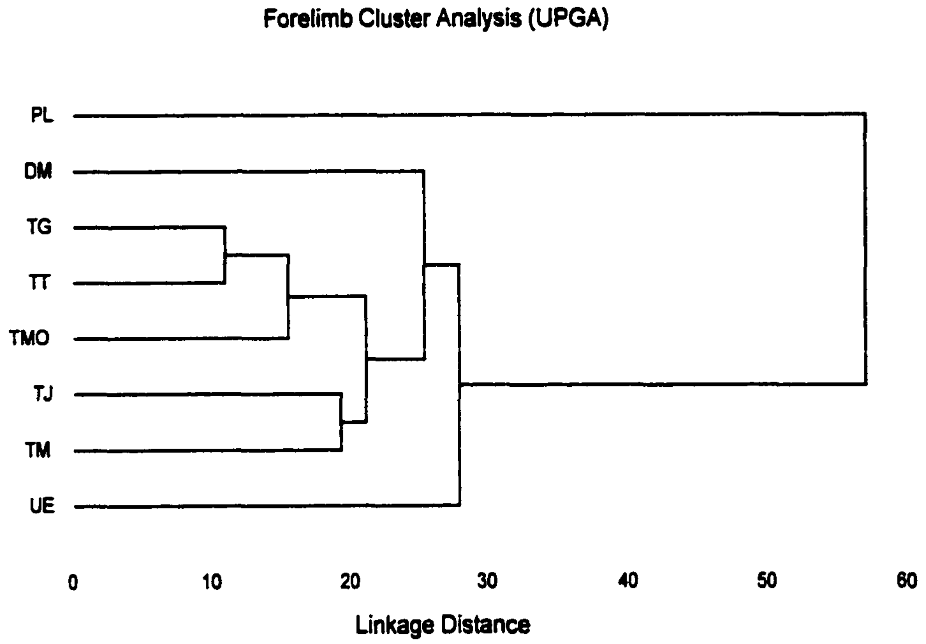


Figure 5.41. Cluster analysis of the variables included in twenty forelimb indices. Note the difference between *Ptilocercus* and the tupaiines.

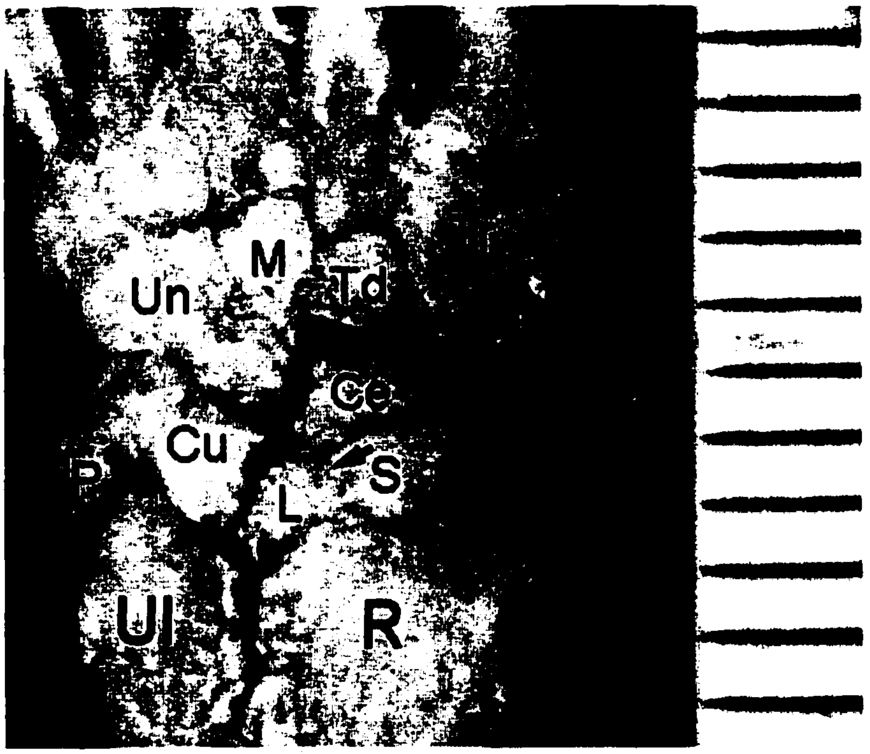


Figure 5.42. Articulated left carpus of *Ptilocercus* (USNM 121885). Subdivisions on scale are 0.5 mm. R: radius, Ul: ulna, S: scaphoid, L: lunate, Cu: cuneiform, P: pisiform, Ce: centrale, Tr: trapezium, Td: trapezoid, M: magnum, Un: unciform. Arrowhead designates groove between scaphoid and lunate.

fused, the magnum and unciform are fused, and the centrale has been lost, which leaves a total of five carpal bones (three in the proximal row and two in the distal row). This would obviously be an extremely derived condition, but Stafford and Thorington (1998, fig. 4b) have clearly shown that only the scaphoid and lunate are fused in *Anathana* and that this taxon is very similar to *Tupaia* and *Urogale* in its carpal morphology. Davis' (1938) comments concerning the fusion of the scaphoid and lunate in *Dendrogale* are confusing because he said that "the scaphoid and lunar are separate," and then later in the same paragraph he referred to "the fused condition of the scaphoid and lunar in *Dendrogale*" (p. 386). Also, despite the fact that Flower (1885), Lyon (1913), and Davis (1938), for example, had reported the fusion of the scaphoid and lunate in *Tupaia* and George (1977) had reported the fusion of these bones in *Tupaia*, *Urogale*, and *Anathana*, Novacek (1980) still scored these bones as being unfused in Tupaiinae for his phylogenetic analysis (see Novacek, 1980, fig. 23; table 5). Hence, Stafford and Thorington's (1998, table 1) definitive statements concerning tupaiid carpal fusion are in sharp contrast to many of the confusing statements made previously about this topic. Stafford and Thorington (1998) were in complete agreement with George (1977) in concluding that the scaphoid and lunate are fused into a scapholunate in *Tupaia*, *Urogale*, and *Anathana*, while the scaphoid and lunate are unfused in *Dendrogale* (see Davis, 1938) and *Ptilocercus* (see Le Gros Clark, 1926). Stafford and Thorington (1998), however, did not attempt to disarticulate the articulated *Ptilocercus* carpus in their care (which they have figured extremely well; see fig. 2a). This is unfortunate because hypotheses concerning carpal fusion (in adults) can be most robustly tested by attempts at disarticulation.

I have examined several disarticulated tupaiid wrists, including those of *Ptilocercus* (NHM 67.1479, 1960.8.4.6), *D. melanura* (MCZ 36746), *D. murina* (FMNH 46630), *T. glis* (MHN 801.95), *T. gracilis* (USNM 449963), *T. minor* (MNHN 1981-186, USNM 396669), *T. montana* (USNM 449964), *T. nicobarica* (USNM 111782), *T. palawanensis* (FMNH 62950), *T. tana* (USNM 396660), and *Urogale* (FMNH 57311, 57312), and I agree with some of Stafford and Thorington's (1998) conclusions, but disagree with others. I agree with their assessment of the fusion of the scaphoid and lunate in *Tupaia*, *Urogale*, and *Anathana*, and I also agree that there is a groove between the scaphoid and lunate of *Ptilocercus* and *Dendrogale* (see arrows on Figs. 5.42-5.44; see also fig. 2a in Stafford and Thorington, 1998, for a scanning electron micrograph of the same carpus shown in Fig. 5.42 that shows the groove between the scaphoid and lunate better than the figure presented here). However, while the scaphoid and lunate of *Ptilocercus* and *Dendrogale* are not as completely fused as they are in *Tupaia*, *Anathana*, and *Urogale* (see Fig. 5.44), they are indeed fused (Figs. 5.43-5.44; contra Le Gros Clark, 1926; Davis, 1938; George, 1977; Novacek, 1980; Stafford and Thorington, 1998). I suspect that any attempt to separate the scapholunate of *Ptilocercus* or *Dendrogale* would result in breakage.

It is possible (albeit unlikely) that the groove on the scapholunate of these taxa (Figs. 5.43-5.44) allows more mobility in the carpus than is present in the carpus of *Tupaia*, *Urogale*, and *Anathana*, in which the groove has been completely obliterated (Fig. 5.44). The presence of a scapholunate is a synapomorphy that unites all living tupaiids. This is clearly a derived condition within Archonta, while the condition found primitively in primates, nine unfused carpal bones, represents the primitive condition for

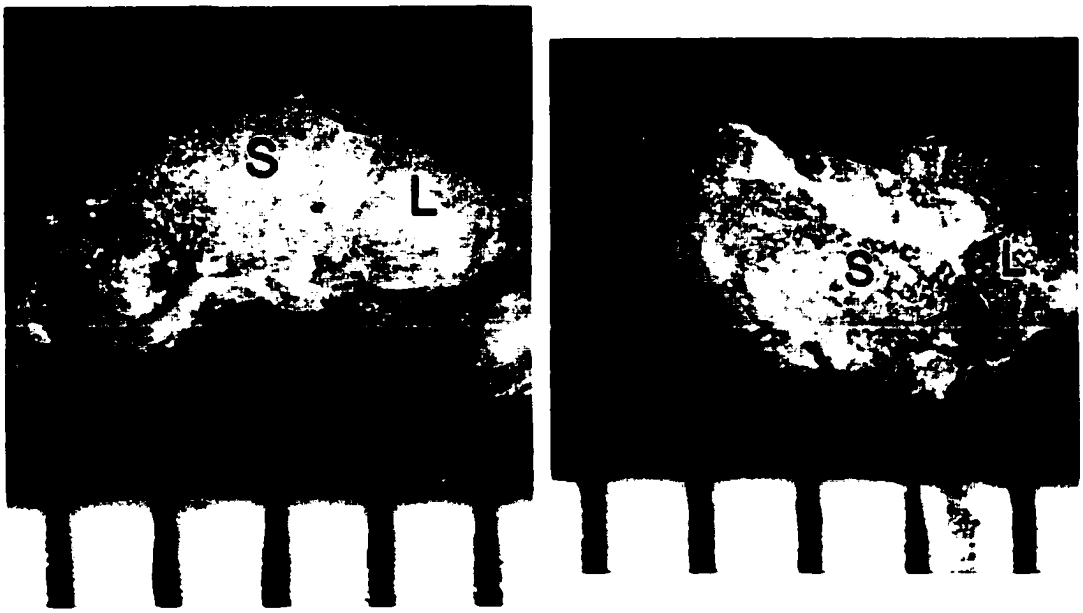


Figure 5.43. Scapholunate of *Ptilocercus* (NHM 67.1479; left: proximal view, right: distal view). Subdivisions on scale are 0.5 mm. S: scaphoid, L: lunate. Arrowhead designates groove between scaphoid and lunate. Note that the scaphoid and lunate are fused in *Ptilocercus*.

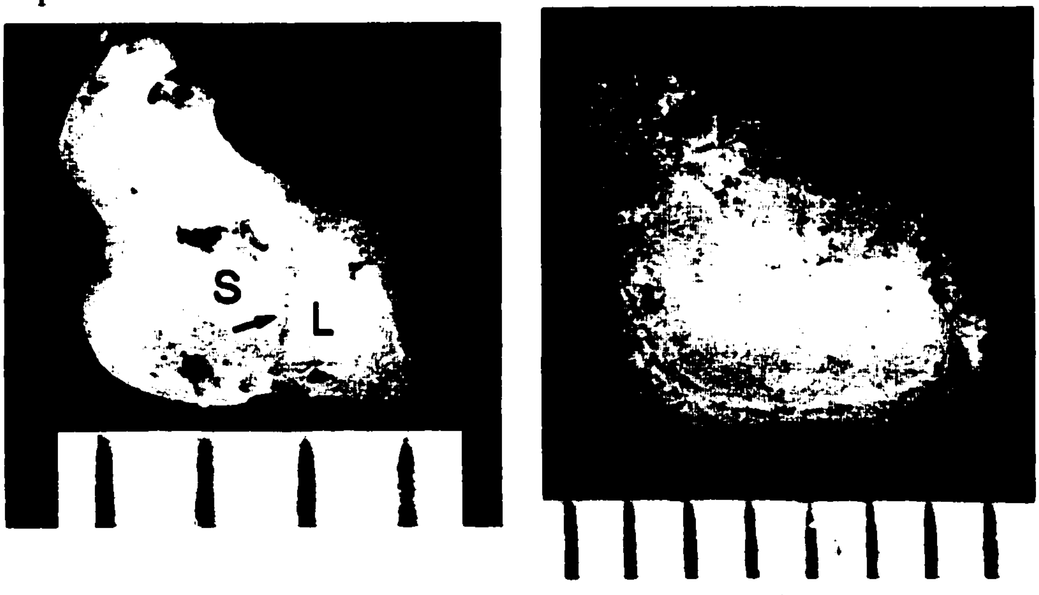


Figure 5.44. Distal view of scapholunate of *Dendrogale melanura* (left; MCZ 36746) and *Urogale* (right; FMNH 57311). Subdivisions on scale are 0.5 mm. S: scaphoid, L: lunate. Arrowhead designates groove between scaphoid and lunate. Note that the scaphoid and lunate are fused in both taxa. The groove between these bones is retained in *Dendrogale*, while it has been completely obliterated in *Urogale*.

Archonta. However, carpal fusion is relatively common in therian mammals (see below), and the incomplete fusion of the scapholunate in *Ptilocercus* and *Dendrogale* could indicate that the ancestral tupaiid had an unfused scaphoid and lunate (although this is perhaps unlikely). Dermopterans and chiropterans both exhibit fusion of the scaphoid, centrale, and lunate into a scaphocentralunate (Stafford and Thorington, 1998), a synapomorphy uniting these groups in Volitantia (Szalay and Lucas, 1993, 1996; Simmons, 1995). The fusion of the scaphoid and lunate into the scapholunate of tupaiids could represent the antecedent condition to that seen in volitantians (though this seems unlikely; see chapter 7). This will be discussed further in the character analysis in chapter 7.

The trapezium of *Ptilocercus* is large relative to that of tupaiines (compare Fig. 5.42 or Stafford and Thorington, 1998, fig. 2a to their figs. 2b-4). An enlarged trapezium may be related to the grasping capabilities of the pollex (Matthew, 1904), which would make sense in the case of *Ptilocercus* because it is capable of grasping with its hand (see chapter 3; Zitzmann, pers. comm.). In fact, the large trapezium, the ulnarly expanded centrale (Fig. 5.42; Stafford and Thorington, 1998), and the fused scapholunate of *Ptilocercus* may have all evolved in response to greater loads placed on the radial side of the carpus during movements in which the pollex is divergent and branches are grasped between the pollex and the other four digits. If the ability to grasp is primitive for tupaiids (see above), then these features present in *Ptilocercus* may be primitive as well. Also, the evolution of grasping in tupaiids may explain why the scaphoid and lunate initially fused in this group because the fusion of these bones may allow them to better incur the loads generated in the wrist when the pollex is habitually divergent.

Stafford and Thorington (1998) identified two features in the carpus of *Ptilocercus* that they considered to be derived: 1) a dorsal process present on the pisiform, which forms a cup with the cuneiform that the ulnar styloid process fits into; and 2) an extension of the unciform that articulates with the ulnarly expanded centrale and restricts the proximal articulation of the magnum to the unciform and centrale, so that it does not contact the lunate (Fig. 5.42; see also Stafford and Thorington, 1998, fig. 2a, which is of better quality than the figure presented here).

Stafford and Thorington (1998) have interpreted the first feature as an adaptation to arboreal locomotion in *Ptilocercus*, which often uses vertical supports. When descending these supports, the forelimb is abducted and pronated, and the hand is ulnarly deviated. In this position, the pisiform-cuneiform cup that the ulnar styloid process sits in would resist carpal dislocation ulnarly, as well as restrict ulnar deviation of the hand (Stafford and Thorington, 1998). If the ancestral tupaiid was arboreal, then this unique condition seen in *Ptilocercus* may be primitive for Scandentia, although Stafford and Thorington (1998) interpreted it as being derived.

The radial expansion of the unciform, its contact with the ulnarly expanded centrale, and the resulting lack of contact between the magnum and lunate in *Ptilocercus* (Fig. 5.42) are difficult to explain functionally and may be derived (Stafford and Thorington, 1998). However, the *Ptilocercus* specimens studied by Le Gros Clark (1926) apparently did not exhibit this condition based on his description of the carpus because he noted contact between the magnum and lunate. Hence, it is possible that the carpus examined by Stafford and Thorington (1998) was an aberrant specimen. Also, contact between the unciform and an ulnarly expanded centrale is seen in lemuriforms (Jouffroy, 1975; Beard and Godinot, 1988) and contact between a radially expanded unciform and an ulnarly expanded scaphocentrale (separating the lunate and magnum) is seen in some marsupials like the arboreal *Dromiciops* (Szalay and Trofimov, 1996; Szalay and Sargis, submitted).

Stafford and Thorington (1998) proposed that the carpus of *Dendrogale* represents the primitive condition for tupaiids because it lacks the two "derived" features that are present in *Ptilocercus* and because they believed that *Dendrogale* has an unfused lunate, unlike other tupaiines. However, the fact that the scaphoid and lunate are fused in *Dendrogale* means that this taxon is no different from the other tupaiines. The question concerning whether the tupaiine carpal pattern or that of *Ptilocercus* is primitive is very difficult to evaluate with the present evidence (especially considering the current poor samples; see above). The carpus is a complex region that warrants detailed investigation beyond an examination of the carpal patterns viewed from the dorsal side. The polarization of carpal characters like those identified in *Ptilocercus* by Stafford and Thorington (1998) will require an investigation that incorporates more mammalian taxa (including metatherians and fossils), more specimens of each taxon, and an analysis of every carpal bone from every view (*i.e.*, an examination of every carpal joint rather than just the dorsal carpal patterns). In other words, further investigation is required before a robust understanding of character evolution in the tupaiid carpus can be fully understood. Because such an investigation has been started (Szalay and Sargis, in prep.), I will await the results of this analysis before concluding on the polarity of the features found in the carpus of *Ptilocercus*.

Martin (1984) has previously discussed the relationship between claw length and substrate preference in tupaiids. Arboreal tupaiids have shorter and deeper claws, while terrestrial tupaiids have longer and shallower claws for rooting (see Fig. 5.45; Martin, 1984). *Urogale* has particularly long claws (and ungual phalanges; Fig. 5.45) that are likely adaptations for scratch digging (see above), as long claws and unguals are typical of diggers (Taylor, 1974; Hildebrand, 1985; MacLeod and Rose, 1993). The ungual phalanges of the arboreal *Ptilocercus* are short and deep (Fig. 5.45), while those of tupaiines are longer and more shallow. Arboreal mammals typically have shorter and deeper unguals, and terrestrial mammals usually have longer unguals that are more shallow (MacLeod and Rose, 1993). The short, deep ungual phalanges of *Ptilocercus* and other arboreal mammals are dorsopalmarly reinforced to better resist bending loads (Beard, 1989) incurred especially during claw clinging and climbing on vertical supports (Hamrick *et al.*, 1999). The condition of the ungual phalanges in *Ptilocercus* is similar to that seen in plesiadapiforms (Fig. 7.1) and dermopterans (see Szalay *et al.*, 1975; Beard, 1989, 1993b; Szalay and Lucas, 1993, 1996; Hamrick *et al.*, 1999), as well as chiropterans (Szalay and Lucas, 1993, 1996; Simmons, 1995; contra Beard, 1993b). This is probably the primitive condition for Archonta, while the replacement of claws by nails in euprimates is derived (Szalay *et al.*, 1987; Dagosto, 1988; Martin, 1990; Szalay and Lucas, 1996). This will be discussed further in the character analysis in chapter 7.

Summary

This analysis of the tupaiid forelimb has clearly shown that the forelimb of the arboreal *Ptilocercus* is better adapted for arboreal locomotion, while that of tupaiines is better adapted for terrestrial (or scansorial) locomotion. Even the most arboreal tupaiines

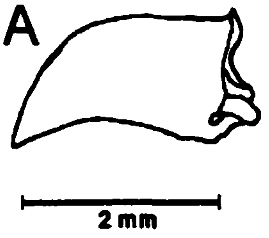
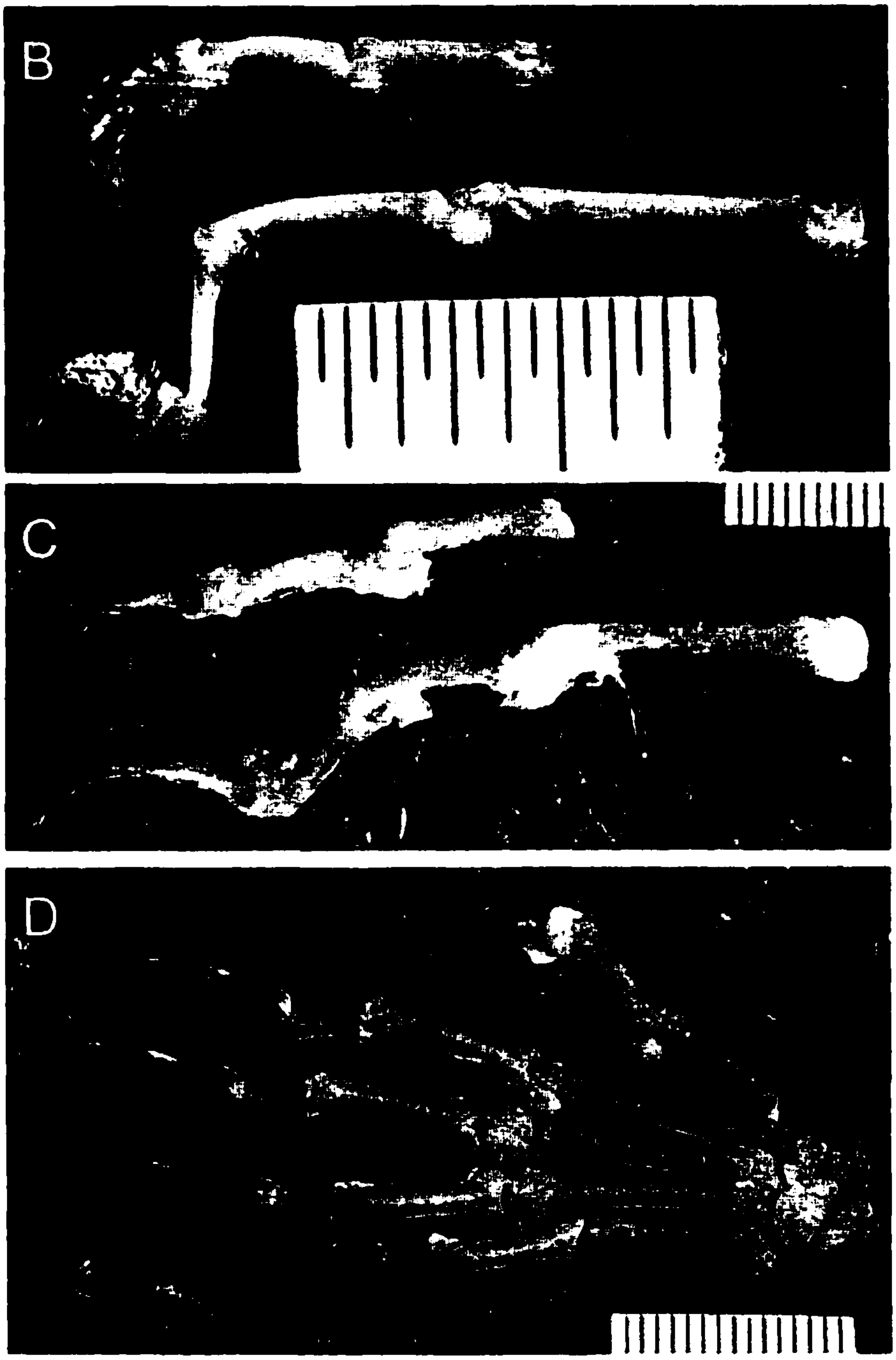


Figure 5.45. A) Ungual phalanx of 3rd manual digit of *Ptilocercus* (redrawn after Szalay, unpublished). 1st and 3rd manual digits of *T. minor* (B) and *Urogale* (C). Left manus of *T. tana* (D). B-D have the falculae on the ungual phalanges. Subdivisions on scale are 0.5 mm. Note the short, deep ungual phalanx of *Ptilocercus*.



remain similar to their terrestrial relatives in their forelimb morphology, providing strong evidence for the terrestrial ancestry of Tupaiinae (but not Tupaiidae). It seems clear that the forelimb morphology of tupaiines has been constrained by their terrestrial heritage. While the forelimb of *Ptilocercus* appears to be habitually flexed and exhibits more mobility in its joints, a necessity for movement on uneven, discontinuous arboreal supports, tupaiines are characterized by more extended forelimbs and more stability in their joints. These stable joints restrict movements more to the parasagittal plane, which increases the efficiency of locomotion on a more even and continuous surface like the ground. The forelimb of tupaiines is more adapted for powerful flexion and extension and, consequently, for rapid terrestrial locomotion. Wharton (1950) stated that *Urogale* "exhibited tendencies to root and dig like miniature pigs" (p. 353), so it is not surprising that the forelimb of *Urogale* stands out among tupaiines in that it exhibits adaptations for scratch-digging. Finally, the forelimb character states of *Ptilocercus* are more similar to those of other archontans than are those of tupaiines. The implications of this will be discussed further in the character analysis in chapter 7.

Table 5.25: Forelimb indices.
(see Table 2.4 for index descriptions)

Genus	Species	Subspecies	Museum	Number	1	2	3	5	6	7	8	9	10	11	12	13	14	15
Ptilocercus	*lowii*	*lowii*	FMNH	76855				91	65									
Ptilocercus	*lowii*		MCZ	51736	77	78	103	77	73	111	97	112	98	85	6.6	28	43	51
Ptilocercus	*lowii*		NHM	1934.5.6.1	79	83	102	84	73	107								
Ptilocercus	*lowii*		NHM	67.1479	80	77	112		70	106	96	105	108	99	6.8	29	39	40
Ptilocercus	*lowii*		NHM	1960.8.4.6	81	79	109	84	75	101	93	98	112	106	6.7	30	41	39
Ptilocercus	*lowii*		NNM	a		80	106	82			89					29		
Ptilocercus	***lowii***	**Mean**			**79**	**79**	**107**	**83**	**71**	**106**	**94**	**105**	**106**	**96**	**6.7**	**29**	**41**	**43**
		SD			**1.42**	**2.39**	**4.32**	**5.28**	**3.84**	**3.91**	**3.52**	**6.91**	**6.94**	**10.56**	**0.10**	**0.88**	**1.95**	**6.71**
		n			**4**	**5**	**5**	**5**	**5**	**4**	**4**	**3**	**3**	**3**	**3**	**4**	**3**	**3**
Dendrogale	*melanura*		MCZ	36746	81	84	103	57	52	95	73	85	101	87	8.4	35	49	56
Dendrogale	*murina*	*frenata*	FMNH	46630	78	82	98	57	62	92	69	77	102	92	7.8	36	46	50
Dendrogale	**sp.**	**Mean**			**80**	**83**	**101**	**57**	**57**	**93**	**71**	**81**	**101**	**89**	**8.1**	**35**	**48**	**53**
		SD			**2.01**	**1.80**	**3.47**	**0.14**	**7.07**	**2.59**	**2.39**	**5.70**	**0.10**	**3.37**	**0.36**	**0.09**	**2.01**	**4.27**
		n			**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**
Tupaia	*glis*	*belangeri*	AMNH	113135	74	80	95	57	65	103	77	72	91	98		32	51	52
Tupaia	*glis*		AMNH	55561		79		63	71	104	71	82	111	96	7.6	40	49	51
Tupaia	*glis*		AMNH	55562		78		60	72	101	75	80	104	98	8.3	38	51	52
Tupaia	*glis*	*glis*	FMNH	98470	73	77	96	55	68	104	78	69	92	105		33	56	53
Tupaia	*glis*	*glis*	FMNH	98469	73	78	93	54	65	97	78	76	92	95		32	50	53
Tupaia	*glis*	*glis*	FMNH	98468	74	79	93	60	69	88	82		86			31		56
Tupaia	*glis*	*belangeri*	FMNH	46642	72	79	91	54	80	94	51	61	125	103		42	51	49
Tupaia	*glis*	*wilkinsoni*	FMNH	66019	70	76	91	62	71	95	55	68	127	102		42	51	50
Tupaia	*glis*	*longipes*	FMNH	76815		77		55	66	93	56	66	125	107		42	52	49
Tupaia	*glis*	*longipes*	FMNH	76819	71	77	96	59	63	91	49	54	123	112		43	58	52
Tupaia	*glis*	*longipes*	FMNH	76824		76	80	56	70	93	55	66	120	101		43	51	50
Tupaia	*glis*	*longipes*	FMNH	76825		76		59	67	95	63	69	111	102		40	53	52
Tupaia	*glis*	*demissa*	MHN	801.95	73	78	90	64	63	101	75	70	91	97	8.0	31	50	51
Tupaia	*glis*	*belangeri*	MNHN	1990-510		79			73	100	75	67	92	103		32	50	49
Tupaia	*glis*	*longipes*	USNM	198043	72	77	96	63	69	98	67	71	116	109	8.4	39	55	50
Tupaia	*glis*	*longipes*	USNM	396665	71	77	95	59	73	98	77	77	99	100	8.1	39	56	56
Tupaia	*glis*	*longipes*	USNM	396673	72	78	93	62	70	97	75	78	106	102	7.6	39	53	52
Tupaia	*glis*		SMNH	A620505	71	76	95	57	69	105	67	63	93	99		32	54	54

Genus	Species	Subspecies	Museum	Number	1	2	3	5	6	7	8	9	10	11	12	13	14	15
Tupaia	*glis*	*discolor*	ZS	1905/13	70	77	92	58	67	98	77	68	88	99		32	52	53
Tupaia	***glis***	**Mean**			**72**	**78**	**93**	**59**	**69**	**98**	**69**	**70**	**105**	**101**	**8.0**	**37**	**52**	**52**
		SD			**1.21**	**1.23**	**4.06**	**3.21**	**4.02**	**4.68**	**10.57**	**6.97**	**14.42**	**4.54**	**0.34**	**4.72**	**2.55**	**2.03**
		n			**13**	**19**	**14**	**18**	**19**	**19**	**19**	**18**	**19**	**18**	**6**	**19**	**18**	**19**
Tupaia	*gracilis*	*gracilis*	FMNH	140925	68	73	99	52	63	90	79		89			32		53
Tupaia	*gracilis*	*gracilis*	FMNH	140928	67	73	97	51	70	87	80		90			33		52
Tupaia	*gracilis*		USNM	449963	70	76	99	72	64	104	62	73	111	95	7.8	41	52	55
Tupaia	***gracilis***	**Mean**			**68**	**74**	**98**	**59**	**66**	**93**	**73**	**73**	**97**	**95**	**7.8**	**35**	**52**	**54**
		SD			**1.44**	**1.82**	**0.76**	**11.47**	**3.73**	**8.84**	**9.97**		**12.49**			**5.06**		**1.73**
		n			**3**	**3**	**3**	**3**	**3**	**3**	**3**	**1**	**3**	**1**	**1**	**3**	**1**	**3**
Tupaia	*javanica*	*occidentalis*	AMNH	106505				48	65									
Tupaia	*javanica*	*occidentalis*	AMNH	106506				53	63									
Tupaia	*javanica*	*occidentalis*	AMNH	106507				49	68									
Tupaia	*javanica*		MCZ	12949				71	64									
Tupaia	*javanica*		MHN	450.15	72	77	94	62	70	110	67	68	92	90	9.1	28	46	51
Tupaia	*javanica*		USNM	154593		81		65	67	96	50	61	124	101	8.7	43	51	50
Tupaia	*javanica*		SMNH	A630506	74	80	97	58	69	103	58	65	97	87		34	47	54
Tupaia	***javanica***	**Mean**			**73**	**79**	**95**	**58**	**67**	**103**	**58**	**65**	**105**	**93**	**8.9**	**35**	**48**	**52**
		SD			**1.64**	**2.08**	**2.23**	**8.46**	**2.71**	**7.01**	**8.69**	**3.75**	**17.19**	**7.31**	**0.30**	**7.35**	**2.53**	**2.22**
		n			**2**	**3**	**2**	**7**	**7**	**3**	**3**	**3**	**3**	**3**	**2**	**3**	**3**	**3**
Tupaia	*minor*	*caedis*	FMNH	140929		80	92	63	64	105	62		102			38		54
Tupaia	*minor*	*caedis*	FMNH	76865	75	81	91	58	63		59	77	118	90		40	47	53
Tupaia	*minor*	*malaccana*	MHN	801.94	73	78	96	54	62	106	69	70	98	96	9.2	33	51	53
Tupaia	*minor*		MNHN	1981-186	73	80	90	61	68	102	70	71	99	99		31	49	50
Tupaia	*minor*		USNM	396668	74	81	92	66	63	106	69	87	116	92	8.6	38	45	49
Tupaia	*minor*		USNM	396669	67	73	95	67	70	104	67	79	109	92	7.8	40	48	52
Tupaia	*minor*		USNM	396672	74	79	92	53	71	104	66	73	106	96	8.7	36	51	53
Tupaia	*minor*		NNM	36048(a)		81	94	65			62	91	129	88		41	41	47
Tupaia	***minor***	**Mean**			**73**	**79**	**93**	**61**	**66**	**104**	**66**	**78**	**110**	**93**	**8.6**	**37**	**48**	**51**
		SD			**2.94**	**2.65**	**2.15**	**5.27**	**3.72**	**1.56**	**4.15**	**8.11**	**10.70**	**3.93**	**0.59**	**3.62**	**3.46**	**2.34**
		n			**6**	**8**	**8**	**8**	**7**	**6**	**8**	**7**	**8**	**7**	**4**	**8**	**7**	**8**
Tupaia	*montana*		USNM	449964	75	79	99	63	68	101	71	66	94	102	8.6	34	61	60
Tupaia	*montana*	*baluensis*	FS	82081	72	76	97	60	60	103	70	72	103	100		35	53	53
Tupaia	***montana***	**Mean**			**73**	**77**	**98**	**62**	**64**	**102**	**70**	**69**	**99**	**101**	**8.6**	**35**	**57**	**56**

Genus	Species	Subspecies	Museum	Number	1	2	3	5	6	7	8	9	10	11	12	13	14	15
		SD			**1.66**	**2.28**	**1.32**	**2.15**	**6.09**	**1.39**	**0.58**	**4.86**	**6.17**	**1.63**		**0.77**	**5.93**	**4.98**
		n			**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**1**	**2**	**2**	**2**
Tupaia	***nicobarica***	***nicobarica***	**USNM**	**111782**		**82**	**99**	**62**	**67**	**99**	**70**	**82**	**133**	**114**	**8.3**	**34**	**45**	**39**
Tupaia	*palawanensis*	*palawanensis*	FMNH	62950	72	77	94	57	69	96	85	84	94	96		33	49	51
Tupaia	*palawanensis*	*palawanensis*	FMNH	63018	71	75	96	56	71	91	72	73	99	97		33	50	52
Tupaia	*palawanensis*	*palawanensis*	FMNH	62976	70	74	95	59	68	99	59	64	116	108		39	54	50
Tupaia	*palawanensis*	*palawanensis*	FMNH	63020	72	77	95	59	72	90	56	61	117	107		40	57	53
Tupaia	*palawanensis*	*palawanensis*	FMNH	62977	72	77	93	67	69	92	55	64	120	103		43	54	52
Tupaia	*palawanensis*	*palawanensis*	FMNH	62978	73	78	94	59	67	96	55	63	119	103		42	54	52
Tupaia	*palawanensis*	*palawanensis*	FMNH	63019	72	77	95	59	67	94	67	69	110	107		40	58	54
Tupaia	*palawanensis*	*palawanensis*	FMNH	63017	73	77	97	63	64	87	64	65	117	114		38	55	48
Tupaia	*palawanensis*	*palawanensis*	FMNH	63016	73	80	90	53	68	95	59	69	122	103		40	52	51
Tupaia	*palawanensis*	*palawanensis*	FMNH	63011	72	78	93	59	77	90	66	74	117	104		39	51	50
Tupaia	*palawanensis*	*palawanensis*	FMNH	63010		78		55	72	94	60	62	107	103		41	57	56
Tupaia	***palawanensis***	**Mean**			**72**	**77**	**94**	**59**	**69**	**93**	**63**	**68**	**113**	**104**		**39**	**54**	**52**
		SD			**0.76**	**1.45**	**1.86**	**3.68**	**3.44**	**3.52**	**8.95**	**6.76**	**9.01**	**5.07**		**3.34**	**2.95**	**2.13**
		n			**10**	**11**	**10**	**11**	**11**	**11**	**11**	**11**	**11**	**11**		**11**	**11**	**11**
Tupaia	*tana*		AMNH	106483				62	72									
Tupaia	*tana*		AMNH	106485				61	71									
Tupaia	*tana*	*utara*	AMNH	35921	73	78	92		70	101	69	68	100	101	8.5	38	56	56
Tupaia	*tana*	*kretami*	FMNH	68793	71	73	97	62	67	95	65	63	96	101		32	52	51
Tupaia	*tana*	*paitana*	FMNH	76892	70	72	98	57	66	93	77	75	98	100		32	51	51
Tupaia	*tana*	*banguei*	FMNH	140935	72	74	98	62	73	91	72		102			35		50
Tupaia	*tana*	*banguei*	FMNH	140936	73	75	100	60	71	91	65		105			36		51
Tupaia	*tana*	*paitana*	FMNH	33031	72	74	100	55	72	97	60	58	114	118		37	62	53
Tupaia	*tana*	*kretami*	FMNH	68797		73		67	66	89	55	63	122	107		40	55	51
Tupaia	*tana*	*paitana*	FMNH	76813	71	73	96	57	68	90	59	64	114	104		39	57	54
Tupaia	*tana*		MHN	746.11	72	74	100	59	64	115	66	63	96	101	9.5	32	52	52
Tupaia	*tana*		MNHN	1977-361	72	74	97	57	72	107	67	62	96	104		35	57	55
Tupaia	*tana*	*tana*	USNM	174611				68	64									
Tupaia	*tana*	*paitana*	USNM	396660	73	73	101	64	66	97	71	67	108	114	8.4	36	60	53
Tupaia	*tana*		USNM	449965	71	72	101	65	64	86	63	69	115	104	8.6	39	53	51
Tupaia	*tana*		USNM	449966	72	73	100	54	76	92	71	86	117	97	9.1	38	46	48
Tupaia	*tana*		USNM	449968	72	72	101	65	75	96	68	75	109	99	9.6	36	51	51

Genus	Species	Subspecies	Museum	Number	1	2	3	5	6	7	8	9	10	11	12	13	14	15
Tupaia	*tana*		USNM	449969	73	75	98	58	66	88	63	63	110	110	9.4	36	56	51
Tupaia	*tana*	*utara*	USNM	83938						97	64	73	121	107	8.4	39	51	48
Tupaia	*tana*	*tana*	USNM	154341		74		55	68	96	72	75	110	107	8.0	37	54	51
Tupaia	*tana*		ZS	1910/1462				66	61									
Tupaia	***tana***	**Mean**			**72**	**74**	**99**	**61**	**69**	**95**	**66**	**68**	**108**	**105**	**8.8**	**36**	**54**	**52**
		SD			**0.91**	**1.42**	**2.49**	**4.22**	**4.01**	**7.23**	**5.43**	**7.29**	**8.68**	**5.80**	**0.58**	**2.56**	**4.07**	**2.20**
		n			**14**	**16**	**14**	**19**	**20**	**17**	**17**	**15**	**17**	**15**	**9**	**17**	**15**	**17**
Urogale	*everetti*		FMNH	57312	71	75	101	53	74	90	60	63	114	109	10.1	37	58	53
Urogale	*everetti*		FMNH	57148	74	74	113	58	70	95	69	78	126	112		36	52	46
Urogale	*everetti*		FMNH	57307	72	74	106	61	76	89	62	72	121	105		37	51	48
Urogale	*everetti*		FMNH	57308	73	76	105	56	72	92	57	67	126	107		39	52	48
Urogale	*everetti*		FMNH	61418	71	74	107	57	67	89	60	66	118	108		36	54	50
Urogale	*everetti*		FMNH	61419	72	77	106	61	65	93	56	69	124	100		40	51	51
Urogale	*everetti*		FMNH	61420	74	76	108	55	72	91	60	73	131	107		39	49	46
Urogale	*everetti*		FMNH	57329	71	74	107	56	68	96	57	72	122	96		40	49	51
Urogale	*everetti*		FMNH	57464	71	75	101	56	66	93	60	68	122	107		39	52	48
Urogale	*everetti*		FMNH	57465	72	74	106	59	65	86	64	67	114	109		37	56	51
Urogale	*everetti*		FMNH	57311	72	73	107	63	71	92	68	82	113	95		34	51	54
Urogale	***everetti***	**Mean**			**72**	**75**	**106**	**58**	**70**	**91**	**61**	**71**	**121**	**105**	**10.1**	**38**	**52**	**50**
		SD			**1.02**	**1.10**	**3.39**	**2.86**	**3.62**	**2.74**	**4.37**	**5.36**	**5.78**	**5.66**		**1.78**	**2.65**	**2.53**
		n			**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**1**	**11**	**11**	**11**
Tupaiinae		**Mean**			**73**	**78**	**98**	**59**	**66**	**97**	**67**	**72**	**109**	**100**	**8.6**	**36**	**51**	**51**
		n			**63**	**76**	**67**	**82**	**83**	**75**	**77**	**71**	**77**	**71**	**27**	**77**	**71**	**77**

Table 5.25: Forelimb indices.
(see Table 2.4 for index descriptions)

Genus	Species	Subspecies	Museum	Number	16	17	18	19	20	21	22	23
Ptilocercus	*lowii*	*lowii*	FMNH	76855								
Ptilocercus	*lowii*		MCZ	51736	25	43	7.9	91	47	85	9.1	4.3
Ptilocercus	*lowii*		NHM	1934.5.6.1		42						
Ptilocercus	*lowii*		NHM	67.1479	25	40	7.7	91	42	82	9.2	4.2
Ptilocercus	*lowii*		NHM	1960.8.4.6	24	43	7.8	77	43	85	7.7	4.6
Ptilocercus	*lowii*		NNM	a	26	43						
Ptilocercus	***lowii***	**Mean**			**25**	**42**	**7.8**	**86**	**44**	**84**	**8.7**	**4.4**
		SD			**0.85**	**1.48**	**0.14**	**8.28**	**2.55**	**1.70**	**0.85**	**0.17**
		n			**4**	**5**	**3**	**3**	**3**	**3**	**3**	**3**
Dendrogale	*melanura*		MCZ	36746	21	44	9.1	96	45	71	6.7	4.1
Dendrogale	*murina*	*frenata*	FMNH	46630	19	40	8.8	77	47	79	9.2	4.7
Dendrogale	**sp.**	**Mean**			**20**	**42**	**8.9**	**87**	**46**	**75**	**8.0**	**4.4**
		SD			**1.46**	**2.89**	**0.21**	**13.52**	**1.39**	**5.38**	**1.75**	**0.42**
		n			**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**
Tupaia	*glis*	*belangeri*	AMNH	113135	21	44	9.9	89	38	72	8.0	4.1
Tupaia	*glis*		AMNH	55561	18	43						
Tupaia	*glis*		AMNH	55562	19	44						
Tupaia	*glis*	*glis*	FMNH	98470	21	42	9.6	95	43	74	8.8	4.0
Tupaia	*glis*	*glis*	FMNH	98469	21	42	10.2	96	43	72	9.2	4.4
Tupaia	*glis*	*glis*	FMNH	98468	20		11.0			70	7.9	4.1
Tupaia	*glis*	*belangeri*	FMNH	46642	20		11.3	85	39	69	10.6	4.7
Tupaia	*glis*	*wilkinsoni*	FMNH	66019	21		11.8	72	47	65	11.2	4.3
Tupaia	*glis*	*longipes*	FMNH	76815	19							
Tupaia	*glis*	*longipes*	FMNH	76819	19		10.4	78	43	68	9.5	4.4
Tupaia	*glis*	*longipes*	FMNH	76824	18		11.0	90	39	70	10.7	5.6
Tupaia	*glis*	*longipes*	FMNH	76825	19					64		
Tupaia	*glis*	*demissa*	MHN	801.95	20	42	9.9	80	39	69	7.8	3.5
Tupaia	*glis*	*belangeri*	MNHN	1990-510	20	44		90	44	71		
Tupaia	*glis*	*longipes*	USNM	198043	19	46	8.7	94	40	69	10.7	3.9
Tupaia	*glis*	*longipes*	USNM	396665	18	43	9.1	99	46	76	9.8	4.1
Tupaia	*glis*	*longipes*	USNM	396673	17	43	8.5	94	41	75	10.2	3.9
Tupaia	*glis*		SMNH	A620505	22	38	10.7	91	47	68	8.6	3.9

Genus	Species	Subspecies	Museum	Number	16	17	18	19	20	21	22	23
Tupaia	*glis*	*discolor*	ZS	1905/13	20	38	10.4	87	45	72	9.8	4.1
Tupaia	***glis***	**Mean**			**20**	**42**	**10.2**	**89**	**42**	**70**	**9.5**	**4.2**
		SD			**1.19**	**2.21**	**0.97**	**7.62**	**3.16**	**3.47**	**1.13**	**0.50**
		n			**19**	**12**	**14**	**14**	**14**	**16**	**14**	**14**
Tupaia	*gracilis*	*gracilis*	FMNH	140925	19		9.9	68		70		4.0
Tupaia	*gracilis*	*gracilis*	FMNH	140928	19		9.3	72		70		4.1
Tupaia	*gracilis*		USNM	449963	18		9.2	100	48	69	7.9	3.5
Tupaia	***gracilis***	**Mean**			**19**		**9.4**	**80**	**48**	**70**	**7.9**	**3.9**
		SD			**0.33**		**0.39**	**17.24**		**0.41**		**0.32**
		n			**3**		**3**	**3**	**1**	**3**	**1**	**3**
Tupaia	*javanica*	*occidentalis*	AMNH	106505								
Tupaia	*javanica*	*occidentalis*	AMNH	106506								
Tupaia	*javanica*	*occidentalis*	AMNH	106507								
Tupaia	*javanica*		MCZ	12949								
Tupaia	*javanica*		MHN	450.15	24	34	9.9	90	39	74	8.4	3.7
Tupaia	*javanica*		USNM	154593	21	38						
Tupaia	*javanica*		SMNH	A630506	21	31	9.1	99	43	74	8.8	4.6
Tupaia	***javanica***	**Mean**			**22**	**34**	**9.5**	**94**	**41**	**74**	**8.6**	**4.2**
		SD			**1.48**	**3.66**	**0.60**	**6.26**	**3.35**	**0.33**	**0.24**	**0.63**
		n			**3**	**3**	**2**	**2**	**2**	**2**	**2**	**2**
Tupaia	*minor*	*caedis*	FMNH	140929	21			85		72	9.7	4.3
Tupaia	*minor*	*caedis*	FMNH	76865	20		8.7	120	34	74	10.2	4.2
Tupaia	*minor*	*malaccana*	MHN	801.94	22	36	9.3	89	39	73	8.3	3.8
Tupaia	*minor*		MNHN	1981-186	23	42	8.6	82	47	77	8.1	3.9
Tupaia	*minor*		USNM	396668	23	45	7.6	76	40	77	10.3	5.5
Tupaia	*minor*		USNM	396669	18		7.7	87	34	73	9.5	5.3
Tupaia	*minor*		USNM	396672	23	40	8.1	90	37	82	9.0	5.8
Tupaia	*minor*		NNM	36048(a)	22	43						
Tupaia	***minor***	**Mean**			**21**	**41**	**8.3**	**90**	**38**	**75**	**9.3**	**4.7**
		SD			**1.66**	**3.68**	**0.64**	**14.15**	**4.58**	**3.56**	**0.88**	**0.81**
		n			**8**	**5**	**6**	**7**	**6**	**7**	**7**	**7**
Tupaia	*montana*		USNM	449964	21	45	8.9	87	35	72	6.4	4.8
Tupaia	*montana*	*baluensis*	FS	82081	22	43	8.6	97	39	73	10.1	4.8
Tupaia	***montana***	**Mean**			**21**	**44**	**8.7**	**92**	**37**	**73**	**8.3**	**4.8**

Genus	Species	Subspecies	Museum	Number	16	17	18	19	20	21	22	23
		SD			**0.64**	**1.06**	**0.25**	**6.69**	**3.52**	**0.42**	**2.65**	**0.01**
		n			**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**
Tupaia	***nicobarica***	***nicobarica***	**USNM**	**111782**	**22**		**8.1**	**87**	**43**	**72**	**10.8**	**4.8**
Tupaia	*palawanensis*	*palawanensis*	FMNH	62950	20	38	9.6	92	42	73	8.9	3.8
Tupaia	*palawanensis*	*palawanensis*	FMNH	63018	22	41	10.3	90	48	70	8.8	4.3
Tupaia	*palawanensis*	*palawanensis*	FMNH	62976	21		11.1	106	39	70	9.9	5.0
Tupaia	*palawanensis*	*palawanensis*	FMNH	63020	21		11.9	90	41	69	9.6	4.9
Tupaia	*palawanensis*	*palawanensis*	FMNH	62977	21		12.0	100	42	74	9.5	4.6
Tupaia	*palawanensis*	*palawanensis*	FMNH	62978	20		11.4	93	38	70	7.4	3.7
Tupaia	*palawanensis*	*palawanensis*	FMNH	63019	20		11.7	88	38	73	10.3	4.7
Tupaia	*palawanensis*	*palawanensis*	FMNH	63017	20		10.7	94	36	70	9.1	4.4
Tupaia	*palawanensis*	*palawanensis*	FMNH	63016	20	42	11.4	81	43	72	11.0	4.2
Tupaia	*palawanensis*	*palawanensis*	FMNH	63011	21		11.8	87	38	74	9.2	4.8
Tupaia	*palawanensis*	*palawanensis*	FMNH	63010	19							
Tupaia	***palawanensis***	**Mean**			**20**	**40**	**11.2**	**92**	**40**	**71**	**9.4**	**4.4**
		SD			**0.76**	**2.07**	**0.78**	**7.03**	**3.33**	**2.11**	**0.98**	**0.44**
		n			**11**	**3**	**10**	**10**	**10**	**10**	**10**	**10**
Tupaia	*tana*		AMNH	106483								
Tupaia	*tana*		AMNH	106485								
Tupaia	*tana*	*utara*	AMNH	35921	19	44	8.9	147	44	72	9.3	5.5
Tupaia	*tana*	*kretami*	FMNH	68793	25	46	11.6	96	43	67	8.7	4.6
Tupaia	*tana*	*paitana*	FMNH	76892	26	45	11.8	94	46	67	9.2	4.8
Tupaia	*tana*	*banguei*	FMNH	140935	24		12.0	90		73	8.7	4.2
Tupaia	*tana*	*banguei*	FMNH	140936	24		12.0	67		73		4.6
Tupaia	*tana*	*paitana*	FMNH	33031	25		11.6	90	35	74	9.5	4.9
Tupaia	*tana*	*kretami*	FMNH	68797	24			90	38			
Tupaia	*tana*	*paitana*	FMNH	76813	23		12.9	72	40	69	9.0	4.8
Tupaia	*tana*		MHN	746.11	23	46	10.4	90	44	69	8.3	4.2
Tupaia	*tana*		MNHN	1977-361	22	49	10.6	98	47	70	8.9	4.4
Tupaia	*tana*	*tana*	USNM	174611								
Tupaia	*tana*	*paitana*	USNM	396660	23	48	10.1	91	36	74	8.6	5.1
Tupaia	*tana*		USNM	449965	23	48	9.9	94	42	78	8.5	5.0
Tupaia	*tana*		USNM	449966	23	50	10.1	92	42	77	8.6	4.7
Tupaia	*tana*		USNM	449968	23	45	9.2	77	41	78	8.8	5.0

Genus	Species	Subspecies	Museum	Number	16	17	18	19	20	21	22	23
Tupaia	*tana*		USNM	449969	23	50	10.6	78	42	71	8.6	5.2
Tupaia	*tana*	*utara*	USNM	83938	22	47		80	46	71		
Tupaia	*tana*	*tana*	USNM	154341	21	47	9.4	74	40	72		
Tupaia	*tana*		ZS	1910/1462								
Tupaia	***tana***	**Mean**			**23**	**47**	**10.7**	**90**	**42**	**72**	**8.8**	**4.8**
		SD			**1.43**	**2.09**	**1.19**	**17.59**	**3.44**	**3.44**	**0.36**	**0.37**
		n			**17**	**12**	**15**	**17**	**15**	**16**	**13**	**14**
Urogale	*everetti*		FMNH	57312	25	36	12.5	79	43	74	8.0	4.8
Urogale	*everetti*		FMNH	57148	26		12.4	99	37	70	7.8	4.1
Urogale	*everetti*		FMNH	57307	26		13.0	88	43	73	8.8	5.2
Urogale	*everetti*		FMNH	57308	25		12.1	86	36	72	8.9	5.8
Urogale	*everetti*		FMNH	61418	27		13.0	87	40	75	9.3	5.2
Urogale	*everetti*		FMNH	61419	26		12.8	120	37	70	8.2	3.9
Urogale	*everetti*		FMNH	61420	25		11.8	99	38	69	9.0	4.7
Urogale	*everetti*		FMNH	57329	27		12.9	88	43	70	7.4	5.1
Urogale	*everetti*		FMNH	57464	26		13.9	91	42	72	8.7	5.1
Urogale	*everetti*		FMNH	57465	26		12.4	72	39	70	8.5	5.2
Urogale	*everetti*		FMNH	57311	27	44	11.5	99	40	70	8.8	4.2
Urogale	***everetti***	**Mean**			**26**	**40**	**12.6**	**92**	**40**	**71**	**8.5**	**4.8**
		SD			**0.68**	**6.28**	**0.66**	**12.59**	**2.65**	**1.80**	**0.58**	**0.58**
		n			**11**	**2**	**11**	**11**	**11**	**11**	**11**	**11**
Tupaiinae		**Mean**			**21**	**41**	**9.8**	**89**	**42**	**72**	**8.9**	**4.5**
		n			**77**	**41**	**66**	**69**	**64**	**70**	**63**	**66**

Table 5.26: Forelimb measurements.
(see Table 2.3 for measurement descriptions)

Genus	Species	Subspecies	Museum	Number	SL	SW	SGL	SGW	HL	HHW	HHL	HMSML	HMSAP	HTW	HCW	HTL	HCL
Ptilocercus	*lowii*	*lowii*	FMNH	76855	12.54	11.45	2.97	1.93									
Ptilocercus	*lowii*		MCZ	51736	13.50	10.34	2.80	2.04	22.41	3.35	3.02	2.06		1.52	1.57	1.36	1.60
Ptilocercus	*lowii*		NHM	1934.5.6.1	12.69	10.60	2.84	2.06	22.22	3.05	2.86		1.98				
Ptilocercus	*lowii*		NHM	67.1479	13.98		2.90	2.02	21.19	3.12	2.94	1.96		1.47	1.53	1.40	1.42
Ptilocercus	*lowii*		NHM	1960.8.4.6	12.64	10.56	2.63	1.97	21.23	2.98	2.94	2.03		1.43	1.54	1.46	1.38
Ptilocercus	*lowii*		NNM	a	13.03	10.66			20.60			1.73	1.90	1.39	1.56		
Ptilocercus	***lowii***	**Mean**			**13.06**	**10.72**	**2.83**	**2.00**	**21.53**	**3.13**	**2.94**	**1.95**	**1.94**	**1.45**	**1.55**	**1.41**	**1.47**
		SD			**0.57**	**0.42**	**0.13**	**0.05**	**0.76**	**0.16**	**0.07**	**0.15**	**0.06**	**0.06**	**0.02**	**0.05**	**0.12**
		n			**6**	**5**	**5**	**5**	**5**	**4**	**4**	**4**	**2**	**4**	**4**	**3**	**3**
Dendrogale	*melanura*		MCZ	36746	14.23	8.07	2.86	1.50	19.51	2.38	2.50	1.55		1.07	1.47	1.26	1.45
Dendrogale	*murina*	*frenata*	FMNH	46630	14.48	8.24	2.61	1.63	19.63	2.49	2.72	1.56	1.68	0.93	1.34	1.21	1.32
Dendrogale	**sp.**	**Mean**			**14.36**	**8.16**	**2.74**	**1.57**	**19.57**	**2.44**	**2.61**	**1.56**	**1.68**	**1.00**	**1.41**	**1.24**	**1.39**
		SD			**0.18**	**0.12**	**0.18**	**0.09**	**0.08**	**0.08**	**0.16**	**0.01**		**0.10**	**0.09**	**0.04**	**0.09**
		n			**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**1**	**2**	**2**	**2**	**2**
Tupaia	*glis*	*belangeri*	AMNH	113135	22.55	12.93	3.96	2.57	31.33	4.39	4.27	2.34	2.52	1.61	2.09	2.24	2.29
Tupaia	*glis*		AMNH	55561	19.40	12.28	3.61	2.56	27.86	3.71	3.58	2.14		1.44	2.04	1.76	1.84
Tupaia	*glis*		AMNH	55562	20.30	12.26	3.65	2.62	29.48	3.77	3.74	2.28		1.63	2.17	2.04	2.08
Tupaia	*glis*	*glis*	FMNH	98470	21.34	11.71	3.84	2.63	30.28	4.33	4.16	2.15	2.33	1.59	2.03	2.32	2.21
Tupaia	*glis*	*glis*	FMNH	98469	20.73	11.19	3.86	2.50	29.24	3.98	4.11	2.10	2.24	1.52	1.94	1.99	2.10
Tupaia	*glis*	*glis*	FMNH	98468	21.22	12.67	3.86	2.68	29.93	3.74	4.24	2.09	2.20	1.53	1.87		2.17
Tupaia	*glis*	*belangeri*	FMNH	46642	22.54	12.18	3.77	3.02	30.84	4.13	4.39	2.39	2.24	1.30	2.57	2.13	2.06
Tupaia	*glis*	*wilkinsoni*	FMNH	66019	20.48	12.71	3.55	2.51	27.45	3.73	3.94	2.23	2.32	1.30	2.37	1.91	1.87
Tupaia	*glis*	*longipes*	FMNH	76815	23.12	12.70	4.50	2.96	35.51	4.32	4.66	2.61	2.72	1.54	2.76	2.35	2.20
Tupaia	*glis*	*longipes*	FMNH	76819	22.28	13.24	4.49	2.85	33.05	4.13	4.53	2.25	2.50	1.34	2.72	2.47	2.21
Tupaia	*glis*	*longipes*	FMNH	76824	24.02	13.35	4.29	2.99	35.02	4.36	4.67	2.26	2.59	1.53	2.76	2.32	2.30
Tupaia	*glis*	*longipes*	FMNH	76825	23.76	14.07	4.54	3.06	35.24	4.52	4.74	2.20	2.51	1.65	2.60	2.38	2.34
Tupaia	*glis*	*demissa*	MHN	801.95	21.82	13.93	4.07	2.56	32.44	4.10	4.04	2.27	3.07	1.45	1.94	2.07	2.14
Tupaia	*glis*	*belangeri*	MNHN	1990-510			3.94	2.88	31.01	4.13	4.15	2.32	2.41	1.50	1.99	2.23	2.17
Tupaia	*glis*	*longipes*	USNM	198043	22.83	14.27	4.32	2.97	34.74	4.24	4.33	2.11		1.73	2.60	2.45	2.25
Tupaia	*glis*	*longipes*	USNM	396665	23.89	14.14	4.29	3.13	36.43	4.40	4.49	2.29		1.99	2.57	2.59	2.59
Tupaia	*glis*	*longipes*	USNM	396673	23.48	14.53	4.34	3.05	36.14	4.09	4.20	2.23		1.83	2.43	2.34	2.29
Tupaia	*glis*		SMNH	A620505	19.32	11.06	3.56	2.47	27.71	4.11	3.90	2.08	2.27	1.30	1.94	2.06	2.09

Genus	Species	Subspecies	Museum	Number	SL	SW	SGL	SGW	HL	HHW	HHL	HMSML	HMSAP	HTW	HCW	HTL	HCL
Tupaia	*glis*	*discolor*	ZS	1905/13	20.53	12.00	3.95	2.66	32.37	4.13	4.20	2.17	2.20	1.58	2.06	2.32	2.34
Tupaia	***glis***	**Mean**			**21.87**	**12.85**	**4.02**	**2.77**	**31.90**	**4.12**	**4.23**	**2.24**	**2.44**	**1.55**	**2.29**	**2.22**	**2.19**
		SD			**1.52**	**1.05**	**0.33**	**0.23**	**2.96**	**0.24**	**0.31**	**0.13**	**0.24**	**0.18**	**0.32**	**0.22**	**0.17**
		n			**18**	**18**	**19**	**19**	**19**	**19**	**19**	**19**	**14**	**19**	**19**	**18**	**19**
Tupaia	*gracilis*	*gracilis*	FMNH	140925	16.03	8.40	3.13	1.98	23.57	2.86	3.19	1.65	1.56	1.10	1.40		1.57
Tupaia	*gracilis*	*gracilis*	FMNH	140928	16.57	8.53	3.02	2.12	23.42	2.85	3.27	1.78	1.68	1.14	1.43		1.59
Tupaia	*gracilis*		USNM	449963	15.95	11.45	3.34	2.15	25.44	3.20	3.09	1.71		1.17	1.89	1.61	1.70
Tupaia	***gracilis***	**Mean**			**16.18**	**9.46**	**3.16**	**2.08**	**24.14**	**2.97**	**3.18**	**1.71**	**1.62**	**1.14**	**1.57**	**1.61**	**1.62**
		SD			**0.34**	**1.72**	**0.16**	**0.09**	**1.13**	**0.20**	**0.09**	**0.07**	**0.08**	**0.04**	**0.27**		**0.07**
		n			**3**	**3**	**3**	**3**	**3**	**3**	**3**	**3**	**2**	**3**	**3**	**1**	**3**
Tupaia	*javanica*	*occidentalis*	AMNH	106505	13.78	6.65	2.98	1.95									
Tupaia	*javanica*	*occidentalis*	AMNH	106506	17.42	9.21	3.28	2.06									
Tupaia	*javanica*	*occidentalis*	AMNH	106507	16.12	7.83	3.08	2.10									
Tupaia	*javanica*		MCZ	12949	17.04	12.05	3.26	2.10									
Tupaia	*javanica*		MHN	450.15	14.51	8.96	2.76	1.94	21.81	3.01	2.74	1.61	1.59	0.97	1.45	1.42	1.57
Tupaia	*javanica*		USNM	154593	16.07	10.39	3.36	2.26	23.44	3.22	3.36	1.84		1.04	2.10	1.71	1.69
Tupaia	*javanica*		SMNH	A630506	16.64	9.60	3.13	2.17	24.39	3.63	3.54	1.76	1.75	1.02	1.75	1.57	1.80
Tupaia	***javanica***	**Mean**			**15.94**	**9.24**	**3.12**	**2.08**	**23.21**	**3.29**	**3.21**	**1.74**	**1.67**	**1.01**	**1.77**	**1.57**	**1.69**
		SD			**1.33**	**1.74**	**0.21**	**0.11**	**1.30**	**0.32**	**0.42**	**0.12**	**0.11**	**0.04**	**0.33**	**0.15**	**0.12**
		n			**7**	**7**	**7**	**7**	**3**	**3**	**3**	**3**	**2**	**3**	**3**	**3**	**3**
Tupaia	*minor*	*caedis*	FMNH	140929	14.48	9.14	2.75	1.76	20.43	2.98	2.84	1.60	1.52	1.01	1.62		1.59
Tupaia	*minor*	*caedis*	FMNH	76865	14.55	8.40	2.86	1.79	22.14			1.65	1.72	1.04	1.77	1.35	1.50
Tupaia	*minor*	*malaccana*	MHN	801.94	15.48	8.41	3.00	1.87	21.97	3.09	2.91	1.68	1.62	1.12	1.63	1.61	1.67
Tupaia	*minor*		MNHN	1981-186	14.62	8.99	2.96	2.01	22.07	2.97	2.91	1.71	1.66	1.09	1.55	1.54	1.56
Tupaia	*minor*		USNM	396668	14.71	9.73	3.10	1.94	21.61	3.04	2.87	1.79		1.30	1.88	1.49	1.62
Tupaia	*minor*		USNM	396669	16.22	10.90	3.09	2.15	25.22	3.25	3.13	1.97		1.25	1.86	1.58	1.71
Tupaia	*minor*		USNM	396672	15.58	8.33	2.91	2.07	21.69	3.16	3.05	1.81		1.18	1.78	1.61	1.68
Tupaia	*minor*		NNM	36048(a)	14.84	9.58			22.31			1.60	1.66	1.27	2.06	1.40	1.60
Tupaia	***minor***	**Mean**			**15.06**	**9.19**	**2.95**	**1.94**	**22.18**	**3.08**	**2.95**	**1.73**	**1.64**	**1.16**	**1.77**	**1.51**	**1.62**
		SD			**0.63**	**0.88**	**0.13**	**0.14**	**1.36**	**0.11**	**0.11**	**0.13**	**0.07**	**0.11**	**0.17**	**0.10**	**0.07**
		n			**8**	**8**	**7**	**7**	**8**	**6**	**6**	**8**	**5**	**8**	**8**	**7**	**8**
Tupaia	*montana*		USNM	449964	21.00	13.27	3.97	2.71	28.96	3.79	3.77	2.49		1.45	2.05	2.21	2.17
Tupaia	*montana*	*baluensis*	FS	82081	21.23	12.77	4.51	2.69	29.64	4.10	4.00	2.55	2.49	1.58	2.26	2.18	2.19
Tupaia	***montana***	**Mean**			**21.12**	**13.02**	**4.24**	**2.70**	**29.30**	**3.95**	**3.89**	**2.52**	**2.49**	**1.52**	**2.16**	**2.20**	**2.18**

Genus	Species	Subspecies	Museum	Number	SL	SW	SGL	SGW	HL	HHW	HHL	HMSML	HMSAP	HTW	HCW	HTL	HCL
		SD			**0.16**	**0.35**	**0.38**	**0.01**	**0.48**	**0.22**	**0.16**	**0.04**		**0.09**	**0.15**	**0.02**	**0.01**
		n			**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**1**	**2**	**2**	**2**	**2**
Tupaia	***nicobarica***	***nicobarica***	**USNM**	**111782**	**20.99**	**12.91**	**4.13**	**2.75**	**31.25**	**4.37**	**4.41**	**2.38**		**1.63**	**2.34**	**2.00**	**1.76**
Tupaia	*palawanensis*	*palawanensis*	FMNH	62950	21.18	12.14	3.89	2.70	29.14	4.04	4.21	2.26	2.35	1.62	1.91	1.94	2.03
Tupaia	*palawanensis*	*palawanensis*	FMNH	63018	20.02	11.30	3.81	2.69	28.17	3.75	4.11	2.13	2.17	1.41	1.97	1.93	1.98
Tupaia	*palawanensis*	*palawanensis*	FMNH	62976	19.82	11.66	3.78	2.58	27.50	4.05	4.08	2.12	2.06	1.35	2.27	2.10	1.95
Tupaia	*palawanensis*	*palawanensis*	FMNH	63020	19.73	11.62	3.63	2.61	27.75	3.58	3.97	2.16	2.12	1.31	2.36	2.16	2.01
Tupaia	*palawanensis*	*palawanensis*	FMNH	62977	18.47	12.31	3.62	2.51	27.44	3.61	3.93	2.01	1.98	1.34	2.43	2.09	2.02
Tupaia	*palawanensis*	*palawanensis*	FMNH	62978	18.49	10.83	3.61	2.41	28.10	3.65	3.81	2.01	1.84	1.31	2.40	2.08	2.01
Tupaia	*palawanensis*	*palawanensis*	FMNH	63019	20.17	11.87	3.80	2.53	27.55	3.68	3.92	2.17	2.01	1.48	2.21	2.16	2.01
Tupaia	*palawanensis*	*palawanensis*	FMNH	63017	19.90	12.46	3.83	2.46	28.41	3.46	3.99	2.12	2.14	1.36	2.14	2.09	1.83
Tupaia	*palawanensis*	*palawanensis*	FMNH	63016	20.44	10.82	3.85	2.60	29.33	3.98	4.18	2.13		1.38	2.35	1.99	1.93
Tupaia	*palawanensis*	*palawanensis*	FMNH	63011	20.70	12.14	3.67	2.83	28.25	3.92	4.36	2.12	2.20	1.53	2.32	2.06	1.99
Tupaia	*palawanensis*	*palawanensis*	FMNH	63010	19.65	10.73	3.76	2.69	28.96	3.85	4.09	2.17	2.06	1.34	2.23	2.15	2.08
Tupaia	***palawanensis***	**Mean**			**19.87**	**11.63**	**3.75**	**2.60**	**28.24**	**3.78**	**4.06**	**2.13**	**2.09**	**1.40**	**2.24**	**2.07**	**1.99**
		SD			**0.82**	**0.63**	**0.10**	**0.12**	**0.67**	**0.20**	**0.16**	**0.07**	**0.14**	**0.10**	**0.17**	**0.08**	**0.07**
		n			**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**10**	**11**	**11**	**11**	**11**
Tupaia	*tana*		AMNH	106483	23.48	14.45	4.51	3.23									
Tupaia	*tana*		AMNH	106485	23.38	14.31	4.49	3.21									
Tupaia	*tana*	*utara*	AMNH	35921			3.90	2.73	30.37	4.09	4.03	2.07		1.56	2.26	2.28	2.26
Tupaia	*tana*	*kretami*	FMNH	68793	24.21	14.90	5.04	3.36	34.94	5.03	5.27	3.29	3.11	1.80	2.75	2.87	2.85
Tupaia	*tana*	*paitana*	FMNH	76892	24.50	13.87	4.97	3.27	32.91	4.94	5.29	3.01	3.24	2.06	2.68	2.75	2.74
Tupaia	*tana*	*banguei*	FMNH	140935	21.16	13.05	4.14	3.02	30.55	4.29	4.73	2.77	2.66	1.81	2.53		2.47
Tupaia	*tana*	*banguei*	FMNH	140936	22.66	13.67	4.20	2.97	30.85	4.25	4.68	3.00	2.70	1.68	2.60		2.48
Tupaia	*tana*	*paitana*	FMNH	33031	24.49	13.53	4.54	3.25	34.06	5.00	5.18	3.16	3.01	1.86	3.11	3.23	2.74
Tupaia	*tana*	*kretami*	FMNH	68797	22.88	15.22	4.65	3.09	32.45	4.59	5.17	2.89	2.86	1.72	3.10	2.71	2.54
Tupaia	*tana*	*paitana*	FMNH	76813	25.32	14.33	4.79	3.24	34.21	4.69	5.19	3.24	3.36	1.79	3.05	2.79	2.68
Tupaia	*tana*		MHN	746.11	25.38	14.98	5.22	3.33	36.30	5.37	4.67	3.28	3.24	1.78	2.70	2.84	2.82
Tupaia	*tana*		MNHN	1977-361	24.85	14.19	4.43	3.17	34.62	4.99	4.65	2.89	2.81	1.73	2.59	2.80	2.70
Tupaia	*tana*	*tana*	USNM	174611	21.95	14.93	4.95	3.17									
Tupaia	*tana*	*paitana*	USNM	396660	24.84	15.88	4.93	3.23	35.13	4.89	5.04	3.10		2.09	2.96	3.12	2.74
Tupaia	*tana*		USNM	449965	24.24	15.84	4.71	3.02	32.00	4.54	5.26	3.00		1.79	2.84	2.58	2.47
Tupaia	*tana*		USNM	449966	24.55	13.36	4.43	3.35	32.01	4.41	4.78	2.94		1.98	2.78	2.30	2.38
Tupaia	*tana*		USNM	449968	25.01	16.22	4.31	3.24	30.95	4.57	4.78	2.73		1.76	2.60	2.36	2.39

Genus	Species	Subspecies	Museum	Number	SL	SW	SGL	SGW	HL	HHW	HHL	HMSML	HMSAP	HTW	HCW	HTL	HCL
Tupaia	*tana*		USNM	449969	25.94	15.15	4.73	3.11	34.72	4.48	5.10	2.98		1.82	2.87	2.87	2.60
Tupaia	*tana*	*utara*	USNM	83938					36.14	4.88	5.03	3.00		1.99	3.10	2.74	2.56
Tupaia	*tana*	*tana*	USNM	154341	23.92	13.27	4.51	3.08	34.25	4.54	4.71	3.00		1.96	2.71	2.63	2.46
Tupaia	*tana*		ZS	1910/1462	23.70	15.70	5.81	3.56									
Tupaia	***tana***	**Mean**			**24.02**	**14.57**	**4.66**	**3.18**	**33.32**	**4.68**	**4.92**	**2.96**	**3.00**	**1.83**	**2.78**	**2.72**	**2.58**
		SD			**1.22**	**0.96**	**0.43**	**0.17**	**1.95**	**0.34**	**0.33**	**0.28**	**0.25**	**0.14**	**0.24**	**0.27**	**0.17**
		n			**19**	**19**	**20**	**20**	**17**	**17**	**17**	**17**	**9**	**17**	**17**	**15**	**17**
Urogale	*everetti*		FMNH	57312	24.59	13.06	4.62	3.43	32.86	4.92	5.47	3.07	2.93	1.86	3.08	2.94	2.69
Urogale	*everetti*		FMNH	57148	24.06	14.01	4.13	2.90	30.39	4.37	4.61	2.67	2.46	1.97	2.86	2.54	2.27
Urogale	*everetti*		FMNH	57307	26.08	15.79	4.40	3.34	32.06	4.38	4.94	3.06	2.89	1.91	3.07	2.67	2.54
Urogale	*everetti*		FMNH	57308	25.75	14.38	4.61	3.33	33.62	4.60	4.98	3.03	2.70	1.91	3.33	2.83	2.65
Urogale	*everetti*		FMNH	61418	26.64	15.08	4.70	3.17	31.81	4.42	4.96	3.08	3.12	1.89	3.13	2.87	2.66
Urogale	*everetti*		FMNH	61419	25.33	15.46	4.80	3.13	31.50	4.57	4.94	3.18	3.05	1.80	3.22	2.59	2.59
Urogale	*everetti*		FMNH	61420	27.86	15.46	4.54	3.26	32.58	4.51	4.96	2.86	2.80	1.92	3.21	2.63	2.45
Urogale	*everetti*		FMNH	57329	24.74	13.96	4.51	3.05	30.85	4.54	4.75	2.93	2.75	1.85	3.27	2.56	2.67
Urogale	*everetti*		FMNH	57464	25.95	14.59	5.05	3.35	32.43	4.83	5.22	2.89	2.90	1.97	3.30	2.89	2.70
Urogale	*everetti*		FMNH	57465	25.50	15.16	4.70	3.07	31.87	4.42	5.13	2.69	2.95	1.98	3.08	2.95	2.71
Urogale	*everetti*		FMNH	57311	24.76	15.52	4.73	3.34	31.38	4.50	4.91	3.13	2.81	1.97	2.88	2.41	2.55
Urogale	***everetti***	**Mean**			**25.57**	**14.77**	**4.62**	**3.22**	**31.94**	**4.55**	**4.99**	**2.96**	**2.85**	**1.91**	**3.13**	**2.72**	**2.59**
		SD			**1.07**	**0.85**	**0.23**	**0.16**	**0.92**	**0.18**	**0.23**	**0.17**	**0.18**	**0.06**	**0.16**	**0.19**	**0.13**
		n			**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**

Table 5.26: Forelimb measurements.
(see Table 2.3 for measurement descriptions)

Genus	Species	Subspecies	Museum	Number	HTD	HDASW	HDEW	HDCL	UL	UOPL	UTNW	URFL	URFW	USPL	UTND	UTNL
Ptilocercus	*lowii*	*lowii*	FMNH	76855												
Ptilocercus	*lowii*		MCZ	51736	1.49	3.14	5.60	9.64	26.21	2.08	1.59	1.49	1.64	1.03	0.90	1.92
Ptilocercus	*lowii*		NHM	1934.5.6.1				9.34	25.83							
Ptilocercus	*lowii*		NHM	67.1479	1.45	3.55	5.24	8.42	27.17	2.08	1.66	1.54	1.69	0.79	0.83	1.97
Ptilocercus	*lowii*		NHM	1960.8.4.6	1.43	3.56	5.10	9.14	26.28	2.05	1.60	1.28	1.67	1.00	0.84	1.96
Ptilocercus	*lowii*		NNM	a		3.46	5.37	8.93	25.06							
Ptilocercus	***lowii***	**Mean**			**1.46**	**3.43**	**5.33**	**9.09**	**26.11**	**2.07**	**1.62**	**1.44**	**1.67**	**0.94**	**0.86**	**1.95**
		SD			**0.03**	**0.20**	**0.21**	**0.46**	**0.77**	**0.02**	**0.04**	**0.14**	**0.03**	**0.13**	**0.04**	**0.03**
		n			**3**	**4**	**4**	**5**	**5**	**3**	**3**	**3**	**3**	**3**	**3**	**3**
Dendrogale	*melanura*		MCZ	36746	1.63	2.57	4.15	8.65	23.05	2.09	1.42	1.03	1.07		0.78	1.72
Dendrogale	*murina*	*frenata*	FMNH	46630	1.54	2.62	3.77	7.90	22.35	1.96	1.48	0.81	1.05		0.88	1.86
Dendrogale	**sp.**	**Mean**			**1.59**	**2.60**	**3.96**	**8.28**	**22.70**	**2.03**	**1.45**	**0.92**	**1.06**		**0.83**	**1.79**
		SD			**0.06**	**0.04**	**0.27**	**0.53**	**0.49**	**0.09**	**0.04**	**0.16**	**0.01**		**0.07**	**0.10**
		n			**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**		**2**	**2**
Tupaia	*glis*	*belangeri*	AMNH	113135		4.40	6.51	13.63	34.92	3.44	2.67	1.83	2.05	1.79	1.13	2.99
Tupaia	*glis*		AMNH	55561	2.11	3.60	5.08	11.90								
Tupaia	*glis*		AMNH	55562	2.45	3.98	5.73	13.03								
Tupaia	*glis*	*glis*	FMNH	98470		4.14	6.24	12.71	33.87	3.24	2.31	2.06	2.16	1.85	1.21	2.79
Tupaia	*glis*	*glis*	FMNH	98469		3.99	6.14	12.26	31.71	3.24	2.59	1.71	1.78	1.82	1.09	2.56
Tupaia	*glis*	*glis*	FMNH	98468		3.90	5.97		32.72	3.59	2.95					
Tupaia	*glis*	*belangeri*	FMNH	46642		4.17	6.06		33.22	3.76	2.86	1.83	2.15		1.17	3.03
Tupaia	*glis*	*wilkinsoni*	FMNH	66019		3.74	5.66		29.69	3.50	3.01	1.45	2.01		1.29	2.75
Tupaia	*glis*	*longipes*	FMNH	76815		4.50	6.63			3.84	2.57					
Tupaia	*glis*	*longipes*	FMNH	76819		4.23	6.38		37.24	3.87	3.27	1.83	2.36		1.39	3.20
Tupaia	*glis*	*longipes*	FMNH	76824		4.58	6.42		33.10	3.65	3.12	2.00	2.23		1.22	3.11
Tupaia	*glis*	*longipes*	FMNH	76825		4.50	6.54			3.77	2.64					
Tupaia	*glis*	*demissa*	MHN	801.95	2.58	4.16	6.36	13.48	34.19	3.38	2.60	1.68	2.10	1.75	1.08	2.75
Tupaia	*glis*	*belangeri*	MNHN	1990-510		4.46	6.26	13.55		3.63	2.58	1.75	1.94		1.12	2.54
Tupaia	*glis*	*longipes*	USNM	198043	2.91	4.47	6.60	15.85	39.19	3.41	2.44	1.76	1.88		1.31	3.27
Tupaia	*glis*	*longipes*	USNM	396665	2.96	4.65	6.66	15.57	40.65	3.71	2.85	1.60	1.62		1.54	3.36
Tupaia	*glis*	*longipes*	USNM	396673	2.75	4.38	6.20	15.49	39.04	3.31	2.74	1.69	1.79		1.30	3.16
Tupaia	*glis*		SMNH	A620505		3.84	6.11	10.51	31.05	3.31	2.30	1.43	1.58	1.68	1.19	2.52

Genus	Species	Subspecies	Museum	Number	HTD	HDASW	HDEW	HDCL	UL	UOPL	UTNW	URFL	URFW	USPL	UTND	UTNL
Tupaia	*glis*	*discolor*	ZS	1905/13		4.43	6.47	12.44	34.05	3.53	2.51	1.94	2.24		1.29	2.86
Tupaia	***glis***	**Mean**			**2.63**	**4.22**	**6.21**	**13.37**	**34.62**	**3.54**	**2.71**	**1.75**	**1.99**	**1.78**	**1.24**	**2.92**
		SD			**0.32**	**0.31**	**0.39**	**1.61**	**3.26**	**0.21**	**0.27**	**0.18**	**0.24**	**0.07**	**0.13**	**0.28**
		n			**6**	**19**	**19**	**12**	**14**	**17**	**17**	**14**	**14**	**5**	**14**	**14**
Tupaia	*gracilis*	*gracilis*	FMNH	140925		2.95	4.42		26.71	2.64	2.23	0.97	1.42			
Tupaia	*gracilis*	*gracilis*	FMNH	140928		3.06	4.40		26.10	2.42	2.27	0.97	1.34			
Tupaia	*gracilis*		USNM	449963	1.98	3.07	4.63		28.93	2.65	1.99	1.54	1.54		0.98	2.03
Tupaia	***gracilis***	**Mean**			**1.98**	**3.03**	**4.48**		**27.25**	**2.57**	**2.16**	**1.16**	**1.43**		**0.98**	**2.03**
		SD				**0.07**	**0.13**		**1.49**	**0.13**	**0.15**	**0.33**	**0.10**			
		n			**1**	**3**	**3**		**3**	**3**	**3**	**3**	**3**		**1**	**1**
Tupaia	*javanica*	*occidentalis*	AMNH	106505												
Tupaia	*javanica*	*occidentalis*	AMNH	106506												
Tupaia	*javanica*	*occidentalis*	AMNH	106507												
Tupaia	*javanica*		MCZ	12949												
Tupaia	*javanica*		MHN	450.15	1.99	3.09	5.16	7.37	23.90	2.37	1.97	1.34	1.49	0.88	0.82	2.12
Tupaia	*javanica*		USNM	154593	2.04	3.36	4.92	8.96								
Tupaia	*javanica*		SMNH	A630506		3.31	5.17	7.55	27.48	2.49	1.92	1.62	1.64	1.25	0.99	2.28
Tupaia	***javanica***	**Mean**			**2.02**	**3.25**	**5.08**	**7.96**	**25.69**	**2.43**	**1.95**	**1.48**	**1.57**	**1.07**	**0.91**	**2.20**
		SD			**0.04**	**0.14**	**0.14**	**0.87**	**2.53**	**0.08**	**0.04**	**0.20**	**0.11**	**0.26**	**0.12**	**0.11**
		n			**2**	**3**	**3**	**3**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**
Tupaia	*minor*	*caedis*	FMNH	140929		2.96	4.26			2.09	1.94	1.05	1.24			
Tupaia	*minor*	*caedis*	FMNH	76865		2.85	4.39		23.52	2.04	1.96	1.38	1.15		0.72	2.12
Tupaia	*minor*	*malaccana*	MHN	801.94	2.02	3.15	4.89	7.82	24.70	2.30	1.67	1.33	1.50	1.42	0.81	2.10
Tupaia	*minor*		MNHN	1981-186		3.13	5.00	9.24	23.18	1.99	1.79	1.02	1.24	1.15	0.88	1.89
Tupaia	*minor*		USNM	396668	1.86	3.28	4.92	9.83	23.41	1.79	1.72	1.12	1.48		0.87	2.20
Tupaia	*minor*		USNM	396669	1.96	3.26	4.60		27.41	2.12	1.86	1.32	1.51		0.80	2.32
Tupaia	*minor*		USNM	396672	1.89	3.17	4.90	8.76	23.54	1.90	1.77	1.23	1.36		0.84	2.27
Tupaia	*minor*		NNM	36048(a)		3.40	5.00	9.59	24.45							
Tupaia	***minor***	**Mean**			**1.93**	**3.15**	**4.75**	**9.05**	**24.32**	**2.03**	**1.82**	**1.21**	**1.35**	**1.29**	**0.82**	**2.15**
		SD			**0.07**	**0.18**	**0.29**	**0.80**	**1.48**	**0.16**	**0.11**	**0.14**	**0.15**	**0.19**	**0.06**	**0.15**
		n			**4**	**8**	**8**	**5**	**7**	**7**	**7**	**7**	**7**	**2**	**6**	**6**
Tupaia	*montana*		USNM	449964	2.50	3.62	6.02	13.01	33.64	3.00	2.49	1.57	1.80		1.08	3.13
Tupaia	*montana*	*baluensis*	FS	82081		4.14	6.43	12.87	33.30	2.85	2.34	1.75	1.81	1.66	1.07	2.71
Tupaia	***montana***	**Mean**			**2.50**	**3.88**	**6.23**	**12.94**	**33.47**	**2.93**	**2.42**	**1.66**	**1.81**	**1.66**	**1.08**	**2.92**

Genus	Species	Subspecies	Museum	Number	HTD	HDASW	HDEW	HDCL	UL	UOPL	UTNW	URFL	URFW	USPL	UTND	UTNL
		SD				**0.37**	**0.29**	**0.10**	**0.24**	**0.11**	**0.11**	**0.13**	**0.01**		**0.01**	**0.30**
		n			**1**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**1**	**2**	**2**
Tupaia	***nicobarica***	***nicobarica***	**USNM**	**111782**	**2.59**	**4.47**	**6.95**		**35.74**	**2.90**	**2.37**	**1.79**	**2.06**		**1.26**	**2.91**
Tupaia	*palawanensis*	*palawanensis*	FMNH	62950		3.99	5.82	11.16	32.35	3.09	2.38	1.56	1.70	1.75	1.11	2.67
Tupaia	*palawanensis*	*palawanensis*	FMNH	63018		3.84	6.06	11.48	31.55	3.24	2.41	1.70	1.89	1.86	1.23	2.58
Tupaia	*palawanensis*	*palawanensis*	FMNH	62976		3.88	5.78		30.84	3.41	2.67	2.07	1.95		1.10	2.80
Tupaia	*palawanensis*	*palawanensis*	FMNH	63020		3.81	5.87		31.24	3.71	2.78	1.73	1.92		1.12	2.73
Tupaia	*palawanensis*	*palawanensis*	FMNH	62977		3.86	5.68		30.25	3.62	2.78	1.77	1.77		1.16	2.78
Tupaia	*palawanensis*	*palawanensis*	FMNH	62978		3.83	5.72		31.25	3.55	2.65	1.71	1.83		1.08	2.88
Tupaia	*palawanensis*	*palawanensis*	FMNH	63019		3.74	5.48		31.06	3.63	2.73	1.53	1.73		1.08	2.82
Tupaia	*palawanensis*	*palawanensis*	FMNH	63017		3.83	5.65		31.84	3.42	2.59	1.66	1.76		1.06	2.92
Tupaia	*palawanensis*	*palawanensis*	FMNH	63016		3.82	5.83	12.44	31.28	3.57	2.62	1.60	1.98		1.15	2.67
Tupaia	*palawanensis*	*palawanensis*	FMNH	63011		4.01	5.98		31.59	3.73	2.83	1.57	1.81		1.12	2.94
Tupaia	*palawanensis*	*palawanensis*	FMNH	63010		3.74	5.50									
Tupaia	***palawanensis***	**Mean**				**3.85**	**5.76**	**11.69**	**31.33**	**3.50**	**2.64**	**1.69**	**1.83**	**1.81**	**1.12**	**2.78**
		SD				**0.09**	**0.18**	**0.67**	**0.57**	**0.21**	**0.15**	**0.16**	**0.10**	**0.08**	**0.05**	**0.12**
		n				**11**	**11**	**3**	**10**	**10**	**10**	**10**	**10**	**2**	**10**	**10**
Tupaia	*tana*		AMNH	106483												
Tupaia	*tana*		AMNH	106485												
Tupaia	*tana*	*utara*	AMNH	35921	2.58	4.04	5.89	13.23	32.48	2.88	1.95	2.05	1.39		1.31	3.00
Tupaia	*tana*	*kretami*	FMNH	68793		5.55	8.63	16.16	40.17	4.67	3.17	2.41	2.52	2.00	1.53	3.57
Tupaia	*tana*	*paitana*	FMNH	76892		5.40	8.42	14.94	38.52	4.55	3.14	2.53	2.68	2.09	1.66	3.59
Tupaia	*tana*	*banguei*	FMNH	140935		4.92	7.21		35.11	4.21	3.55	1.37	1.52			
Tupaia	*tana*	*banguei*	FMNH	140936		4.90	7.31		36.60	4.39	3.60	1.47	2.19			
Tupaia	*tana*	*paitana*	FMNH	33031		5.19	8.37		40.43	4.67	3.94	2.07	2.29		1.34	3.78
Tupaia	*tana*	*kretami*	FMNH	68797		4.96	7.73			4.67	3.64	2.30	2.56		1.37	3.59
Tupaia	*tana*	*paitana*	FMNH	76813		4.92	7.82		39.35	5.07	3.85	1.73	2.40		1.38	3.43
Tupaia	*tana*		MHN	746.11	3.44	5.42	8.31	16.70	42.56	4.43	3.56	2.25	2.51	2.18	1.60	3.63
Tupaia	*tana*		MNHN	1977-361		4.88	7.48	16.90	39.37	4.16	3.14	1.93	1.96	2.08	1.57	3.34
Tupaia	*tana*	*tana*	USNM	174611												
Tupaia	*tana*	*paitana*	USNM	396660	2.95	5.21	8.14	16.69	42.14	4.24	2.89	1.92	2.11		1.30	3.58
Tupaia	*tana*		USNM	449965	2.76	4.89	7.34	15.50	38.44	3.79	3.00	2.07	2.21		1.38	3.32
Tupaia	*tana*		USNM	449966	2.91	4.99	7.31	16.07	37.57	3.81	2.48	2.08	2.25		1.33	3.15
Tupaia	*tana*		USNM	449968	2.98	4.67	7.18	13.87	37.79	3.47	2.84	1.81	2.36		1.36	3.31

Genus	Species	Subspecies	Museum	Number	HTD	HDASW	HDEW	HDCL	UL	UOPL	UTNW	URFL	URFW	USPL	UTND	UTNL
Tupaia	*tana*		USNM	449969	3.27	5.09	8.04	17.49	40.41	4.28	2.69	1.81	2.31		1.46	3.44
Tupaia	*tana*	*utara*	USNM	83938	3.05	5.33	7.89	17.14		4.15	2.92	1.80	2.24		1.60	3.46
Tupaia	*tana*	*tana*	USNM	154341	2.74	4.84	7.30	16.25	39.74	3.72	2.98	1.48	2.00		1.37	3.40
Tupaia	*tana*		ZS	1910/1462												
Tupaia	***tana***	**Mean**			**2.96**	**5.01**	**7.67**	**15.91**	**38.71**	**4.19**	**3.14**	**1.95**	**2.21**	**2.09**	**1.44**	**3.44**
		SD			**0.27**	**0.35**	**0.66**	**1.31**	**2.60**	**0.53**	**0.52**	**0.33**	**0.34**	**0.07**	**0.12**	**0.20**
		n			**9**	**17**	**17**	**12**	**15**	**17**	**17**	**17**	**17**	**4**	**15**	**15**
Urogale	*everetti*		FMNH	57312	3.33	5.08	8.37	11.67	39.79	4.99	3.03	2.11	2.66		1.74	4.01
Urogale	*everetti*		FMNH	57148		4.89	7.86		40.95	5.06	3.57	2.65	2.68		1.40	3.77
Urogale	*everetti*		FMNH	57307		5.27	8.28		40.76	5.30	3.98	2.37	2.68		1.54	3.58
Urogale	*everetti*		FMNH	57308		5.48	8.47		40.86	4.96	3.96	2.21	2.58		1.39	3.86
Urogale	*everetti*		FMNH	61418		5.31	8.74		40.68	5.30	4.00	2.38	2.75		1.56	3.87
Urogale	*everetti*		FMNH	61419		5.06	8.11		39.91	5.12	3.79	2.48	2.07		1.46	3.98
Urogale	*everetti*		FMNH	61420		5.32	8.29		41.60	4.92	3.91	2.41	2.44		1.48	3.85
Urogale	*everetti*		FMNH	57329		5.20	8.22		39.81	5.13	3.83	2.39	2.71		1.52	3.57
Urogale	*everetti*		FMNH	57464		5.60	8.55		39.89	5.54	4.09	2.43	2.66		1.59	3.80
Urogale	*everetti*		FMNH	57465		5.30	8.43		40.24	5.00	3.76	2.11	2.94		1.43	3.71
Urogale	*everetti*		FMNH	57311		4.75	8.39	13.93	39.91	4.57	2.84	2.60	2.62	1.84	1.45	3.66
Urogale	***everetti***	**Mean**			**3.33**	**5.21**	**8.34**	**12.80**	**40.40**	**5.08**	**3.71**	**2.38**	**2.62**	**1.84**	**1.51**	**3.79**
		SD				**0.25**	**0.23**	**1.60**	**0.60**	**0.25**	**0.41**	**0.18**	**0.22**		**0.10**	**0.15**
		n			**1**	**11**	**11**	**2**	**11**	**11**	**11**	**11**	**11**	**1**	**11**	**11**

Table 5.26: Forelimb measurements.
(see Table 2.3 for measurement descriptions)

Genus	Species	Subspecies	Museum	Number	RL	RNL	RHW	RHRL	RSPL	RDEW	RDEL	RHL
Ptilocercus	*lowii*	*lowii*	FMNH	76855								
Ptilocercus	*lowii*		MCZ	51736	22.99	2.10	2.20	1.00	0.67	1.87	1.36	1.86
Ptilocercus	*lowii*		NHM	1934.5.6.1	22.75							
Ptilocercus	*lowii*		NHM	67.1479	23.83	2.19	2.05	1.01	0.50	1.81	1.34	1.68
Ptilocercus	*lowii*		NHM	1960.8.4.6	23.17	1.78	2.02	1.06	0.34	2.01	1.37	1.72
Ptilocercus	*lowii*		NNM	a	21.89							
Ptilocercus	***lowii***	**Mean**			**22.93**	**2.02**	**2.09**	**1.02**	**0.50**	**1.90**	**1.36**	**1.75**
		SD			**0.70**	**0.22**	**0.10**	**0.03**	**0.17**	**0.10**	**0.02**	**0.09**
		n			**5**	**3**	**3**	**3**	**3**	**3**	**3**	**3**
Dendrogale	*melanura*		MCZ	36746	20.09	1.35	2.00	0.82				1.42
Dendrogale	*murina*	*frenata*	FMNH	46630	19.25	1.77	1.87	0.90				1.47
Dendrogale	**sp.**	**Mean**			**19.67**	**1.56**	**1.94**	**0.86**				**1.45**
		SD			**0.59**	**0.30**	**0.09**	**0.06**				**0.04**
		n			**2**	**2**	**2**	**2**				**2**
Tupaia	*glis*	*belangeri*	AMNH	113135	29.83	2.38	3.11	1.21	0.56	2.56	1.93	2.23
Tupaia	*glis*		AMNH	55561								
Tupaia	*glis*		AMNH	55562								
Tupaia	*glis*	*glis*	FMNH	98470	29.00	2.56	2.94	1.17	0.48	2.49	1.84	2.19
Tupaia	*glis*	*glis*	FMNH	98469	27.29	2.51	2.99	1.21	0.43	2.25	2.00	2.16
Tupaia	*glis*	*glis*	FMNH	98468	27.76	2.19	2.83	1.15		2.03	1.53	1.99
Tupaia	*glis*	*belangeri*	FMNH	46642	28.05	2.98	3.01	1.32				2.07
Tupaia	*glis*	*wilkinsoni*	FMNH	66019	25.10	2.80	2.82	1.07				1.82
Tupaia	*glis*	*longipes*	FMNH	76815								
Tupaia	*glis*	*longipes*	FMNH	76819	31.74	3.02	3.17	1.39				2.16
Tupaia	*glis*	*longipes*	FMNH	76824	28.16	3.02	2.97	1.58				2.07
Tupaia	*glis*	*longipes*	FMNH	76825			3.56					2.27
Tupaia	*glis*	*demissa*	MHN	801.95	29.31	2.29	2.98	1.02	0.50	2.08	1.85	2.06
Tupaia	*glis*	*belangeri*	MNHN	1990-510		2.57	2.92	1.17				2.07
Tupaia	*glis*	*longipes*	USNM	198043	33.45	3.58	3.49	1.30				2.42
Tupaia	*glis*	*longipes*	USNM	396665	34.60	3.39	3.61	1.42				2.75
Tupaia	*glis*	*longipes*	USNM	396673	33.65	3.43	3.09	1.32				2.33
Tupaia	*glis*		SMNH	A620505	26.40	2.27	2.98	1.03	0.47	2.15	1.69	2.02

Genus	Species	Subspecies	Museum	Number	RL	RNL	RHW	RHRL	RSPL	RDEW	RDEL	RHL
Tupaia	*glis*	*discolor*	ZS	1905/13	29.73	2.91	3.23	1.22				2.34
Tupaia	***glis***	**Mean**			**29.58**	**2.79**	**3.11**	**1.24**	**0.49**	**2.26**	**1.81**	**2.18**
		SD			**2.84**	**0.45**	**0.25**	**0.15**	**0.05**	**0.22**	**0.17**	**0.21**
		n			**14**	**15**	**16**	**15**	**5**	**6**	**6**	**16**
Tupaia	*gracilis*	*gracilis*	FMNH	140925	23.23		2.13	0.94		1.70	1.17	1.49
Tupaia	*gracilis*	*gracilis*	FMNH	140928	22.81		2.22	0.94		1.85	1.24	1.56
Tupaia	*gracilis*		USNM	449963	25.14	1.99	2.39	0.89				1.66
Tupaia	***gracilis***	**Mean**			**23.73**	**1.99**	**2.25**	**0.92**		**1.78**	**1.21**	**1.57**
		SD			**1.24**		**0.13**	**0.03**		**0.11**	**0.05**	**0.09**
		n			**3**	**1**	**3**	**3**		**2**	**2**	**3**
Tupaia	*javanica*	*occidentalis*	AMNH	106505								
Tupaia	*javanica*	*occidentalis*	AMNH	106506								
Tupaia	*javanica*	*occidentalis*	AMNH	106507								
Tupaia	*javanica*		MCZ	12949								
Tupaia	*javanica*		MHN	450.15	20.45	1.72	2.21	0.76	0.34	1.61	1.39	1.63
Tupaia	*javanica*		USNM	154593								
Tupaia	*javanica*		SMNH	A630506	23.64	2.07	2.56	1.09	0.38	1.88	1.44	1.90
Tupaia	***javanica***	**Mean**			**22.05**	**1.90**	**2.39**	**0.93**	**0.36**	**1.75**	**1.42**	**1.77**
		SD			**2.26**	**0.25**	**0.25**	**0.23**	**0.03**	**0.19**	**0.04**	**0.19**
		n			**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**
Tupaia	*minor*	*caedis*	FMNH	140929	18.86	1.82	2.06	0.82		1.39	1.02	1.48
Tupaia	*minor*	*caedis*	FMNH	76865	20.11	2.06	2.08	0.84				1.53
Tupaia	*minor*	*malaccana*	MHN	801.94	21.12	1.76	2.20	0.80	0.31	1.61	1.36	1.60
Tupaia	*minor*		MNHN	1981-186	19.80	1.60	2.13	0.78	0.40	1.78	1.31	1.65
Tupaia	*minor*		USNM	396668	19.80	2.04	2.30	1.08				1.78
Tupaia	*minor*		USNM	396669	23.86	2.27	2.28	1.27				1.66
Tupaia	*minor*		USNM	396672	19.85	1.78	2.17	1.15				1.77
Tupaia	*minor*		NNM	36048(a)	20.98							
Tupaia	***minor***	**Mean**			**20.55**	**1.90**	**2.17**	**0.96**	**0.36**	**1.59**	**1.23**	**1.64**
		SD			**1.52**	**0.23**	**0.09**	**0.20**	**0.06**	**0.20**	**0.18**	**0.11**
		n			**8**	**7**	**7**	**7**	**2**	**3**	**3**	**7**
Tupaia	*montana*		USNM	449964	28.71	1.83	2.86	1.39				2.07
Tupaia	*montana*	*baluensis*	FS	82081	28.83	2.92	2.96	1.39	0.49	2.64	1.93	2.16
Tupaia	***montana***	**Mean**			**28.77**	**2.38**	**2.91**	**1.39**	**0.49**	**2.64**	**1.93**	**2.12**

Genus	Species	Subspecies	Museum	Number	RL	RNL	RHW	RHRL	RSPL	RDEW	RDEL	RHL
		SD			**0.08**	**0.77**	**0.07**	**0.00**				**0.06**
		n			**2**	**2**	**2**	**2**	**1**	**1**	**1**	**2**
Tupaia	***nicobarica***	***nicobarica***	**USNM**	**111782**	**30.96**	**3.33**	**3.24**	**1.48**				**2.33**
Tupaia	*palawanensis*	*palawanensis*	FMNH	62950	27.50	2.46	2.91	1.05	0.48	2.17	1.73	2.13
Tupaia	*palawanensis*	*palawanensis*	FMNH	63018	26.96	2.37	2.81	1.16	0.43	2.20	1.70	1.96
Tupaia	*palawanensis*	*palawanensis*	FMNH	62976	26.26	2.60	2.79	1.32				1.94
Tupaia	*palawanensis*	*palawanensis*	FMNH	63020	26.26	2.53	2.77	1.29				1.90
Tupaia	*palawanensis*	*palawanensis*	FMNH	62977	25.56	2.44	2.62	1.17				1.95
Tupaia	*palawanensis*	*palawanensis*	FMNH	62978	26.53	1.95	2.77	0.99				1.95
Tupaia	*palawanensis*	*palawanensis*	FMNH	63019	26.27	2.70	2.71	1.24				1.97
Tupaia	*palawanensis*	*palawanensis*	FMNH	63017	27.47	2.49	2.67	1.20				1.86
Tupaia	*palawanensis*	*palawanensis*	FMNH	63016	26.39	2.91	2.74	1.11				1.98
Tupaia	*palawanensis*	*palawanensis*	FMNH	63011	26.39	2.43	2.82	1.26				2.09
Tupaia	*palawanensis*	*palawanensis*	FMNH	63010								
Tupaia	***palawanensis***	**Mean**			**26.56**	**2.49**	**2.76**	**1.18**	**0.46**	**2.19**	**1.72**	**1.97**
		SD			**0.60**	**0.25**	**0.08**	**0.11**	**0.04**	**0.02**	**0.02**	**0.08**
		n			**10**	**10**	**10**	**10**	**2**	**2**	**2**	**10**
Tupaia	*tana*		AMNH	106483								
Tupaia	*tana*		AMNH	106485								
Tupaia	*tana*	*utara*	AMNH	35921	27.93	2.60	2.95	1.54				2.12
Tupaia	*tana*	*kretami*	FMNH	68793	33.92	2.96	3.80	1.57	0.56	2.99	2.40	2.56
Tupaia	*tana*	*paitana*	FMNH	76892	32.13	2.97	3.88	1.54	0.59	2.89	2.21	2.61
Tupaia	*tana*	*banguei*	FMNH	140935	29.90	2.59	3.37	1.27		2.33	1.60	2.47
Tupaia	*tana*	*banguei*	FMNH	140936	30.75		3.27	1.40		2.22	1.65	2.39
Tupaia	*tana*	*paitana*	FMNH	33031	34.15	3.25	3.68	1.68				2.71
Tupaia	*tana*	*kretami*	FMNH	68797								
Tupaia	*tana*	*paitana*	FMNH	76813	32.90	2.97	3.69	1.59				2.53
Tupaia	*tana*		MHN	746.11	36.40	3.01	3.62	1.53	0.54	2.90	2.26	2.50
Tupaia	*tana*		MNHN	1977-361	33.69	2.99	3.62	1.48	0.49	3.00	2.21	2.52
Tupaia	*tana*	*tana*	USNM	174611								
Tupaia	*tana*	*paitana*	USNM	396660	35.54	3.07	3.60	1.81				2.65
Tupaia	*tana*		USNM	449965	32.27	2.74	3.40	1.62				2.65
Tupaia	*tana*		USNM	449966	31.85	2.73	3.47	1.51				2.67
Tupaia	*tana*		USNM	449968	31.28	2.75	3.26	1.56				2.55

Genus	Species	Subspecies	Museum	Number	RL	RNL	RHW	RHRL	RSPL	RDEW	RDEL	RHL
Tupaia	*tana*		USNM	449969	34.16	2.93	3.65	1.77				2.60
Tupaia	*tana*	*utara*	USNM	83938		3.83	3.75	1.52				2.66
Tupaia	*tana*	*tana*	USNM	154341		2.69	3.49	1.49				2.51
Tupaia	*tana*		ZS	1910/1462								
Tupaia	***tana***	**Mean**			**32.63**	**2.94**	**3.53**	**1.56**	**0.55**	**2.72**	**2.06**	**2.54**
		SD			**2.25**	**0.31**	**0.24**	**0.13**	**0.04**	**0.35**	**0.34**	**0.14**
		n			**14**	**15**	**16**	**16**	**4**	**6**	**6**	**16**
Urogale	*everetti*		FMNH	57312	33.07	2.63	3.80	1.60				2.81
Urogale	*everetti*		FMNH	57148	34.49	2.69	3.68	1.42				2.59
Urogale	*everetti*		FMNH	57307	34.08	3.00	3.53	1.77				2.56
Urogale	*everetti*		FMNH	57308	35.17	3.14	3.95	2.05				2.84
Urogale	*everetti*		FMNH	61418	33.89	3.14	3.84	1.75				2.87
Urogale	*everetti*		FMNH	61419	33.31	2.73	3.68	1.30				2.58
Urogale	*everetti*		FMNH	61420	35.11	3.16	3.77	1.66				2.60
Urogale	*everetti*		FMNH	57329	33.08	2.44	3.67	1.69				2.57
Urogale	*everetti*		FMNH	57464	32.88	2.86	3.76	1.67				2.69
Urogale	*everetti*		FMNH	57465	33.86	2.89	3.79	1.75				2.66
Urogale	*everetti*		FMNH	57311	33.73	2.96	3.70	1.40	0.56	2.62	2.12	2.60
Urogale	***everetti***	**Mean**			**33.88**	**2.88**	**3.74**	**1.64**	**0.56**	**2.62**	**2.12**	**2.67**
		SD			**0.79**	**0.23**	**0.11**	**0.21**				**0.12**
		n			**11**	**11**	**11**	**11**	**1**	**1**	**1**	**11**

CHAPTER 6: HINDLIMB

INTRODUCTION

As with the forelimb myology, the hindlimb myology of tupaiids has been well described by Le Gros Clark (1924a, 1926) and George (1973, 1977). Baba (1985) conducted a morphometric analysis of the hindlimb of primates and included *T. glis* tentatively as a primate. Interestingly, when all of Baba's (1985) indices were considered together, *T. glis* was the "primate" that was most similar to the "terrestrial running" carnivorans included in the analysis. This reflected the terrestrial locomotion of *T. glis* and may be yet another indication of the terrestrial ancestry of tupaiines.

Just as the carpus is the best studied region of the forelimb in tupaiids, the tarsus is the only well studied portion of the tupaiid hindlimb. Szalay and Drawhorn (1980) and Szalay and Dagosto (1988) have conducted detailed analyses of the tupaiid tarsus and my discussion builds on their contributions.

RESULTS AND DISCUSSION

Standard Indices

The indices pertaining to both the forelimb and hindlimb, the intermembral and humerofemoral indices, were discussed in chapter five above. An examination of the crural index shows that the terrestrial *T. gracilis* and *Urogale* both have relatively long tibiae, but the terrestrial *T. tana* has a relatively short tibia (Fig. 6.1; Tables 6.1, 6.27). While this is interesting and the crural index is obviously not correlated with differential substrate use, such a gross index is of questionable value when considering relatively less specialized mammals like tupaiids (as stated above).

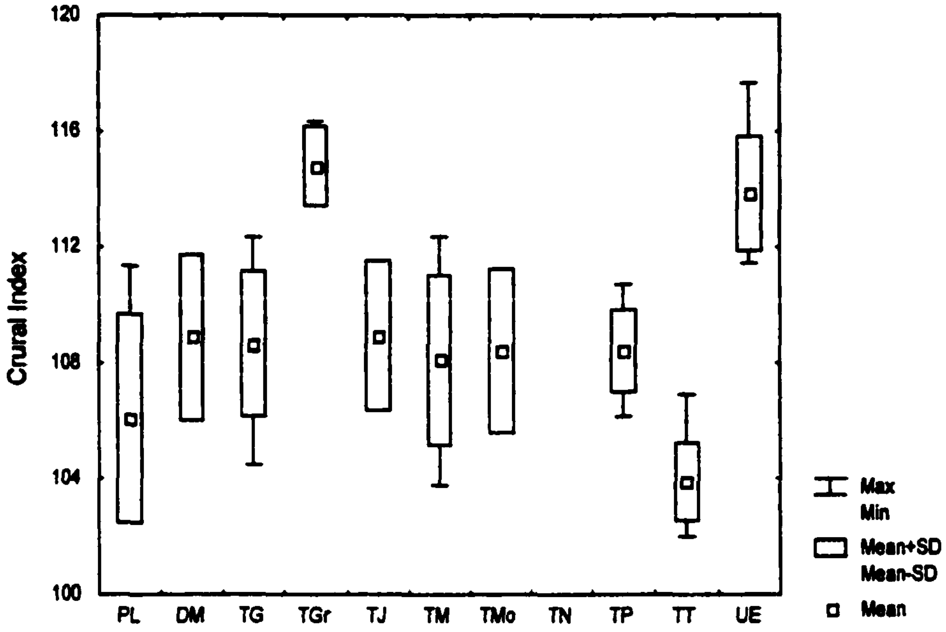


Figure 6.1. Box plot of crural index. Note the high indices of *T. gracilis* and *Urogale*, and the low index of *T. tana*.

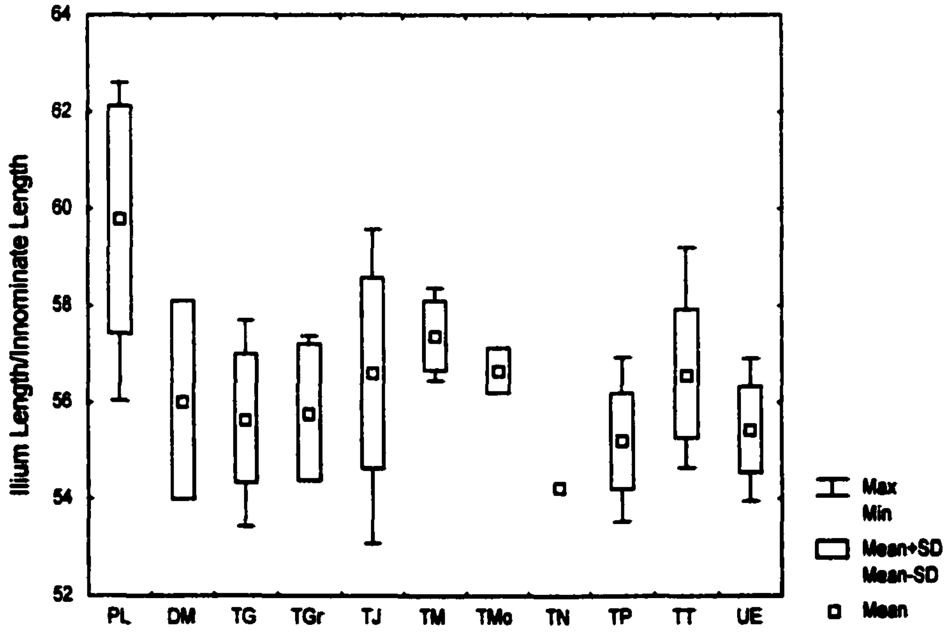


Figure 6.2. Box plot of ilium length index. Note the high index of *Ptilocercus*.

Table 6.1: Probabilities* from Tukey Honest Significant Difference (HSD) post hoc test of crural index.

	Dendrogale melanura	*Dendrogale murina*	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
D. melanura		0.9699	0.6741	0.9965	0.9125	0.9998	0.9854	0.9982	0.9924	0.0929	0.9745
D. murina	0.9699		1.0000	0.9996	0.0831	0.9997	1.0000	1.0000	0.9999	0.9707	0.1026
P. lowii	0.6741	1.0000		0.6207	**0.0002**	0.9195	0.9416	0.9798	0.7885	0.8215	**0.0001**
T. glis	0.9965	0.9996	0.6207		**0.0021**	1.0000	1.0000	1.0000	1.0000	**0.0001**	**0.0001**
T. gracilis	0.9125	0.0831	**0.0002**	**0.0021**		0.1366	**0.0026**	0.0727	**0.0018**	**0.0001**	0.9999
T. javanica	0.9998	0.9997	0.9195	1.0000	0.1366		1.0000	1.0000	1.0000	0.1056	0.1420
T. minor	0.9854	1.0000	0.9416	1.0000	**0.0026**	1.0000		1.0000	1.0000	**0.0089**	**0.0002**
T. montana	0.9982	1.0000	0.9798	1.0000	0.0727	1.0000	1.0000		1.0000	0.2131	0.0670
T. palawanensis	0.9924	0.9999	0.7885	1.0000	**0.0018**	1.0000	1.0000	1.0000		**0.0004**	**0.0001**
T. tana	0.0929	0.9707	0.8215	**0.0001**	**0.0001**	0.1056	**0.0089**	0.2131	**0.0004**		**0.0001**
U. everetti	0.9745	0.1026	**0.0001**	**0.0001**	0.9999	0.1420	**0.0002**	0.0670	**0.0001**	**0.0001**	

*probabilities in bold are significant at the p < .05 level

Table 6.2: Probabilities* from Tukey Honest Significant Difference (HSD) post hoc test of ilium length index.

	Dendrogale melanura	*Dendrogale murina*	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
D. melanura		0.9317	0.9242	0.9735	0.9943	1.0000	1.0000	1.0000	0.8733	0.8996	1.0000	0.9460
D. murina	0.9317		**0.0333**	0.9998	0.9998	0.9629	0.7570	0.9825	1.0000	1.0000	0.9512	1.0000
P. lowii	0.9242	**0.0333**		**0.0001**	**0.0051**	**0.0044**	0.1177	0.2089	**0.0179**	**0.0001**	**0.0004**	**0.0001**
T. glis	0.9735	0.9998	**0.0001**		1.0000	0.9189	0.2629	0.9972	0.9977	0.9995	0.6353	1.0000
T. gracilis	0.9943	0.9998	**0.0051**	1.0000		0.9993	0.8848	0.9999	0.9981	1.0000	0.9982	1.0000
T. javanica	1.0000	0.9629	**0.0044**	0.9189	0.9993		0.9967	1.0000	0.9044	0.6165	1.0000	0.8178
T. minor	1.0000	0.7570	0.1177	0.2629	0.8848	0.9967		1.0000	0.6191	0.0946	0.9856	0.1913
T. montana	1.0000	0.9825	0.2089	0.9972	0.9999	1.0000	1.0000		0.9520	0.9609	1.0000	0.9880
T. nicobarica	0.8733	1.0000	**0.0179**	0.9977	0.9981	0.9044	0.6191	0.9520		0.9999	0.8792	0.9996
T. palawanensis	0.8996	1.0000	**0.0001**	0.9995	1.0000	0.6165	0.0946	0.9609	0.9999		0.2540	1.0000
T. tana	1.0000	0.9512	**0.0004**	0.6353	0.9982	1.0000	0.9856	1.0000	0.8792	0.2540		0.5019
U. everetti	0.9460	1.0000	**0.0001**	1.0000	1.0000	0.8178	0.1913	0.9880	0.9996	1.0000	0.5019	

*probabilities in bold are significant at the p < .05 level

Innominate

The ilium of *Ptilocercus* is relatively long and narrow, while that of tupaiines is wider (expanded laterally) and shorter (Figs. 6.2-6.4; Tables 6.2-6.5, 6.27). In fact, *Ptilocercus* is significantly different from every tupaiine species except *D. melanura* for the ilium shape index (Table 6.3), and *Ptilocercus* is significantly different from *Dendrogale* sp. when the two *Dendrogale* species (specimens) are considered together (Table 6.4). *Dendrogale* is quite variable for this index (Fig. 6.4; Tables 6.3, 6.27) and *D. melanura* is significantly different from several tupaiines including *D. murina* (Table 6.3). The fact that *D. melanura* is more similar to *Ptilocercus* than it is to *D. murina* for this index (Tables 6.3, 6.27) may be an indication that *D. melanura* is more arboreal than *D. murina*, but no definitive conclusions can be made about this because both *Dendrogale* species are represented by only a single specimen.

The relatively long, narrow ilium of *Ptilocercus* compared to that of tupaiines (Tables 6.3, 6.27) is particularly interesting because both Szalay *et al.* (1975) and Muizon (1998) have interpreted a long, narrow ilium as representing the primitive mammalian condition. The ilium is the site of origin of the gluteus medius muscle, which is an extensor of the thigh. The lateral expansion of the ilium in tupaiines provides a broad area of attachment for this large muscle, which may, in turn, indicate powerful extension of the thigh by this muscle for propulsion during terrestrial running. Again, the fact that even arboreal tupaiines like *T. minor* exhibit this feature probably reflects the terrestrial ancestry of this group. The lateral expansion of the ilium in tupaiines may also "reduce the moment of the gluteus medius muscle to abduct and medially rotate the thigh, while increasing its moment to act as an extensor" (Ward, 1993, p. 315). The lateral expansion

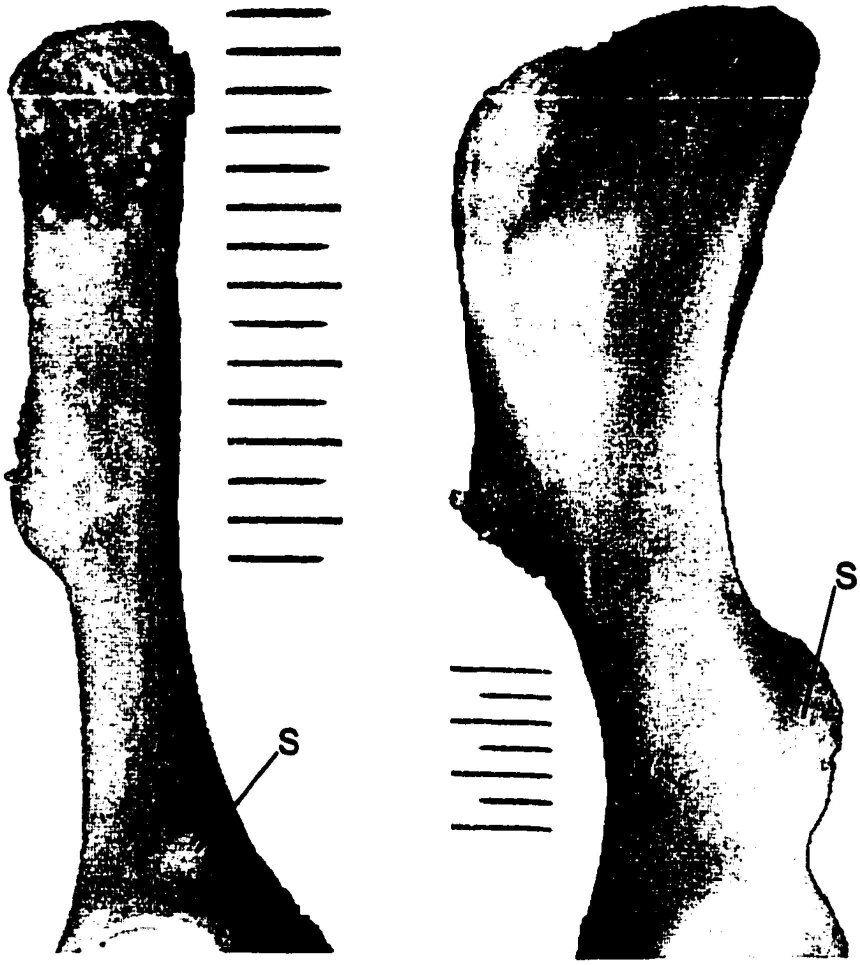


Figure 6.3. Lateral view of the ilia of *Ptilocercus* (left) and *T. tana* (right). S: anterior inferior iliac spine. Subdivisions on scale are 0.5 mm. Note the narrow ilium and small anterior inferior iliac spine of *Ptilocercus*.

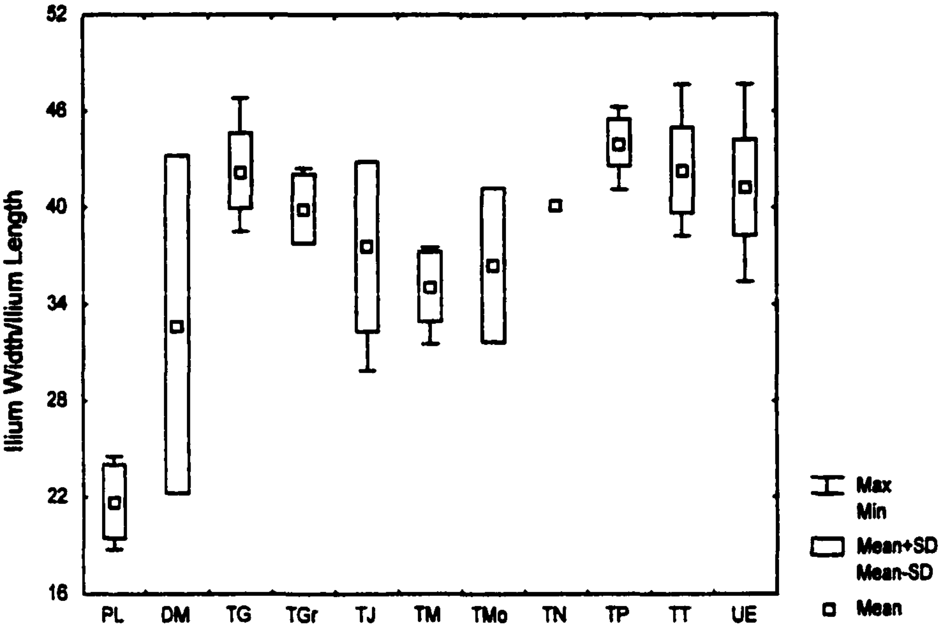


Figure 6.4. Box plot of ilium shape index. Note the low index of *Ptilocercus*.

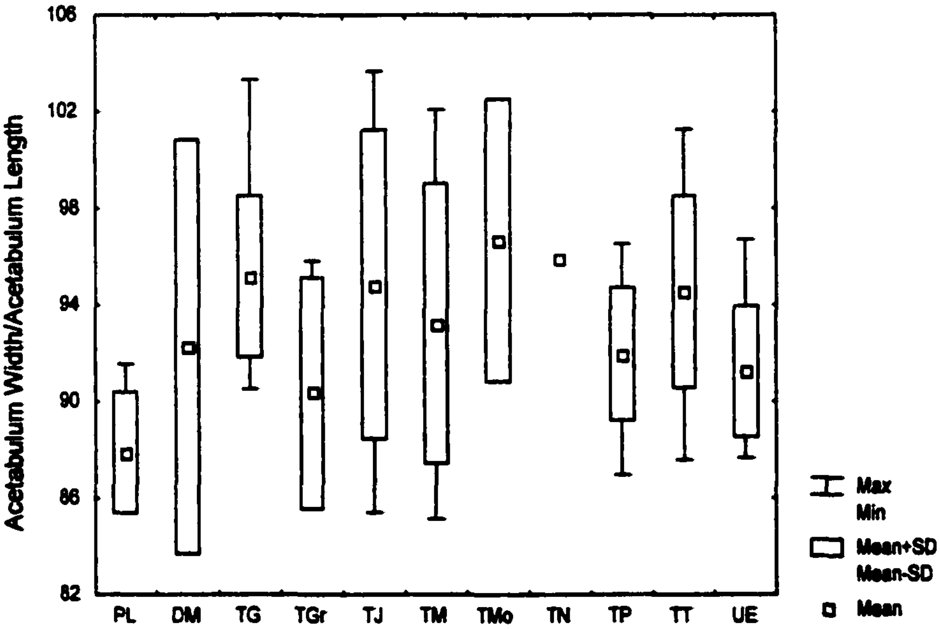


Figure 6.5. Box plot of acetabulum shape index. Note the low index of *Ptilocercus*.

Table 6.3: Probabilities* from Tukey Honest Significant Difference (HSD) post hoc test of ilium shape index.

	Dendrogale melanura	*Dendrogale murina*	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
D. melanura		**0.0166**	0.9861	**0.0001**	**0.0013**	**0.0052**	0.0660	0.0688	**0.0155**	**0.0001**	**0.0001**	**0.0001**
D. murina	**0.0166**		**0.0001**	0.9998	1.0000	0.9994	0.8629	0.9946	1.0000	0.9679	0.9997	1.0000
P. lowii	0.9861	**0.0001**		**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**
T. glis	**0.0001**	0.9998	**0.0001**		0.9752	**0.0177**	**0.0001**	0.1988	0.9999	0.8772	1.0000	0.9986
T. gracilis	**0.0013**	1.0000	**0.0001**	0.9752		0.9833	0.3198	0.9599	1.0000	0.5205	0.9662	0.9999
T. javanica	**0.0052**	0.9994	**0.0001**	**0.0177**	0.9833		0.8610	1.0000	0.9992	**0.0006**	**0.0129**	0.2332
T. minor	0.0660	0.8629	**0.0001**	**0.0001**	0.3198	0.8610		1.0000	0.8482	**0.0001**	**0.0001**	**0.0010**
T. montana	0.0688	0.9946	**0.0001**	0.1988	0.9599	1.0000	1.0000		0.9933	**0.0291**	0.1783	0.5111
T. nicobarica	**0.0155**	1.0000	**0.0001**	0.9999	1.0000	0.9992	0.8482	0.9933		0.9730	0.9998	1.0000
T. palawanensis	**0.0001**	0.9679	**0.0001**	0.8772	0.5205	**0.0006**	**0.0001**	**0.0291**	0.9730		0.9029	0.4497
T. tana	**0.0001**	0.9997	**0.0001**	1.0000	0.9662	**0.0129**	**0.0001**	0.1783	0.9998	0.9029		0.9968
U. everetti	**0.0001**	1.0000	**0.0001**	0.9986	0.9999	0.2332	**0.0010**	0.5111	1.0000	0.4497	0.9968	

*probabilities in bold are significant at the p < .05 level

Table 6.4: Probabilities* from Tukey Honest Significant Difference (HSD) post hoc test of ilium shape index with *Dendrogale* species combined.

	Dendrogale sp.	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
***Dendrogale* sp.**		**0.0014**	**0.0032**	0.2505	0.6404	0.9963	0.9773	0.6325	**0.0004**	**0.0027**	**0.0178**
P. lowii	**0.0014**		**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**
T. glis	**0.0032**	**0.0002**		0.9797	**0.0356**	**0.0002**	0.2743	0.9999	0.9027	1.0000	0.9987
T. gracilis	0.2505	**0.0002**	0.9797		0.9862	0.4049	0.9677	1.0000	0.5994	0.9727	0.9999
T. javanica	0.6404	**0.0002**	**0.0356**	0.9862		0.8898	1.0000	0.9992	**0.0016**	**0.0272**	0.3127
T. minor	0.9963	**0.0002**	**0.0002**	0.4049	0.8898		1.0000	0.8796	**0.0002**	**0.0002**	**0.0029**
T. montana	0.9773	**0.0002**	0.2743	0.9677	1.0000	1.0000		0.9942	0.0546	0.2508	0.5908
T. nicobarica	0.6325	**0.0002**	0.9999	1.0000	0.9992	0.8796	0.9942		0.9780	0.9998	1.0000
T. palawanensis	**0.0004**	**0.0002**	0.9027	0.5994	**0.0016**	**0.0002**	0.0546	0.9780		0.9230	0.5333
T. tana	**0.0027**	**0.0002**	1.0000	0.9727	**0.0272**	**0.0002**	0.2508	0.9998	0.9230		0.9971
U. everetti	**0.0178**	**0.0002**	0.9987	0.9999	0.3127	**0.0029**	0.5908	1.0000	0.5333	0.9971	

*probabilities in bold are significant at the p < .05 level

Table 6.5. Distribution of tupaiid hindlimb features discussed in the text.

Taxon	*Ptilocercus*	Tupaiinae[a]	*Dendrogale*	*Tupaia glis*	*T. minor*	*T. tana*	*Urogale*
Ilio-pubic angle	large (*e.g.*, above 145°)	smaller (*e.g.*, below 130°)	smaller (*e.g.*, below 130°)	smaller (*e.g.*, below 130°)	smaller (*e.g.*, below 130°)	smaller (*e.g.*, below 130°)	smaller (*e.g.*, below 130°)
Pubic symphysis length	short	long	long	long	long	long	long
Anterior, inferior iliac spine	small	large	large	large	large	large	large
Ilium width	very narrow	wide	variable (intermediate to wide)	wide	wide	wide	wide
Acetabulum shape	elliptical	circular	circular	circular	circular	circular	circular
Greater Trochanter size	small	large	large	large	large	large	large
Third Trochanter size	small	large	large	large	large	large	large
Femoral Condyle depth	shallow	deep	deep	deep	deep	deep	deep
Patellar Groove shape	short, wide	long, narrow	long, narrow	long, narrow	long, narrow	long, narrow	long, narrow

[a] This column summarizes the most common character states found among the species included in this subfamily.

of the ilium in tupaiines results in a wider iliac crest, which is where the gluteus superficialis muscle, an extensor of the thigh that is not differentiated from the tensor fasciae femoris muscle in tupaiids (Le Gros Clark, 1924a, 1926), originates. Here again, the laterally expanded ilium in tupaiines may be related to powerful extension of the thigh for propulsion during terrestrial running because a wider iliac crest provides a larger area of attachment for the gluteus superficialis muscle. However, the area of origin of this muscle in tupaiines may not actually be more extensive than in *Ptilocercus*, despite their laterally expanded iliac crest (see Le Gros Clark, 1924a, 1926; George, 1977). Finally, the laterally expanded iliac crest of tupaiines also provides a broader area of attachment for the erector spinae muscles (longissimus and iliocostalis), as well as quadratus lumborum. This could be related to the ventral position of the tupaiine lumbar transverse processes, which allows powerful flexion of the vertebral column by quadratus lumborum and powerful extension of the vertebral column by enlarged erector spinae muscles (see discussion in chapter 4). Powerful spinal flexion and extension in tupaiines is important for terrestrial running because it increases the length of the stride during galloping and bounding (see chapter 4).

Among didelphids, it is the terrestrial *Metachirus* that has a somewhat widened ilium (Muizon, 1998), and cursorial viverrids also exhibit wide ilia (Taylor, 1976). It is also interesting that, as in the axial skeleton, *Ptilocercus* and tupaiines mirror lorisines and galagines, respectively, insofar as ilium width is concerned, albeit in response to different biological roles. The slow climbing lorisines have somewhat narrower ilia than the leaping galagines (McArdle, 1981; Anemone, 1993). The convergence in ilium width between tupaiines and leapers like galagines (and indriids, which have even wider ilia;

Anemone, 1993) makes sense because leaping requires powerful extension of the thigh by the gluteus medius muscle (Anemone, 1993). The narrower ilium of *Ptilocercus* probably reflects a form of arboreal quadrupedalism in which the hindlimbs are habitually in more flexed positions, compared to the more extended hindlimbs of tupaiines during terrestrial locomotion. While it does not reflect the specialized slow climbing of lorisines, the narrower ilium of *Ptilocercus* does reflect a slower form of arboreal locomotion compared to the faster terrestrial locomotion of tupaiines. The condition found in *Ptilocercus* is likely primitive for Scandentia, and the prototupaiine condition probably evolved in response to increased terrestriality in that lineage. In fact, the condition found in *Ptilocercus* is probably primitive for Archonta (Table 6.6), as a narrow ilium is also found in dermopterans (see Fig. 7.4; Beard, 1989, fig. 75), some plesiadapiforms (see Fig. 7.4; Beard, 1989, fig. 75; Beard, 1993b, fig. 10.9), and chiropterans (see Simmons, 1994, fig. 5). The ilium of the ancestral euprimate, on the other hand, was probably expanded in relation to graspleaping (Szalay and Dagosto, 1988; Szalay and Lucas, 1996).

While the acetabulum shape index of *Ptilocercus* is not significantly different from that of tupaiines (Fig. 6.5), the acetabulum of *Ptilocercus* is more elliptical (Fig. 6.6; Table 6.5) and the cranial portion of the articular surface is more expanded than in tupaiines (Fig. 6.6; Table 6.5). The more circular acetabulum of tupaiines restricts the mobility of the hip joint and restricts movements more to the parasagittal plane, which increases the efficiency of terrestrial locomotion. This is yet another indication of the terrestrial ancestry of tupaiines, as even the most arboreal tupaiine, *T. minor*, has a relatively circular acetabulum (Table 6.5). The more elliptical acetabulum of

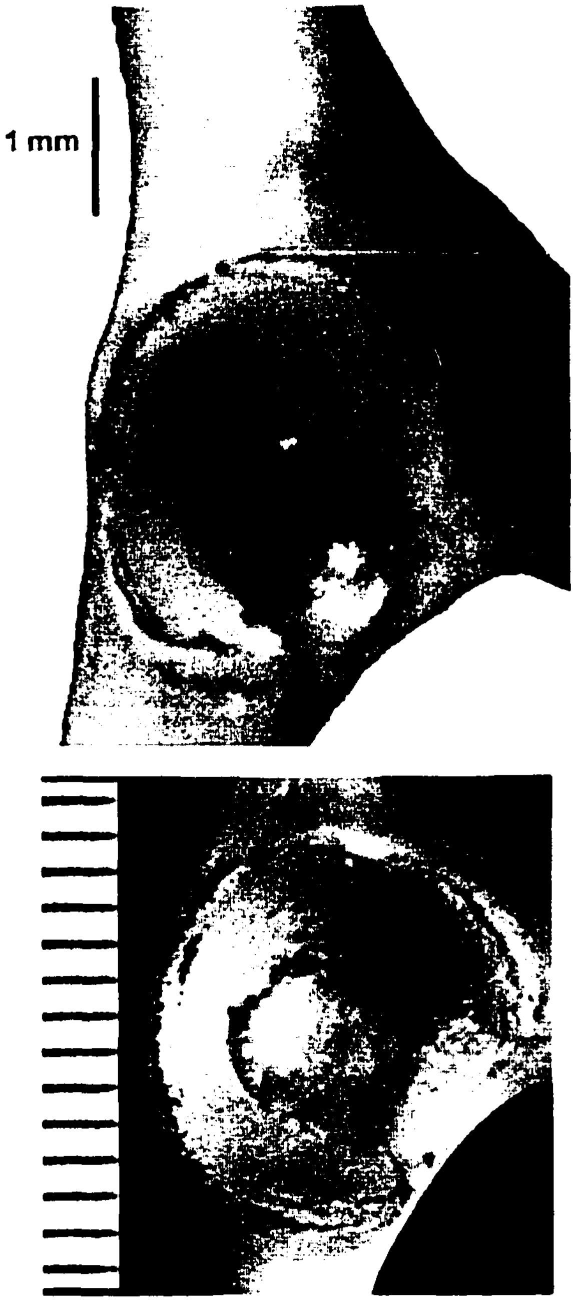


Figure 6.6. Acetabulum of *Ptilocercus* (top) and *T. tana* (bottom). Subdivisions on scale are 0.5 mm. Note the elliptical acetabulum and expansion of the cranial portion of the articular surface in *Ptilocercus*.

Table 6.6. Distribution of archontan hindlimb features discussed in the text.

Taxon	Tupaiinae[a]	*Ptilocercus*	*Cynocephalus*	*Pteropus*	*Microcebus*	Plesiadapiformes
Ilio-pubic angle	smaller (*e.g.*, below 130°)	large (*e.g.*, above 145°)	large	variable	large	large
Pubic symphysis length	long	short	short	short[b]	short	?
Anterior, inferior iliac spine	large	small	small or absent	small or absent	small	small
Ilium width	wide	very narrow	very narrow	narrow	narrow	variable
Acetabulum shape	circular	elliptical	elliptical	elliptical	elliptical	elliptical
Greater Trochanter size	large	small	very small (below head)	very small (below head)	large	small
Third Trochanter size	large	small	very small or absent	very small or absent	small (and high)	small
Femoral Condyle depth	deep	shallow	shallow	shallow	deep	shallow
Patellar Groove shape	long, narrow	short, wide	short, wide	short, narrow	deep, narrow	short, wide

[a] This column summarizes the most common character states found among the species included in this subfamily.

[b] This refers to males only (see Flower, 1885; Vaughan, 1970; Walton and Walton, 1970).

Ptilocercus, on the other hand, allows more mobility at the hip joint (see Szalay and Sargis, submitted), so greater ranges of abduction and lateral rotation are possible at this joint (see Beard, 1989). This is particularly important for an arboreal climber like *Ptilocercus*. The expansion of the cranial portion of the articular surface in *Ptilocercus* reflects loads incurred during climbing on vertical supports (see Beard, 1989; Ward *et al.*, 1993), an activity that *Ptilocercus* commonly engages in (Stafford and Thorington, 1998). Here again, the condition found in *Ptilocercus* appears to represent the primitive condition for Tupaiidae.

The shape of the acetabulum is also related to substrate preference in marsupials, as the arboreal *Caluromys* and *Dromiciops* have an elliptical acetabulum, while that of the terrestrial *Metachirus* (but not caenolestids) is circular (Szalay and Sargis, submitted). For Archonta, the two acetabular character states found in *Ptilocercus* may be primitive as they are also found in euprimates (see Beard, 1993b), dermopterans, chiropterans, and plesiadapiforms (Fig. 7.3; Table 6.6; see Beard, 1989, fig. 75; Beard, 1993b). These characters will be discussed further in the character analysis in chapter 7.

Ptilocercus has a very small anterior inferior iliac spine, while this feature is large in tupaiines (Figs. 6.3, 6.6-6.7; Table 6.5). The rectus femoris muscle, which is an extensor of the leg, originates from this structure. The larger anterior inferior iliac spine of tupaiines provides a larger area of attachment for this muscle and may indicate powerful extension of the leg by this muscle for propulsion during terrestrial running, while the small size of this feature in *Ptilocercus* is probably indicative of a more habitually flexed hindlimb and a slower form of arboreal locomotion (see Szalay and Sargis, submitted). In this feature, *Ptilocercus* is again more similar to the slow climbing

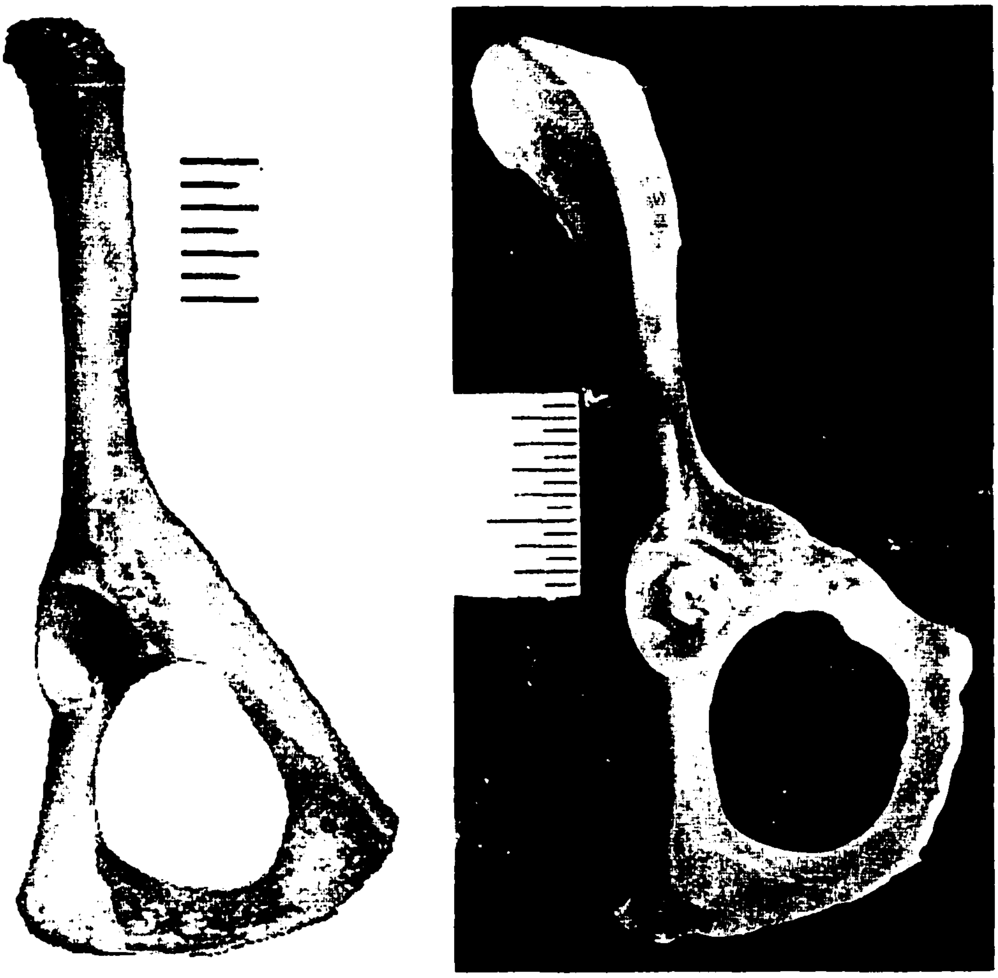


Figure 6.7. Innominates of *Ptilocercus* (left) and *T. tana* (right). Subdivisions on scale are 0.5 mm. Note the large ilio-pubic angle and short pubic symphysis in *Ptilocercus*.

lorisines, and the tupaiines are more similar to the leaping galagines because leaping also requires powerful knee extension by the rectus femoris muscle (see McArdle, 1981; Gebo, 1989; Anemone, 1993). Once again, the fact that even arboreal tupaiines are characterized by a large anterior inferior iliac spine reflects the terrestrial heritage of Tupaiinae, and the condition seen in *Ptilocercus* is probably primitive for Scandentia. The condition found in *Ptilocercus* is also likely primitive for Archonta as this feature is also small in *Microcebus* and plesiadapiforms, and it is small or absent in dermopterans and chiropterans (Table 6.6).

The ilio-pubic angle in *Ptilocercus* is larger (*e.g.*, greater than 145°) than that of tupaiines (*e.g.*, less than 130°) and the pubic symphysis of *Ptilocercus* is shorter than that of tupaiines (Fig. 6.7; Table 6.5). While these features may reflect differences in the attachments of the muscles that originate on the pubis, the thigh adductors and rectus abdominis, they are difficult to interpret functionally without detailed dissections of this region in tupaiids. In tupaiines, there may be a larger area of attachment (and different angle of attachment) for the rectus abdominis muscle, which flexes the trunk, that could be related to some of the vertebral differences discussed above (see chapter 4). The condition of these features found in *Ptilocercus* may be primitive for Tupaiidae, as well as Archonta (Table 6.6) because the same character states are found in dermopterans (see Fig. 7.4; Beard, 1989, fig. 75), chiropterans (see Simmons, 1994, fig. 5), plesiadapiforms (only the ilio-pubic angle character; see Fig. 7.4; Beard, 1989, fig. 75; Beard, 1993b, fig. 10.9), and *Microcebus* (see Jouffroy, 1975, fig. 9).

The pubis length index of *T. montana* and *T. nicobarica* is significantly different from that of several other tupaiids, including *Ptilocercus* (Fig. 6.8; Tables 6.7, 6.27). The

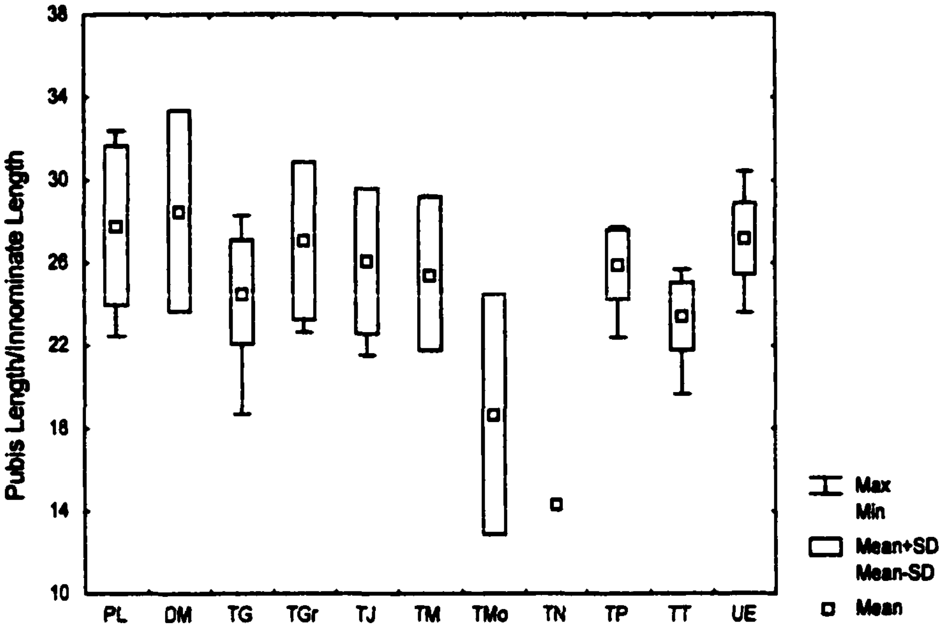


Figure 6.8. Box plot of pubis length index. Note the low indices of *T. montana* and *T. nicobarica*.

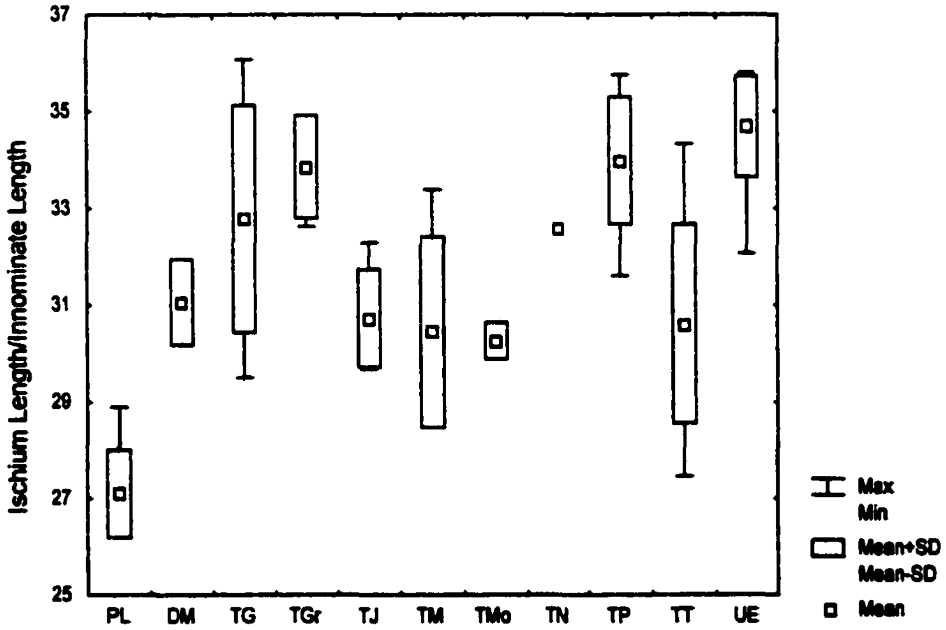


Figure 6.9. Box plot of ischium length index. Note the low index of *Ptilocercus*.

Table 6.7: Probabilities* from Tukey Honest Significant Difference (HSD) post hoc test of pubis length index.

	Dendrogale melanura	*Dendrogale murina*	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
D. melanura		0.7442	0.9341	0.1955	0.8812	0.6257	0.4530	**0.0035**	**0.0005**	0.5066	0.0677	0.8210
D. murina	0.7442		0.9971	1.0000	0.9999	1.0000	1.0000	0.6636	0.1363	1.0000	1.0000	0.9996
P. lowii	0.9341	0.9971		0.2585	1.0000	0.9934	0.9113	**0.0022**	**0.0004**	0.9446	**0.0212**	1.0000
T. glis	0.1955	1.0000	0.2585		0.9127	0.9890	0.9998	0.1035	**0.0104**	0.9668	0.9682	0.2599
T. gracilis	0.8812	0.9999	1.0000	0.9127		1.0000	0.9991	**0.0257**	**0.0026**	0.9999	0.4763	1.0000
T. javanica	0.6257	1.0000	0.9934	0.9890	1.0000		1.0000	**0.0375**	**0.0039**	1.0000	0.6283	0.9996
T. minor	0.4530	1.0000	0.9113	0.9998	0.9991	1.0000		0.0657	**0.0065**	1.0000	0.8449	0.9724
T. montana	**0.0035**	0.6636	**0.0022**	0.1035	**0.0257**	**0.0375**	0.0657		0.9600	**0.0202**	0.3535	**0.0025**
T. nicobarica	**0.0005**	0.1363	**0.0004**	**0.0104**	**0.0026**	**0.0039**	**0.0065**	0.9600		**0.0025**	**0.0373**	**0.0005**
T. palawanensis	0.5066	1.0000	0.9446	0.9668	0.9999	1.0000	1.0000	**0.0202**	**0.0025**		0.3073	0.9881
T. tana	0.0677	1.0000	**0.0212**	0.9682	0.4763	0.6283	0.8449	0.3535	**0.0373**	0.3073		**0.0100**
U. everetti	0.8210	0.9996	1.0000	0.2599	1.0000	0.9996	0.9724	**0.0025**	**0.0005**	0.9881	**0.0100**	

*probabilities in bold are significant at the p < .05 level

Table 6.8: Probabilities* from Tukey Honest Significant Difference (HSD) post hoc test of ischium length index.

	Dendrogale melanura	*Dendrogale murina*	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
D. melanura		1.0000	0.8360	0.9781	0.8732	1.0000	1.0000	1.0000	0.9993	0.7408	1.0000	0.4817
D. murina	1.0000		0.4092	1.0000	0.9956	1.0000	1.0000	0.9999	1.0000	0.9837	1.0000	0.8948
P. lowii	0.8360	0.4092		**0.0001**	**0.0002**	**0.0210**	0.0620	0.5556	0.1659	**0.0001**	**0.0034**	**0.0001**
T. glis	0.9781	1.0000	**0.0001**		0.9979	0.2912	0.2118	0.7503	1.0000	0.8313	**0.0209**	0.2030
T. gracilis	0.8732	0.9956	**0.0002**	0.9979		0.3082	0.2352	0.5347	1.0000	1.0000	0.1429	0.9999
T. javanica	1.0000	1.0000	**0.0210**	0.2912	0.3082		1.0000	1.0000	0.9971	**0.0129**	1.0000	**0.0009**
T. minor	1.0000	1.0000	0.0620	0.2118	0.2352	1.0000		1.0000	0.9923	**0.0094**	1.0000	**0.0007**
T. montana	1.0000	0.9999	0.5556	0.7503	0.5347	1.0000	1.0000		0.9945	0.2267	1.0000	0.0675
T. nicobarica	0.9993	1.0000	0.1659	1.0000	1.0000	0.9971	0.9923	0.9945		0.9998	0.9937	0.9922
T. palawanensis	0.7408	0.9837	**0.0001**	0.8313	1.0000	**0.0129**	**0.0094**	0.2267	0.9998		**0.0003**	0.9985
T. tana	1.0000	1.0000	**0.0034**	**0.0209**	0.1429	1.0000	1.0000	1.0000	0.9937	**0.0003**		**0.0001**
U. everetti	0.4817	0.8948	**0.0001**	0.2030	0.9999	**0.0009**	**0.0007**	0.0675	0.9922	0.9985	**0.0001**	

*probabilities in bold are significant at the p < .05 level

adductor musculature attaches to the pubis, so the moment arm of these muscles is reduced in taxa with a short pubis (Anemone, 1993), such as *T. montana* and *T. nicobarica*. Hence, a short pubis is associated with taxa for which adduction is of less importance, such as terrestrial quadrupeds that restrict movements to flexion and extension in the parasagittal plane (Anemone, 1993). Hence, it is interesting that *T. nicobarica*, which has been classified as arboreal (Table 1.2; Kloss, 1903; Prashanth and Veenakumari, 1996; but see Martin, 1984), is similar to the terrestrial *T. montana* in having a short pubis and is significantly different from *Ptilocercus* for this index. Little more can be said about this because of the lack of research on the mammalian pubis (Anemone, 1993) and because *T. nicobarica* is only represented by a single specimen.

The ischium length index of *Ptilocercus* is significantly different from that of several tupaiines (Fig. 6.9; Tables 6.8, 6.27). The hamstrings (semitendinosus, semimembranosus, and biceps femoris) and the quadratus femoris all originate from the ischium and are all extensors of the thigh. The longer ischium of several terrestrial tupaiines lengthens the moment arm of these muscles (see McArdle, 1981; Anemone, 1993, Muizon, 1998), which probably gives them an advantage in powerfully extending the thigh for propulsion during terrestrial running. The shorter ischium of *Ptilocercus* is yet another indication of its more habitually flexed hindlimb and slower form of arboreal locomotion. The fact that *Urogale* has the longest ischium (Fig. 6.9) may be explained by its digging behavior (see above; Wharton, 1950) because diggers are characterized by a long ischium (Hildebrand, 1985). Again, the condition found in *Ptilocercus* may be primitive for Scandentia and the tupaiine condition probably evolved in relation to increased terrestriality in that lineage.

The ischium shape index is not informative and there are no significant differences between any tupaiid species for this index (Fig. 6.10; Table 6.27). A cluster analysis of the variables included in six innominate indices shows that *Ptilocercus* is quite different from tupaiines in its pelvic morphology (Fig. 6.11).

Femur

There are no significant differences between any tupaiid species for the femoral head shape index (Fig. 6.12; Table 6.27). The femoral head of all tupaiids is spherical and the articular surface does not extend onto the femoral neck (Fig. 6.14). This is somewhat surprising because while terrestrial marsupials exhibit this condition of the femoral head, arboreal marsupials have a more cylindrical head that has an articular surface that extends onto the femoral neck (reflecting the habitually abducted position of the thigh; Szalay and Sargis, submitted). Terrestrial guenons also have a more restricted articular surface than arboreal guenons (Gebo and Sargis, 1994). *Ptilocercus* does seem, however, to have an absolutely larger femoral head than *Dendrogale* (Table 6.28), which is similar in body size to *Ptilocercus* (Table 1.1). This may be related to the increased mobility required at the hip joint for abduction of the thigh on arboreal supports because an enlarged femoral head is also found in arboreal marsupials (Szalay and Sargis, submitted) and arboreal guenons (Gebo and Sargis, 1994).

All tupaiids are characterized by a relatively high femoral neck angle (Fig. 6.14), which may be another indication of the arboreal ancestry of Scandentia. A lower femoral neck angle is found in terrestrial guenons (Gebo and Sargis, 1994), as well as other terrestrial cercopithecids (Harrison, 1989). The latter condition limits abduction of the thigh and restricts movements to the parasagittal plane in terrestrial cercopithecids

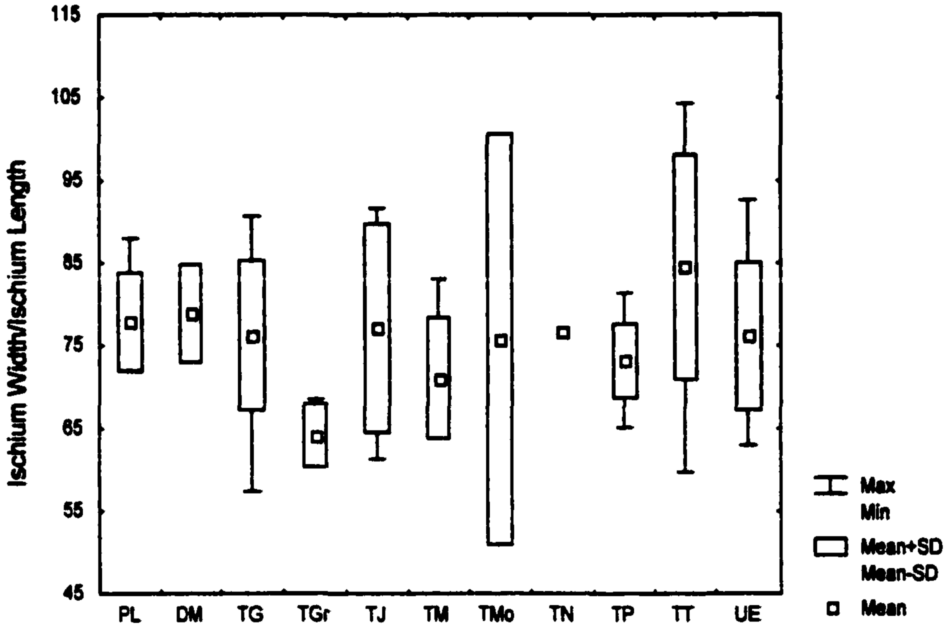


Figure 6.10. Box plot of ischium shape index.

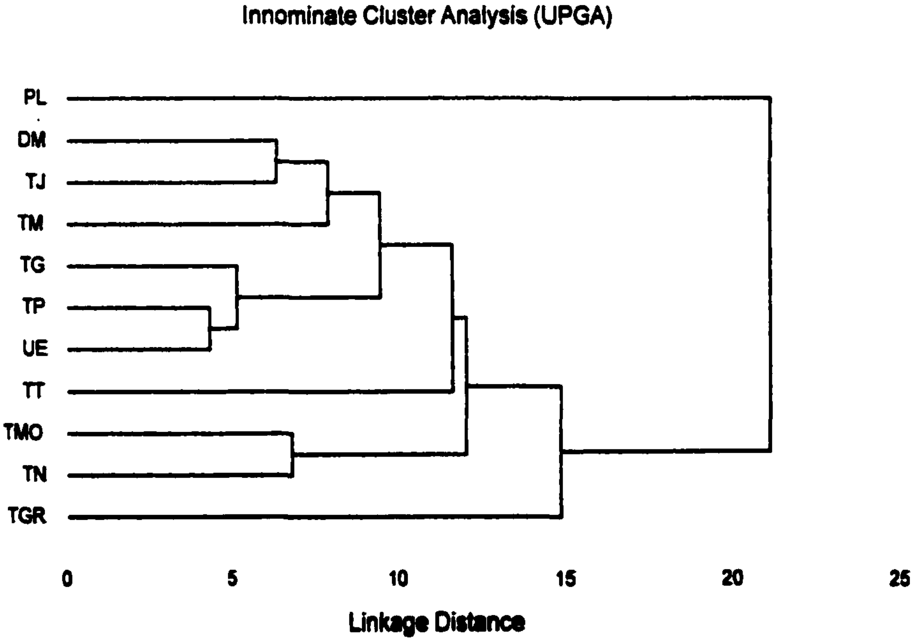


Figure 6.11. Cluster analysis of the variables included in six innominate indices. Note the difference between *Ptilocercus* and the tupaiines.

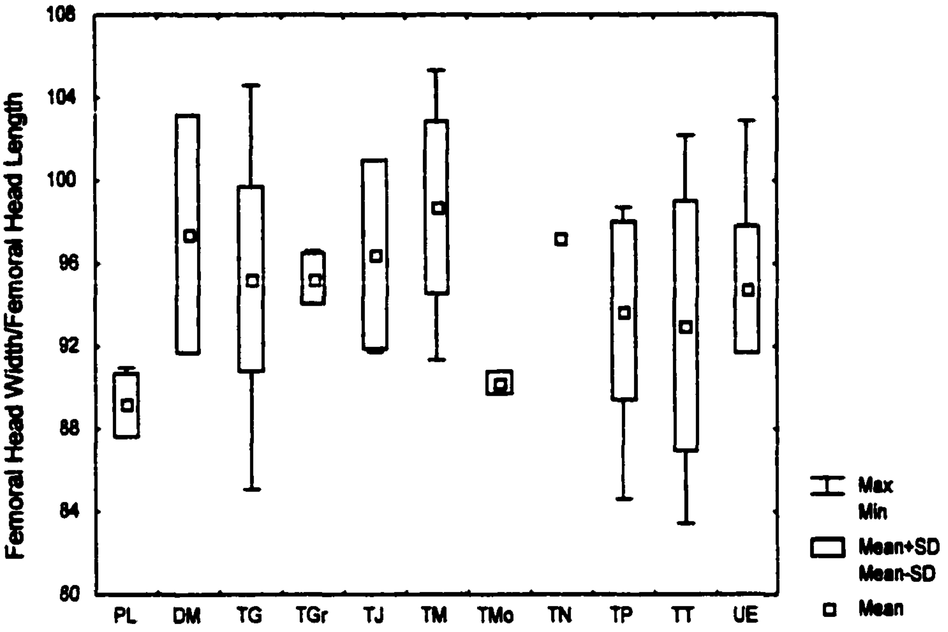


Figure 6.12. Box plot of femoral head shape index.

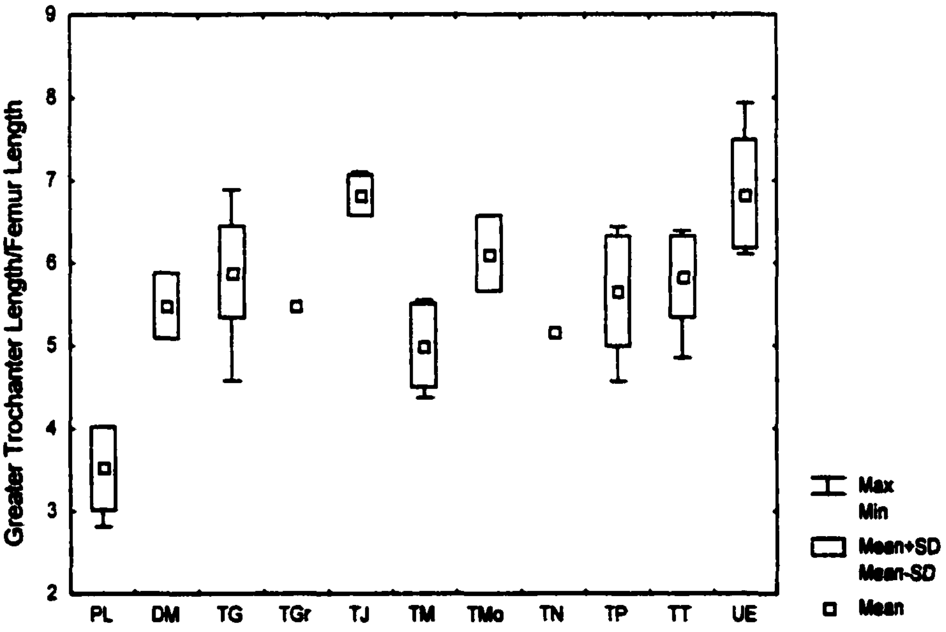


Figure 6.13. Box plot of greater trochanter length index. Note the low index of *Ptilocercus*.

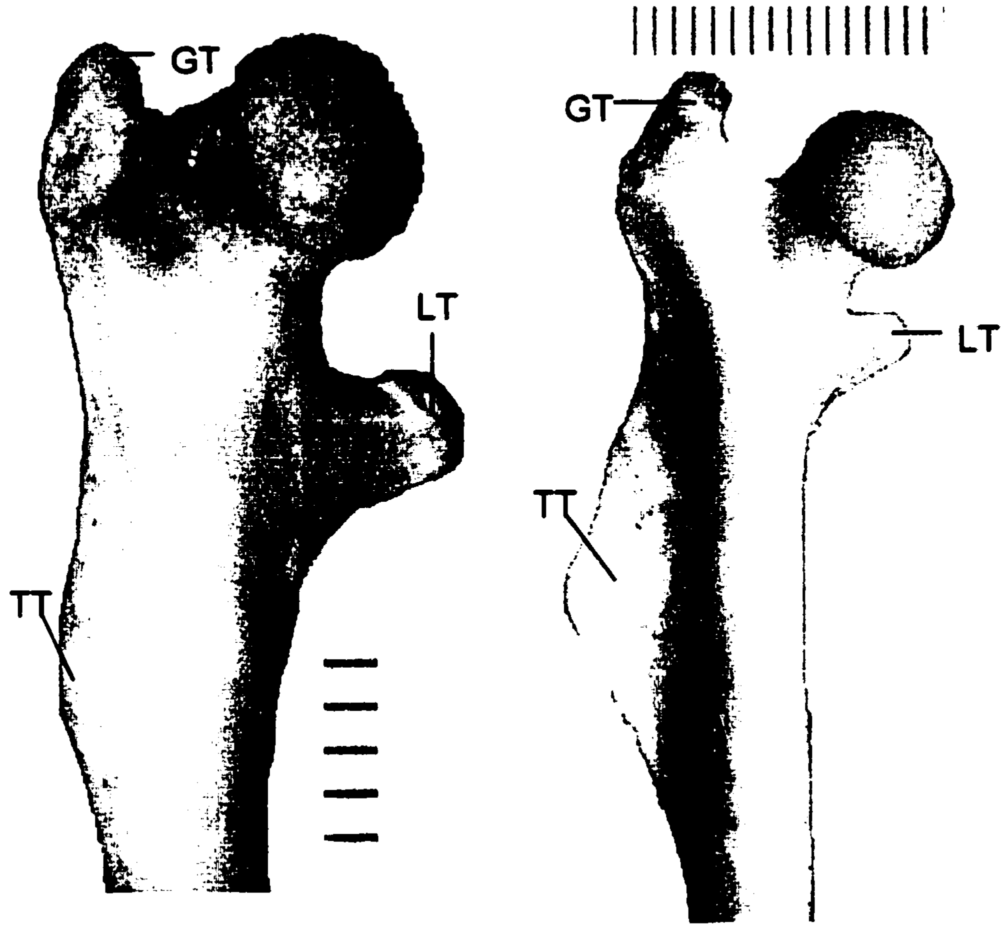


Figure 6.14. Proximal femora of *Ptilocercus* (left) and *T. tana* (right). GT: greater trochanter, LT: lesser trochanter, TT: third trochanter. Subdivisions on scale are 0.5 mm. Note the small greater and third trochanters of *Ptilocercus*.

(Harrison, 1989; Gebo and Sargis, 1994), while the condition seen in tupaiids allows a greater range of abduction at the hip joint.

The greater trochanter of tupaiines projects farther proximally than that of *Ptilocercus* (Figs. 6.13-6.14; Tables 6.5, 6.27), and the greater trochanter length index of *Ptilocercus* is significantly different from every tupaiine species except for the single specimens of *D. melanura*, *T. gracilis*, and *T. nicobarica* (Fig. 6.13; Table 6.9). However, it does seem likely that *Ptilocercus* would be significantly different from the latter two species if larger samples were included (Fig. 6.13) because these species are similar to all other tupaiines in this feature. Also, *Ptilocercus* is significantly different from *Dendrogale* sp. when both *Dendrogale* species (specimens) are considered together (Table 6.10). The greater trochanter is the insertion site for the gluteus medius muscle, an extensor of the thigh (see above). Just as the expanded ilium of tupaiines provides a broader area of origin for this muscle (see above), the large greater trochanter in this group provides a longer lever arm about which this muscle can act and may indicate powerful extension of the thigh by this muscle for propulsion during terrestrial running. The more proximal projection of the greater trochanter in tupaiines also restricts the mobility of the hip joint, which particularly limits the range of abduction. This, in turn, makes the parasagittal hindlimb movements of terrestrial locomotion more efficient. This feature is found in arboreal tupaiines like *T. minor* (Fig. 6.13; Tables 6.5, 6.27), indicating, yet again, the terrestrial ancestry of Tupaiinae. As with the narrower ilium, the shorter greater trochanter of *Ptilocercus* probably reflects its more habitually flexed hindlimb and slower form of arboreal locomotion. Just as a low greater tuberosity allows more mobility in the shoulder joint (see chapter 5; Larson, 1993), a less projecting greater

Table 6.9: Probabilities* from Tukey Honest Significant Difference (HSD) post hoc test of greater trochanter length index.

	Dendrogale melanura	*Dendrogale murina*	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
D. melanura		0.9999	0.2572	0.9900	1.0000	0.3830	1.0000	0.9764	1.0000	0.9998	0.9955	0.2401
D. murina	0.9999		**0.0309**	1.0000	1.0000	0.9012	0.9785	1.0000	0.9998	1.0000	1.0000	0.8249
P. lowii	0.2572	**0.0309**		**0.0001**	0.1032	**0.0001**	**0.0049**	**0.0002**	0.2943	**0.0001**	**0.0001**	**0.0001**
T. glis	0.9900	1.0000	**0.0001**		0.9999	0.2794	**0.0344**	1.0000	0.9833	0.9962	1.0000	**0.0033**
T. gracilis	1.0000	1.0000	0.1032	0.9999		0.6573	0.9997	0.9988	1.0000	1.0000	1.0000	0.5078
T. javanica	0.3830	0.9012	**0.0001**	0.2794	0.6573		**0.0010**	0.9647	0.3409	0.0963	0.2293	1.0000
T. minor	1.0000	0.9785	**0.0049**	**0.0344**	0.9997	**0.0010**		0.3855	1.0000	0.3982	0.0855	**0.0001**
T. montana	0.9764	1.0000	**0.0002**	1.0000	0.9988	0.9647	0.3855		0.9661	0.9964	1.0000	0.8904
T. nicobarica	1.0000	0.9998	0.2943	0.9833	1.0000	0.3409	1.0000	0.9661		0.9994	0.9917	0.2055
T. palawanensis	0.9998	1.0000	**0.0001**	0.9962	1.0000	0.0963	0.3982	0.9964	0.9994		0.9998	**0.0007**
T. tana	0.9955	1.0000	**0.0001**	1.0000	1.0000	0.2293	0.0855	1.0000	0.9917	0.9998		**0.0030**
U. everetti	0.2401	0.8249	**0.0001**	**0.0033**	0.5078	1.0000	**0.0001**	0.8904	0.2055	**0.0007**	**0.0030**	

*probabilities in bold are significant at the p < .05 level

Table 6.10: Probabilities* from Tukey Honest Significant Difference (HSD) post hoc test of greater trochanter length index with *Dendrogale* species combined.

	Dendrogale sp.	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
***Dendrogale* sp.**		**0.0062**	0.9970	1.0000	0.2805	0.9899	0.9897	1.0000	1.0000	0.9993	0.0995
P. lowii	**0.0062**		**0.0002**	0.0871	**0.0002**	**0.0039**	**0.0002**	0.2584	**0.0002**	**0.0002**	**0.0002**
T. glis	0.9970	**0.0002**		0.9998	0.2447	**0.0283**	1.0000	0.9743	0.9933	1.0000	**0.0026**
T. gracilis	1.0000	0.0871	0.9998		0.6090	0.9993	0.9976	1.0000	1.0000	0.9999	0.4603
T. javanica	0.2805	**0.0002**	0.2447	0.6090		**0.0009**	0.9495	0.3015	0.0812	0.1991	1.0000
T. minor	0.9899	**0.0039**	**0.0283**	0.9993	**0.0009**		0.3433	1.0000	0.3551	0.0719	**0.0002**
T. montana	0.9897	**0.0002**	1.0000	0.9976	0.9495	0.3433		0.9513	0.9936	0.9999	0.8595
T. nicobarica	1.0000	0.2584	0.9743	1.0000	0.3015	1.0000	0.9513		0.9988	0.9864	0.1776
T. palawanensis	1.0000	**0.0002**	0.9933	1.0000	0.0812	0.3551	0.9936	0.9988		0.9996	**0.0006**
T. tana	0.9993	**0.0002**	1.0000	0.9999	0.1991	0.0719	0.9999	0.9864	0.9996		**0.0024**
U. everetti	0.0995	**0.0002**	**0.0026**	0.4603	1.0000	**0.0002**	0.8595	0.1776	**0.0006**	**0.0024**	

*probabilities in bold are significant at the p < .05 level

trochanter like that of *Ptilocercus* allows greater mobility in the hip joint (especially for abduction of the thigh in arboreal quadrupedalism and climbing). The greater trochanter of the ancestral tupaiid was probably like that of *Ptilocercus*, and this feature likely became elongated in the tupaiine lineage in response to increased terrestriality.

Similar differences in the height of the greater trochanter are also found in arboreal and terrestrial marsupials (Szalay and Sargis, submitted), as well as arboreal and terrestrial guenons (Gebo and Sargis, 1994). Among archontans, the condition seen in *Ptilocercus* is likely primitive as it is also found in plesiadapiforms, and the greater trochanter of dermopterans and chiropterans is even shorter (Table 6.6). The greater trochanter may have become further shortened in volitantians to create even more hip mobility for hindlimb suspensory (hanging) behavior (see Szalay and Lucas, 1993, 1996; Simmons and Quinn, 1994; Simmons, 1995).

The lesser trochanter is relatively similar in all tupaiids, insofar as its size, orientation, and distal extent are concerned (Figs. 6.14-6.16; Tables 6.11-6.12, 6.27). The lesser trochanter length index of *D. melanura* is significantly different from every other tupaiid species (Table 6.11). The fact that *D. melanura* has such a long lesser trochanter, while that of *D. murina* is much shorter (Tables 6.11, 6.27-6.28), is difficult to explain especially because both of these species are only represented by single specimens. As with the ilium shape index, this may be another indication that *D. melanura* is more arboreal than *D. murina* because large lesser trochanters are also found in arboreal marsupials (Szalay and Sargis, submitted) and more arboreal viverrids (Taylor, 1976). However, no definitive conclusions can be made about this without larger samples of these taxa. The lesser trochanter is also oriented more posteriorly in

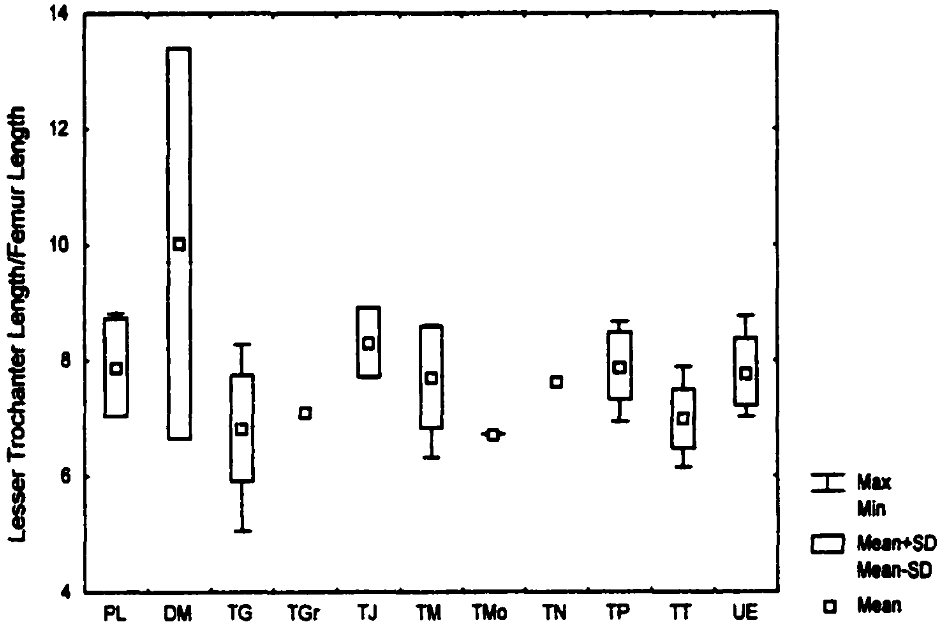


Figure 6.15. Box plot of lesser trochanter length index. Note the high index of *Dendrogale*.

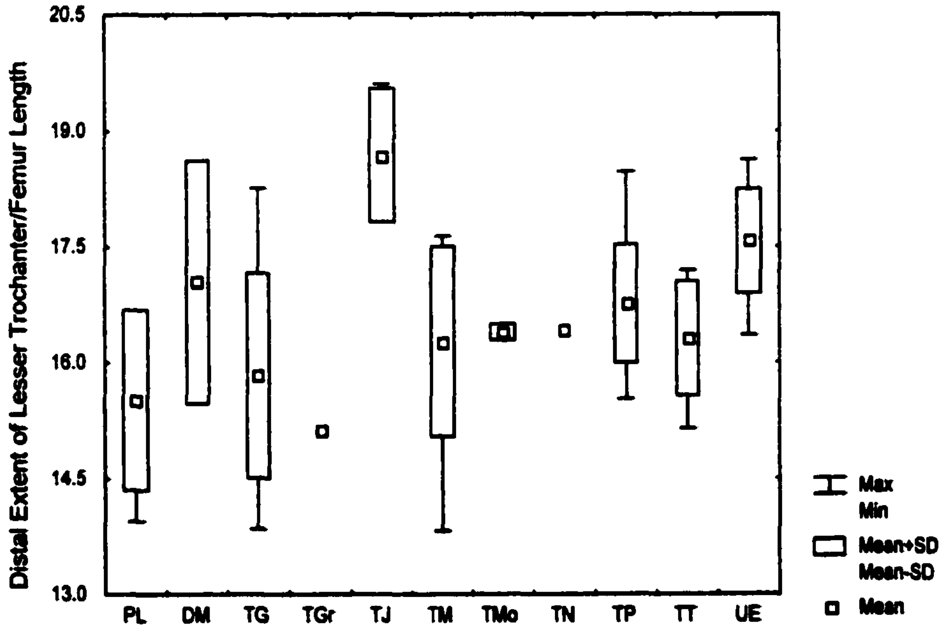


Figure 6.16. Box plot of distal extent of lesser trochanter index. Note the high index of *T. javanica*.

Table 6.11: Probabilities* from Tukey Honest Significant Difference (HSD) post hoc test of lesser trochanter length index.

	Dendrogale melanura	*Dendrogale murina*	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
D. melanura		**0.0008**	**0.0001**	**0.0001**	**0.0002**	**0.0004**	**0.0001**	**0.0001**	**0.0008**	**0.0001**	**0.0001**	**0.0001**
D. murina	**0.0008**		1.0000	0.9923	1.0000	0.9996	1.0000	0.9944	1.0000	1.0000	0.9990	1.0000
P. lowii	**0.0001**	1.0000		0.2554	0.9975	0.9997	1.0000	0.7416	1.0000	1.0000	0.5407	1.0000
T. glis	**0.0001**	0.9923	0.2554		1.0000	0.0566	0.2268	1.0000	0.9938	**0.0115**	1.0000	**0.0395**
T. gracilis	**0.0002**	1.0000	0.9975	1.0000		0.9410	0.9997	1.0000	1.0000	0.9948	1.0000	0.9987
T. javanica	**0.0004**	0.9996	0.9997	0.0566	0.9410		0.9822	0.3697	0.9994	0.9989	0.1570	0.9907
T. minor	**0.0001**	1.0000	1.0000	0.2268	0.9997	0.9822		0.8368	1.0000	1.0000	0.5829	1.0000
T. montana	**0.0001**	0.9944	0.7416	1.0000	1.0000	0.3697	0.8368		0.9954	0.5643	1.0000	0.7086
T. nicobarica	**0.0008**	1.0000	1.0000	0.9938	1.0000	0.9994	1.0000	0.9954		1.0000	0.9993	1.0000
T. palawanensis	**0.0001**	1.0000	1.0000	**0.0115**	0.9948	0.9989	1.0000	0.5643	1.0000		0.0892	1.0000
T. tana	**0.0001**	0.9990	0.5407	1.0000	1.0000	0.1570	0.5829	1.0000	0.9993	0.0892		0.2220
U. everetti	**0.0001**	1.0000	1.0000	**0.0395**	0.9987	0.9907	1.0000	0.7086	1.0000	1.0000	0.2220	

***probabilities in bold are significant at the p < .05 level**

Table 6.12: Probabilities* from Tukey Honest Significant Difference post hoc test of distal extent of lesser trochanter index.

	Dendrogale melanura	*Dendrogale murina*	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
D. melanura		0.9049	0.4313	0.5044	0.5753	1.0000	0.8180	0.9454	0.9832	0.9685	0.8136	1.0000
D. murina	0.9049		1.0000	1.0000	1.0000	0.4184	1.0000	1.0000	1.0000	0.9996	1.0000	0.9033
P. lowii	0.4313	1.0000		1.0000	1.0000	**0.0051**	0.9866	0.9968	0.9996	0.5885	0.9540	**0.0316**
T. glis	0.5044	1.0000	1.0000		0.9999	**0.0014**	0.9981	0.9998	1.0000	0.4172	0.9708	**0.0016**
T. gracilis	0.5753	1.0000	1.0000	0.9999		0.1025	0.9943	0.9958	0.9985	0.9057	0.9893	0.4339
T. javanica	1.0000	0.4184	**0.0051**	**0.0014**	0.1025		**0.0350**	0.3395	0.7087	0.1433	**0.0189**	0.8602
T. minor	0.8180	1.0000	0.9866	0.9981	0.9943	**0.0350**		1.0000	1.0000	0.9961	1.0000	0.2305
T. montana	0.9454	1.0000	0.9968	0.9998	0.9958	0.3395	1.0000		1.0000	1.0000	1.0000	0.9141
T. nicobarica	0.9832	1.0000	0.9996	1.0000	0.9985	0.7087	1.0000	1.0000		1.0000	1.0000	0.9926
T. palawanensis	0.9685	0.9996	0.5885	0.4172	0.9057	0.1433	0.9961	1.0000	1.0000		0.9929	0.7325
T. tana	0.8136	1.0000	0.9540	0.9708	0.9893	**0.0189**	1.0000	1.0000	1.0000	0.9929		0.0909
U. everetti	1.0000	0.9033	**0.0316**	**0.0016**	0.4339	0.8602	0.2305	0.9141	0.9926	0.7325	0.0909	

***probabilities in bold are significant at the p < .05 level**

terrestrial marsupials (Szalay and Sargis, submitted), terrestrial viverrids (Taylor, 1976), and terrestrial guenons (Gebo and Sargis, 1994), while it is oriented more medially in their arboreal relatives. While *Ptilocercus*, like several other arboreal mammals, may have a somewhat less posteriorly oriented lesser trochanter than that of tupaiines (Fig. 6.14), no consistent relationship seems to exist for this feature in tupaiids. Similarly, although the lesser trochanter of *T. javanica* is found more distally on the femur than in some other tupaiids (Fig. 6.16; Tables 6.12, 6.27), this is difficult to interpret functionally because of a lack of information on the substrate use and locomotion of this species.

The third trochanter of tupaiines projects farther laterally than in *Ptilocercus* (Figs. 6.14; 6.17; Tables 6.5, 6.27) and the third trochanter length index of *Ptilocercus* is significantly different from every tupaiine species except for the single specimen of *T. nicobarica* (Table 6.13). Again, this may indicate that *T. nicobarica* is arboreal like *Ptilocercus*, but more likely is the result of the extremely small sample of *T. nicobarica* because this species is similar to other tupaiines in its third trochanter morphology (Fig. 6.17). The third trochanter is the insertion site for the gluteus superficialis muscle, which is an extensor of the thigh (see above). The laterally expanded third trochanter of tupaiines provides a longer lever arm for this muscle to act on (as well as a broad area of insertion), which may be yet another indicator of the powerful extension of the thigh for propulsion during terrestrial running in tupaiines. The shorter third trochanter of *Ptilocercus* is another indication of its habitually flexed hindlimb and slower arboreal locomotion. As with several of the hip features discussed above, *Ptilocercus* likely exhibits the primitive tupaiid condition for this feature and the tupaiine condition likely evolved in response to increased terrestriality. The long third trochanter of arboreal

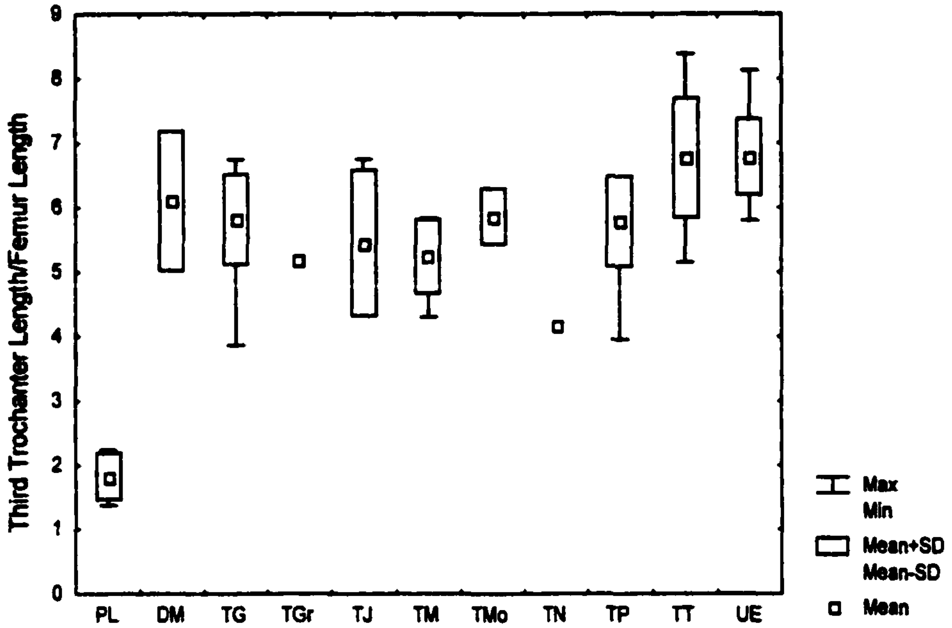


Figure 6.17. Box plot of third trochanter length index. Note the low index of *Ptilocercus*.

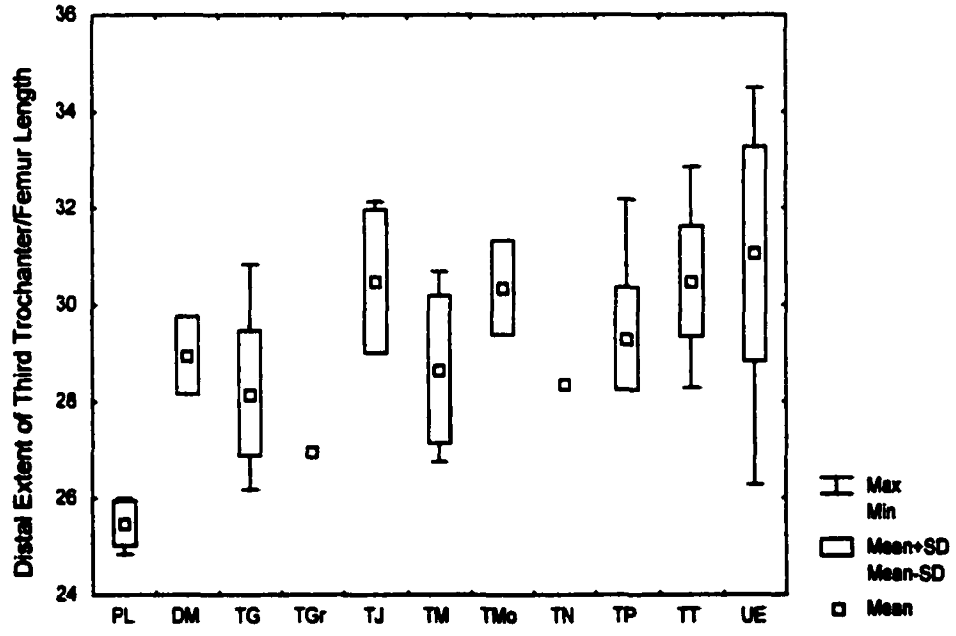


Figure 6.18. Box plot of distal extent of third trochanter index. Note the low index of *Ptilocercus*.

Table 6.13: Probabilities* from Tukey Honest Significant Difference (HSD) post hoc test of third trochanter length index.

	Dendrogale melanura	*Dendrogale murina*	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
D. melanura		0.9439	**0.0031**	1.0000	1.0000	1.0000	1.0000	1.0000	0.9912	1.0000	0.7573	0.7587
D. murina	0.9439		**0.0001**	0.9616	0.8934	0.8707	0.6463	0.9927	0.2971	0.9569	1.0000	1.0000
P. lowii	**0.0031**	**0.0001**		**0.0001**	**0.0058**	**0.0001**	**0.0001**	**0.0001**	0.1705	**0.0001**	**0.0001**	**0.0001**
T. glis	1.0000	0.9616	**0.0001**		0.9994	0.9996	0.8410	1.0000	0.5565	1.0000	**0.0252**	**0.0447**
T. gracilis	1.0000	0.8934	**0.0058**	0.9994		1.0000	1.0000	0.9998	0.9975	0.9997	0.6178	0.6207
T. javanica	1.0000	0.8707	**0.0001**	0.9996	1.0000		1.0000	1.0000	0.9298	0.9999	0.1779	0.1947
T. minor	1.0000	0.6463	**0.0001**	0.8410	1.0000	1.0000		0.9957	0.9622	0.9278	**0.0017**	**0.0028**
T. montana	1.0000	0.9927	**0.0001**	1.0000	0.9998	1.0000	0.9957		0.7570	1.0000	0.8776	0.8808
T. nicobarica	0.9912	0.2971	0.1705	0.5565	0.9975	0.9298	0.9622	0.7570		0.6089	**0.0427**	**0.0446**
T. palawanensis	1.0000	0.9569	**0.0001**	1.0000	0.9997	0.9999	0.9278	1.0000	0.6089		0.0526	0.0774
T. tana	0.7573	1.0000	**0.0001**	**0.0252**	0.6178	0.1779	**0.0017**	0.8776	**0.0427**	0.0526		1.0000
U. everetti	0.7587	1.0000	**0.0001**	**0.0447**	0.6207	0.1947	**0.0028**	0.8808	**0.0446**	0.0774	1.0000	

*probabilities in bold are significant at the $p < .05$ level

Table 6.14: Probabilities* from Tukey Honest Significant Difference post hoc test of distal extent of third trochanter index.

	Dendrogale melanura	*Dendrogale murina*	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
D. melanura		1.0000	0.8061	1.0000	0.9999	0.9816	1.0000	0.9923	1.0000	1.0000	0.9576	0.8202
D. murina	1.0000		0.3493	0.9987	0.9807	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	0.9965
P. lowii	0.8061	0.3493		0.0541	0.9987	**0.0016**	**0.0340**	**0.0110**	0.8086	**0.0015**	**0.0001**	**0.0001**
T. glis	1.0000	0.9987	0.0541		0.9996	0.3256	0.9997	0.6606	1.0000	0.6657	**0.0021**	**0.0003**
T. gracilis	0.9999	0.9807	0.9987	0.9996		0.6121	0.9929	0.7309	0.9999	0.9153	0.4415	0.2337
T. javanica	0.9816	1.0000	**0.0016**	0.3256	0.6121		0.8016	1.0000	0.9810	0.9824	1.0000	1.0000
T. minor	1.0000	1.0000	**0.0340**	0.9997	0.9929	0.8016		0.9417	1.0000	0.9988	0.2394	**0.0437**
T. montana	0.9923	1.0000	**0.0110**	0.6606	0.7309	1.0000	0.9417		0.9921	0.9980	1.0000	1.0000
T. nicobarica	1.0000	1.0000	0.8086	1.0000	0.9999	0.9810	1.0000	0.9921		1.0000	0.9566	0.8176
T. palawanensis	1.0000	1.0000	**0.0015**	0.6657	0.9153	0.9824	0.9988	0.9980	1.0000		0.6687	0.1762
T. tana	0.9576	1.0000	**0.0001**	**0.0021**	0.4415	1.0000	0.2394	1.0000	0.9566	0.6687		0.9970
U. everetti	0.8202	0.9965	**0.0001**	**0.0003**	0.2337	1.0000	**0.0437**	1.0000	0.8176	0.1762	0.9970	

*probabilities in bold are significant at the $p < .05$ level

tupaiines like *T. minor* (Fig. 6.17; Tables 6.5, 6.27) is likely retained from the terrestrial tupaiine ancestor.

Comparisons to non-archontan models are difficult for this feature because the third trochanter has been lost in didelphids, *Dromiciops*, and other australidelphian marsupials (Szalay and Sargis, submitted), anthropoids (and hence guenons; Gebo and Sargis, 1994), and, apparently, viverrids (Taylor, 1976). It is interesting that here again the third trochanter length of tupaiines and *Ptilocercus* converges on that of the leaping galagines and slow climbing lorisines, respectively (see McArdle, 1981; Gebo, 1989). Galagines, like tupaiines, require powerful extension of the thigh by the gluteus superficialis muscle, but galagines require this for leaping rather than terrestrial running. On the other hand, lorisines do not require powerful extension of the thigh by the gluteus superficialis muscle in their specialized slow climbing form of locomotion. I should point out, however, that by making this comparison between lorisines and *Ptilocercus*, I am in no way implying that *Ptilocercus* is a specialized slow climber, only that it probably uses a slower form of arboreal quadrupedalism than the faster terrestrial quadrupedalism of tupaiines. The ancestral archontan was probably *Ptilocercus*-like in its third trochanter morphology because this feature is also small in *Microcebus* and plesiadapiforms, and it is very small or absent in dermopterans and chiropterans (Table 6.6). While the third trochanter of *Ptilocercus* appears to be placed more proximally on the femur than that of several tupaiines (Fig. 6.18; Tables 6.14, 6.27), this is more likely the result of the difficulty in finding a homologous point for measurement on the extremely small third trochanter of *Ptilocercus* (see Figs. 2.2, 6.14).

The medial and lateral femoral condyles of *Ptilocercus* are relatively shallow (anteroposteriorly), while those of tupaiines are relatively deep (Figs. 6.19-6.23; Tables 6.5, 6.15-6.16, 6.27). For the medial condyle depth indices, *Ptilocercus* is significantly different from every tupaiine species except for the single specimen of *T. nicobarica* (Figs. 6.19-6.20; Table 6.15), and is significantly different from every tupaiine species for the lateral condyle depth indices (Figs. 6.21-6.22; Table 6.16). The deeper condyles of tupaiines act to increase the moment arm of the tendon of the quadriceps femoris muscle, an extensor of the leg, which, in turn, increases the leverage and mechanical advantage of the quadriceps femoris muscle for knee extension (see Kappelman, 1988; Anemone, 1993). Hence, the "deep knee" of tupaiines allows more powerful extension of the knee by quadriceps femoris for propulsion during terrestrial running (see Kappelman, 1988), while the shallower knee of *Ptilocercus* is indicative of a more flexed hindlimb and a slower form of arboreal quadrupedalism in which powerful extension of the leg is less common. The condition found in *Ptilocercus* is likely primitive for Scandentia and the tupaiine condition probably evolved in response to a shift to more terrestrial locomotion during the evolutionary history of Tupaiinae. Again, a deep knee is found in the most arboreal tupaiines (Figs 6.19-6.22, Table 6.5) and is likely retained from a more terrestrial ancestral tupaiine. Among tupaiines, *Urogale* has the deepest knee (Figs. 6.19-6.22; Tables 6.15-6.16, 6.27), which may be related to the fact that *Urogale* is the most terrestrial tupaiid or it may be related to its digging behavior (see above; Wharton, 1950). Powerful extension of the knee would likely be important for digging if *Urogale* uses its hindlimbs for this behavior.

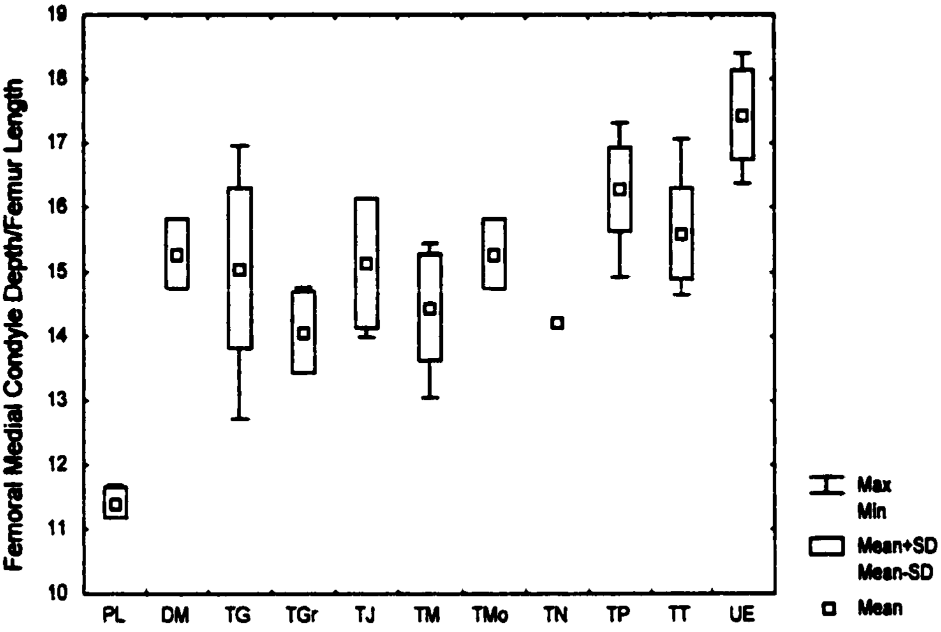


Figure 6.19. Box plot of femoral medial condyle depth index 1. Note the low index of *Ptilocercus*.

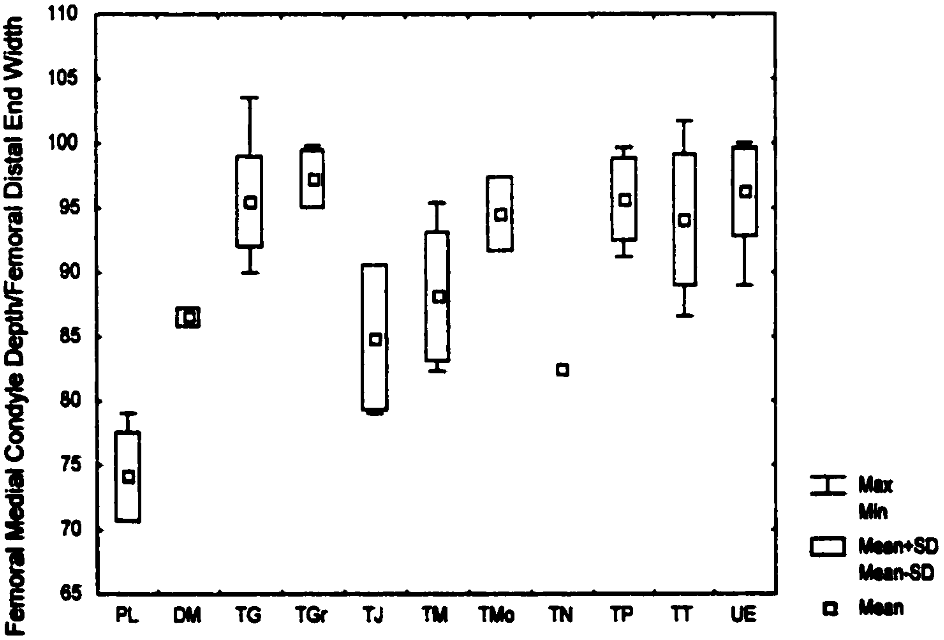


Figure 6.20. Box plot of femoral medial condyle depth index 2. Note the low index of *Ptilocercus*.

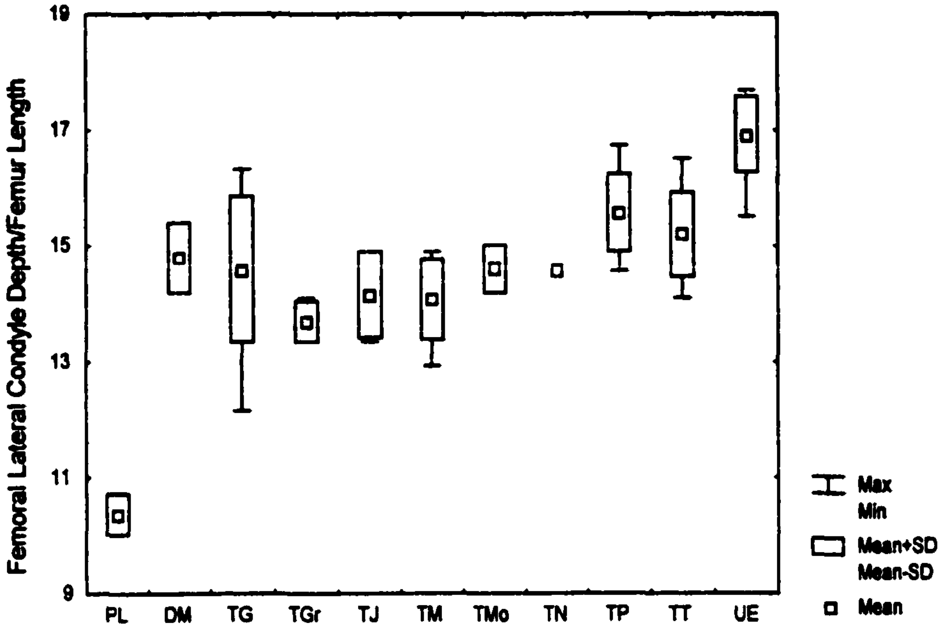


Figure 6.21. Box plot of femoral lateral condyle depth index 1. Note the low index of *Ptilocercus*.

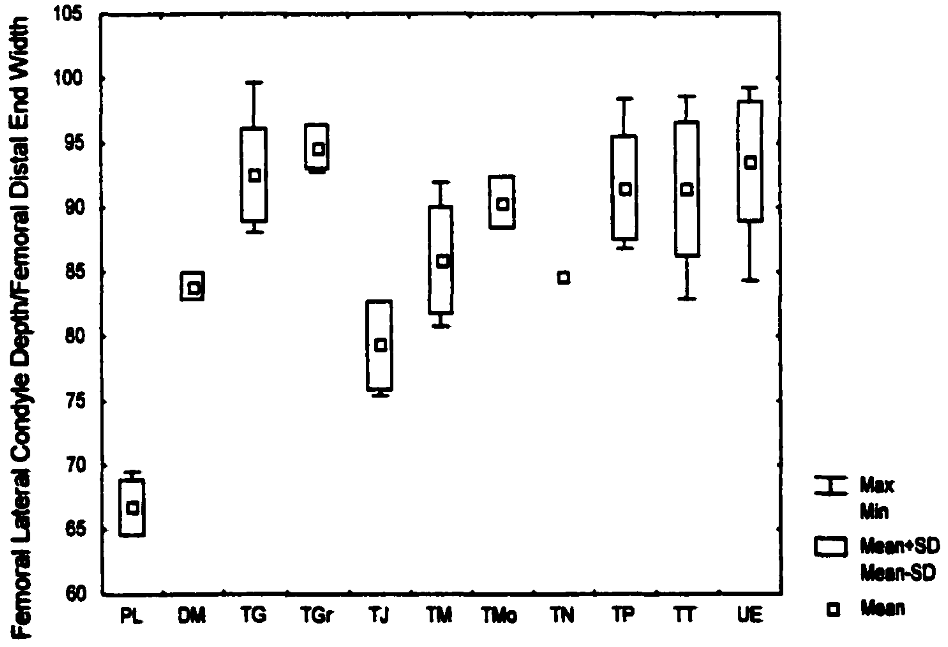


Figure 6.22. Box plot of femoral lateral condyle depth index 2. Note the low index of *Ptilocercus*.

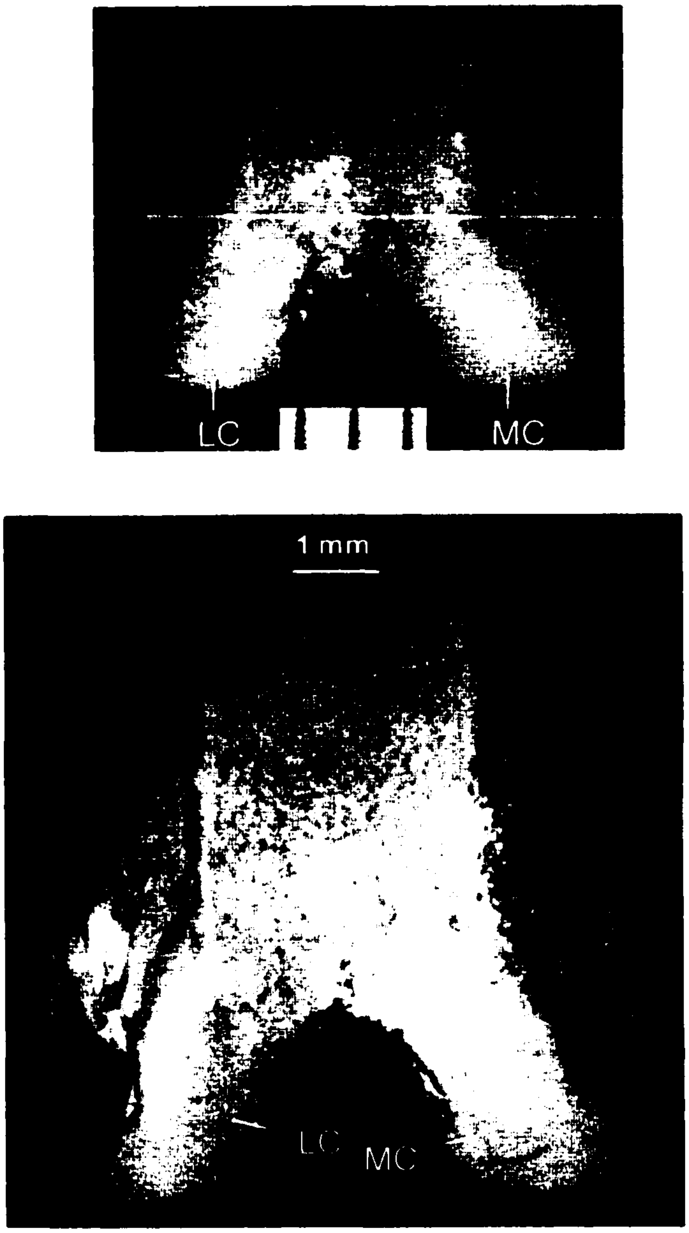


Figure 6.23. Distal view of femora of *Ptilocercus* (top) and *T. tana* (bottom). LC: lateral condyle, MC: medial condyle. Subdivisions on scale are 0.5 mm. Note the shallow condyles of *Ptilocercus*. Also note the wide medial condyle of *Ptilocercus*.

Table 6.15: Probabilities* from Tukey Honest Significant Difference (HSD) post hoc test of medial condyle depth index.

(Femoral Medial Condyle Depth/Femur Length)

	Dendrogale melanura	*Dendrogale murina*	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
D. melanura		1.0000	**0.0052**	1.0000	0.9233	1.0000	0.9791	1.0000	0.9914	0.9999	1.0000	0.7443
D. murina	1.0000		**0.0492**	1.0000	0.9997	1.0000	1.0000	1.0000	1.0000	0.9326	0.9997	0.2239
P. lowii	**0.0052**	**0.0492**		**0.0001**	**0.0212**	**0.0003**	**0.0004**	**0.0007**	0.2248	**0.0001**	**0.0001**	**0.0001**
T. glis	1.0000	1.0000	**0.0001**		0.8182	1.0000	0.9096	1.0000	0.9987	**0.0265**	0.8169	**0.0001**
T. gracilis	0.9233	0.9997	**0.0212**	0.8182		0.9467	1.0000	0.9399	1.0000	**0.0150**	0.2343	**0.0001**
T. javanica	1.0000	1.0000	**0.0003**	1.0000	0.9467		0.9923	1.0000	0.9991	0.7031	0.9994	**0.0089**
T. minor	0.9791	1.0000	**0.0004**	0.9096	1.0000	0.9923		0.9892	1.0000	**0.0034**	0.1709	**0.0001**
T. montana	1.0000	1.0000	**0.0007**	1.0000	0.9399	1.0000	0.9892		0.9979	0.9445	1.0000	0.0907
T. nicobarica	0.9914	1.0000	0.2248	0.9987	1.0000	0.9991	1.0000	0.9979		0.5420	0.9327	**0.0407**
T. palawanensis	0.9999	0.9326	**0.0001**	**0.0265**	**0.0150**	0.7031	**0.0034**	0.9445	0.5420		0.7262	0.1177
T. tana	1.0000	0.9997	**0.0001**	0.8169	0.2343	0.9994	0.1709	1.0000	0.9327	0.7262		**0.0002**
U. everetti	0.7443	0.2239	**0.0001**	**0.0001**	**0.0001**	**0.0089**	**0.0001**	0.0907	**0.0407**	0.1177	**0.0002**	

*probabilities in bold are significant at the $p < .05$ level

(Femoral Medial Condyle Depth/Femoral Distal End Width)

	Dendrogale sp.	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
Dendrogale sp.		**0.0281**	0.1181	0.1394	1.0000	1.0000	0.6615	0.9992	0.1378	0.3270	0.0814
P. lowii	**0.0281**		**0.0002**	**0.0002**	**0.0333**	**0.0002**	**0.0002**	0.7453	**0.0002**	**0.0002**	**0.0002**
T. glis	0.1181	**0.0002**		0.9997	**0.0033**	**0.0047**	1.0000	0.0830	1.0000	0.9915	1.0000
T. gracilis	0.1394	**0.0002**	0.9997		**0.0145**	0.0571	0.9996	0.0765	0.9999	0.9699	1.0000
T. javanica	1.0000	**0.0333**	**0.0033**	**0.0145**		0.9838	0.2601	1.0000	**0.0055**	**0.0217**	**0.0024**
T. minor	1.0000	**0.0002**	**0.0047**	0.0571	0.9838		0.6667	0.9653	**0.0122**	0.0601	**0.0040**
T. montana	0.6615	**0.0002**	1.0000	0.9996	0.2601	0.6667		0.3638	1.0000	1.0000	1.0000
T. nicobarica	0.9992	0.7453	0.0830	0.0765	1.0000	0.9653	0.3638		0.0900	0.1893	0.0595
T. palawanensis	0.1378	**0.0002**	1.0000	0.9999	**0.0055**	**0.0122**	1.0000	0.0900		0.9956	1.0000
T. tana	0.3270	**0.0002**	0.9915	0.9699	**0.0217**	0.0601	1.0000	0.1893	0.9956		0.9375
U. everetti	0.0814	**0.0002**	1.0000	1.0000	**0.0024**	**0.0040**	1.0000	0.0595	1.0000	0.9375	

*probabilities in bold are significant at the $p < .05$ level

Table 6.16: Probabilities* from Tukey Honest Significant Difference (HSD) post hoc test of lateral condyle depth index.

(Femoral Lateral Condyle Depth/Femur Length)

	Dendrogale melanura	*Dendrogale murina*	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
D. melanura		0.9999	**0.0005**	0.9999	0.9262	0.9949	0.9825	1.0000	1.0000	1.0000	1.0000	0.7657
D. murina	0.9999		**0.0075**	1.0000	0.9999	1.0000	1.0000	1.0000	1.0000	0.9740	0.9987	0.1979
P. lowii	**0.0005**	**0.0075**		**0.0001**	**0.0008**	**0.0002**	**0.0001**	**0.0002**	**0.0038**	**0.0001**	**0.0001**	**0.0001**
T. glis	0.9999	1.0000	**0.0001**		0.8747	0.9996	0.9655	1.0000	1.0000	0.1367	0.6360	**0.0001**
T. gracilis	0.9262	0.9999	**0.0008**	0.8747		1.0000	1.0000	0.9902	0.9989	0.0584	0.2156	**0.0001**
T. javanica	0.9949	1.0000	**0.0002**	0.9996	1.0000		1.0000	1.0000	1.0000	0.3470	0.7340	**0.0005**
T. minor	0.9825	1.0000	**0.0001**	0.9655	1.0000	1.0000		0.9997	1.0000	**0.0285**	0.1669	**0.0001**
T. montana	1.0000	1.0000	**0.0002**	1.0000	0.9902	1.0000	0.9997		1.0000	0.9500	0.9988	**0.0391**
T. nicobarica	1.0000	1.0000	**0.0038**	1.0000	0.9989	1.0000	1.0000	1.0000		0.9945	0.9999	0.3119
T. palawanensis	1.0000	0.9740	**0.0001**	0.1367	0.0584	0.3470	**0.0285**	0.9500	0.9945		0.9945	**0.0227**
T. tana	1.0000	0.9987	**0.0001**	0.6360	0.2156	0.7340	0.1669	0.9988	0.9999	0.9945		**0.0003**
U. everetti	0.7657	0.1979	**0.0001**	**0.0001**	**0.0001**	**0.0005**	**0.0001**	**0.0391**	0.3119	**0.0227**	**0.0003**	

*probabilities in bold are significant at the p < .05 level

(Femoral Lateral Condyle Depth/Femoral Distal End Width)

	Dendrogale melanura	*Dendrogale murina*	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
D. melanura		1.0000	**0.0128**	0.7832	0.6258	0.9937	1.0000	0.9917	1.0000	0.9106	0.9083	0.6538
D. murina	1.0000		**0.0327**	0.5553	0.4157	0.9997	1.0000	0.9534	1.0000	0.7421	0.7350	0.4212
P. lowii	**0.0128**	**0.0327**		**0.0001**	**0.0001**	**0.0087**	**0.0001**	**0.0001**	**0.0125**	**0.0001**	**0.0001**	**0.0001**
T. glis	0.7832	0.5553	**0.0001**		0.9995	**0.0003**	**0.0253**	0.9999	0.7878	0.9999	0.9996	1.0000
T. gracilis	0.6258	0.4157	**0.0001**	0.9995		**0.0015**	0.1084	0.9924	0.6306	0.9883	0.9810	1.0000
T. javanica	0.9937	0.9997	**0.0087**	**0.0003**	**0.0015**		0.5050	0.1571	0.9933	**0.0017**	**0.0010**	**0.0002**
T. minor	1.0000	1.0000	**0.0001**	**0.0253**	0.1084	0.5050		0.9656	1.0000	0.2039	0.1395	**0.0138**
T. montana	0.9917	0.9534	**0.0001**	0.9999	0.9924	0.1571	0.9656		0.9921	1.0000	1.0000	0.9977
T. nicobarica	1.0000	1.0000	**0.0125**	0.7878	0.6306	0.9933	1.0000	0.9921		0.9133	0.9111	0.6590
T. palawanensis	0.9106	0.7421	**0.0001**	0.9999	0.9883	**0.0017**	0.2039	1.0000	0.9133		1.0000	0.9896
T. tana	0.9083	0.7350	**0.0001**	0.9996	0.9810	**0.0010**	0.1395	1.0000	0.9111	1.0000		0.9712
U. everetti	0.6538	0.4212	**0.0001**	1.0000	1.0000	**0.0002**	**0.0138**	0.9977	0.6590	0.9896	0.9712	

*probabilities in bold are significant at the p < .05 level

Here again, tupaiines and *Ptilocercus* converge on the leaping galagines and slow climbing lorisines, respectively, although their similarities are related to different biological roles. Galagines are characterized by deep knees, while lorisines are characterized by shallow knees (McArdle, 1981; Gebo, 1989; Anemone, 1993). Galagines require powerful extension of the leg by quadriceps femoris during leaping, while lorisines do not require this for slow climbing. The relationship between depth of the knee and substrate preference seen in tupaiids is also found in viverrids (Taylor, 1976), as well as in marsupials (Szalay and Sargis, submitted). In fact, the terrestrial caenolestids have taken the deepening of the knee to an extreme, in that they are one of the few marsupial groups to have evolved a patella (a bone that is usually absent in marsupials; Szalay and Sargis, submitted). The patella acts to further deepen the knee and further increase the moment arm of the quadriceps femoris muscle, which further increases the leverage and mechanical advantage of this muscle for knee extension (Szalay and Sargis, submitted). The patella of caenolestids, therefore, allows more powerful extension of the knee by quadriceps femoris for propulsion during terrestrial running. The evolution of the patella in eutherians was also likely related to terrestrial locomotion and the presence of a patella in all eutherians likely represents a retention from the terrestrial ancestral eutherian (see Szalay, 1984, 1994; Szalay and Sargis, submitted).

The shallow knee of *Ptilocercus* is probably primitive for Archonta as this condition is also found in plesiadapiforms, dermopterans, and chiropterans (Table 6.6). The deep knee of early euprimates, however, is derived and likely evolved in response to their specialized graspleaping locomotion (see Szalay and Dagosto, 1980, 1988; Dagosto, 1988; Szalay and Lucas, 1996).

In *Ptilocercus*, the medial femoral condyle is slightly wider than the lateral condyle, while the lateral condyle of tupaiines is slightly wider than the medial condyle (Figs. 6.23-6.24, 6.26; Table 6.27). The femoral condyle width index of *Ptilocercus* is significantly different from that of several tupaiines (Table 6.17), and the wider medial condyle of *Ptilocercus* may reflect greater loads incurred medially in the knee during the flexed, abducted hindlimb postures used during arboreal locomotion. More importantly, all tupaiids have medial and lateral femoral condyles that are very similar in width. This is in sharp contrast to the (probably primitive therian) condition seen in marsupials where the lateral condyle is much wider than the medial condyle (Szalay and Trofimov, 1996; Muizon, 1998; Szalay and Sargis, submitted). Only terrestrial marsupials approach the condition seen in tupaiids, in that terrestrial marsupials have a relatively narrowed lateral condyle and a widened medial condyle compared to their arboreal relatives (Szalay and Trofimov, 1996; Muizon, 1998; Szalay and Sargis, submitted). This transformation is likely related to the less abducted hindlimb of terrestrial marsupials, and the fact that the crus is more in line with the femur during the more parasagittal movements of the hindlimb associated with terrestrial locomotion (Szalay and Sargis, submitted). Hence, it seems likely that the ancestral eutherian evolved femoral condyles that are essentially equal in width (compared to the unequal condition found in marsupials) for more efficiency in terrestrial locomotion, especially when one considers that most eutherians are like tupaiids in possessing femoral condyles that are nearly equal in width and that this condition is found only in terrestrial taxa among marsupials (Szalay and Sargis,

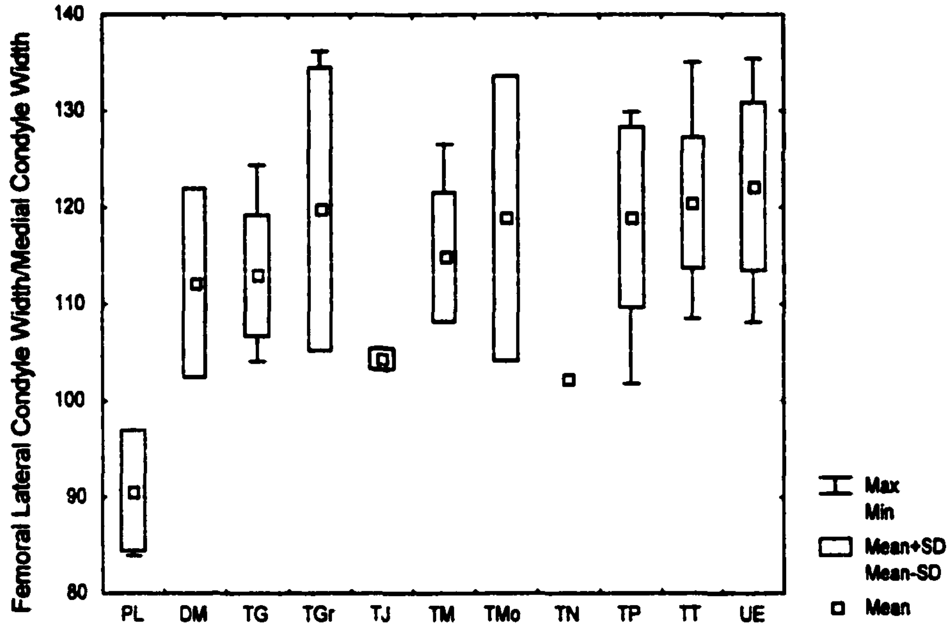


Figure 6.24. Box plot of femoral condyle width index. Note the low index of *Ptilocercus*.

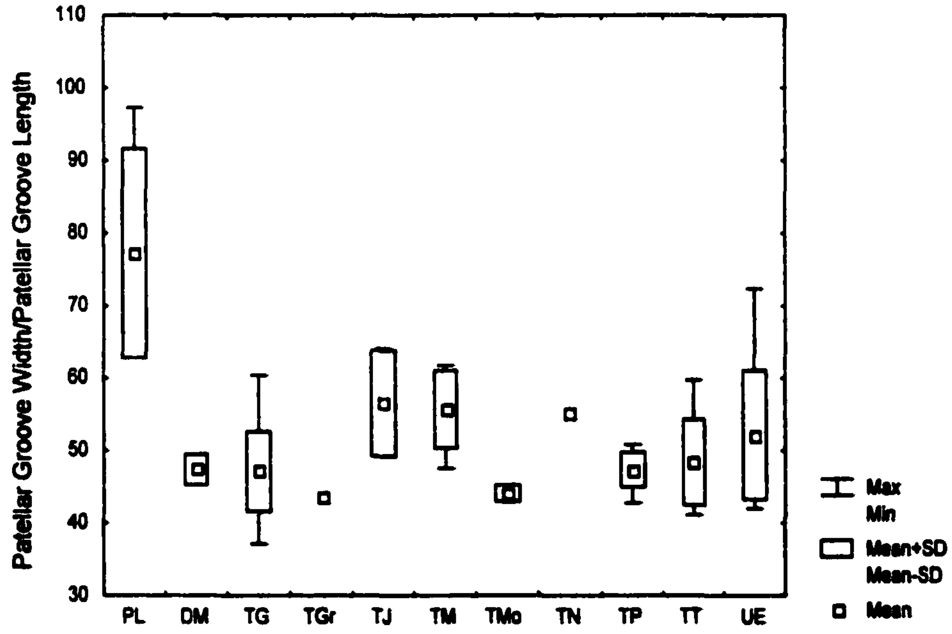


Figure 6.25. Box plot of patellar groove shape index. Note the high index of *Ptilocercus*.

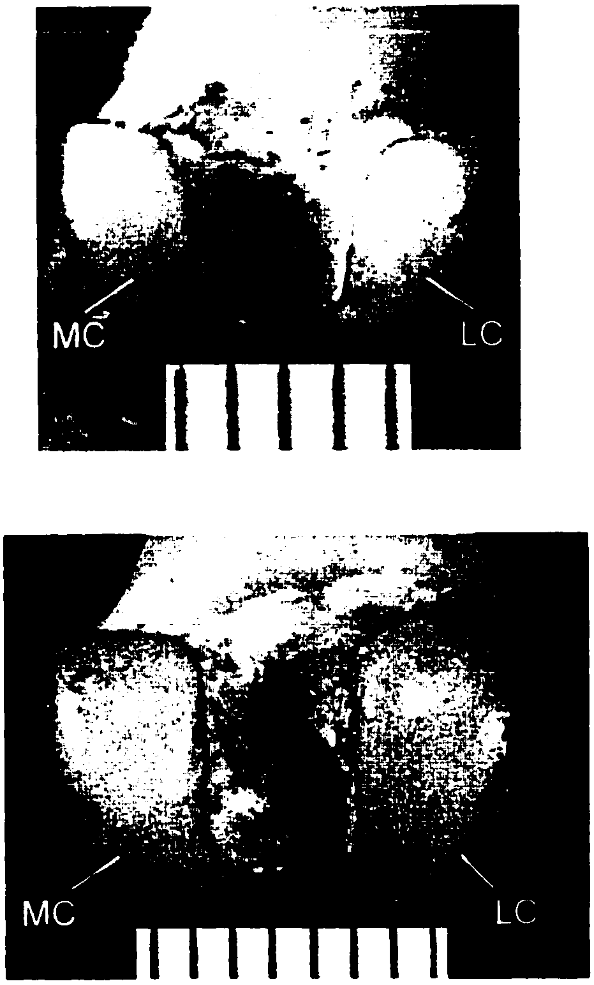


Figure 6.26. Distal femora (posterior view) of *Ptilocercus* (top) and *T. tana* (bottom). LC: lateral condyle, MC: medial condyle. Subdivisions on scale are 0.5 mm. Note the wide medial condyle of *Ptilocercus*.

Table 6.17: Probabilities* from Tukey Honest Significant Difference (HSD) post hoc test of femoral condyle width index.

	Dendrogale melanura	*Dendrogale murina*	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
D. melanura		0.9829	0.8664	0.9984	0.9025	1.0000	0.9917	0.9558	1.0000	0.8752	0.7737	0.6500
D. murina	0.9829		0.0683	0.9998	1.0000	0.8873	1.0000	1.0000	0.9275	1.0000	1.0000	1.0000
P. lowii	0.8664	0.0683		**0.0002**	**0.0005**	0.4863	**0.0004**	**0.0045**	0.9714	**0.0001**	**0.0001**	**0.0001**
T. glis	0.9984	0.9998	**0.0002**		0.9561	0.8262	1.0000	0.9963	0.9717	0.6614	0.1808	0.0969
T. gracilis	0.9025	1.0000	**0.0005**	0.9561		0.4026	0.9987	1.0000	0.7264	1.0000	1.0000	1.0000
T. javanica	1.0000	0.8873	0.4863	0.8262	0.4026		0.7209	0.6596	1.0000	0.1712	0.0656	**0.0353**
T. minor	0.9917	1.0000	**0.0004**	1.0000	0.9987	0.7209		1.0000	0.9328	0.9941	0.9128	0.7304
T. montana	0.9558	1.0000	**0.0045**	0.9963	1.0000	0.6596	1.0000		0.8415	1.0000	1.0000	1.0000
T. nicobarica	1.0000	0.9275	0.9714	0.9717	0.7264	1.0000	0.9328	0.8415		0.6579	0.5174	0.3927
T. palawanensis	0.8752	1.0000	**0.0001**	0.6614	1.0000	0.1712	0.9941	1.0000	0.6579		1.0000	0.9981
T. tana	0.7737	1.0000	**0.0001**	0.1808	1.0000	0.0656	0.9128	1.0000	0.5174	1.0000		1.0000
U. everetti	0.6500	1.0000	**0.0001**	0.0969	1.0000	**0.0353**	0.7304	1.0000	0.3927	0.9981	1.0000	

*probabilities in bold are significant at the p < .05 level

Table 6.18: Probabilities* from Tukey Honest Significant Difference (HSD) post hoc test of patellar groove shape index.

	Dendrogale melanura	*Dendrogale murina*	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
D. melanura		1.0000	**0.0161**	1.0000	1.0000	0.9976	0.9981	1.0000	0.9999	1.0000	1.0000	1.0000
D. murina	1.0000		**0.0047**	1.0000	1.0000	0.9644	0.9636	1.0000	0.9977	1.0000	1.0000	0.9992
P. lowii	**0.0161**	**0.0047**		**0.0001**	**0.0016**	**0.0070**	**0.0003**	**0.0001**	0.1468	**0.0001**	**0.0001**	**0.0001**
T. glis	1.0000	1.0000	**0.0001**		1.0000	0.5121	0.1604	1.0000	0.9887	1.0000	1.0000	0.7329
T. gracilis	1.0000	1.0000	**0.0016**	1.0000		0.8642	0.8502	1.0000	0.9831	1.0000	0.9999	0.9843
T. javanica	0.9976	0.9644	**0.0070**	0.5121	0.8642		1.0000	0.6583	1.0000	0.6080	0.7181	0.9964
T. minor	0.9981	0.9636	**0.0003**	0.1604	0.8502	1.0000		0.5601	1.0000	0.2865	0.3831	0.9905
T. montana	1.0000	1.0000	**0.0001**	1.0000	1.0000	0.6583	0.5601		0.9659	1.0000	0.9994	0.9161
T. nicobarica	0.9999	0.9977	0.1468	0.9887	0.9831	1.0000	1.0000	0.9659		0.9919	0.9970	1.0000
T. palawanensis	1.0000	1.0000	**0.0001**	1.0000	1.0000	0.6080	0.2865	1.0000	0.9919		1.0000	0.8741
T. tana	1.0000	1.0000	**0.0001**	1.0000	0.9999	0.7181	0.3831	0.9994	0.9970	1.0000		0.9527
U. everetti	1.0000	0.9992	**0.0001**	0.7329	0.9843	0.9964	0.9905	0.9161	1.0000	0.8741	0.9527	

*probabilities in bold are significant at the p < .05 level

submitted). In other words, like the presence of the patella in eutherians, the presence of femoral condyles that are almost equal in width is likely retained from a terrestrial eutherian ancestor (see Szalay, 1984, 1994; Szalay and Trofimov, 1996; Szalay and Sargis, submitted).

The patellar groove of *Ptilocercus* is short and relatively wide, while that of tupaiines is longer and narrower (Figs. 6.25, 6.27; Tables 6.5, 6.27). The patellar groove shape index of *Ptilocercus* is significantly different from every tupaiine species except for the single specimen of *T. nicobarica* (Table 6.18). Again, this may indicate that *T. nicobarica* is arboreal like *Ptilocercus*, but more likely is the result of the extremely small sample of *T. nicobarica* because this species is similar to other tupaiines in its patellar groove morphology (Fig. 6.25). The tupaiine condition is likely related to extensive excursions of the knee (Beard, 1989) during fast terrestrial running, while the condition seen in *Ptilocercus* may be related to a slower form of quadrupedalism and climbing as it is also seen in lorisines (see Beard, 1989). The tupaiine condition is found even in the arboreal *T. minor* (Table 6.5), which is yet another indication of the terrestrial heritage of Tupaiinae.

Despite the fact that didelphids lack a patella, the groove for the tendon of the quadriceps femoris muscle is narrower, like that of tupaiines, in the terrestrial *Metachirus*, while it is wider, like that of *Ptilocercus*, in the arboreal *Caluromys* (Szalay and Sargis, submitted). The patellar groove is also narrower in terrestrial guenons than in arboreal guenons (Gebo and Sargis, 1994), and it is wider in arboreal viverrids than in terrestrial viverrids (Taylor, 1976). The condition seen in *Ptilocercus* may be primitive for Tupaiidae, as well as Archonta. A short, wide patellar groove is also found in

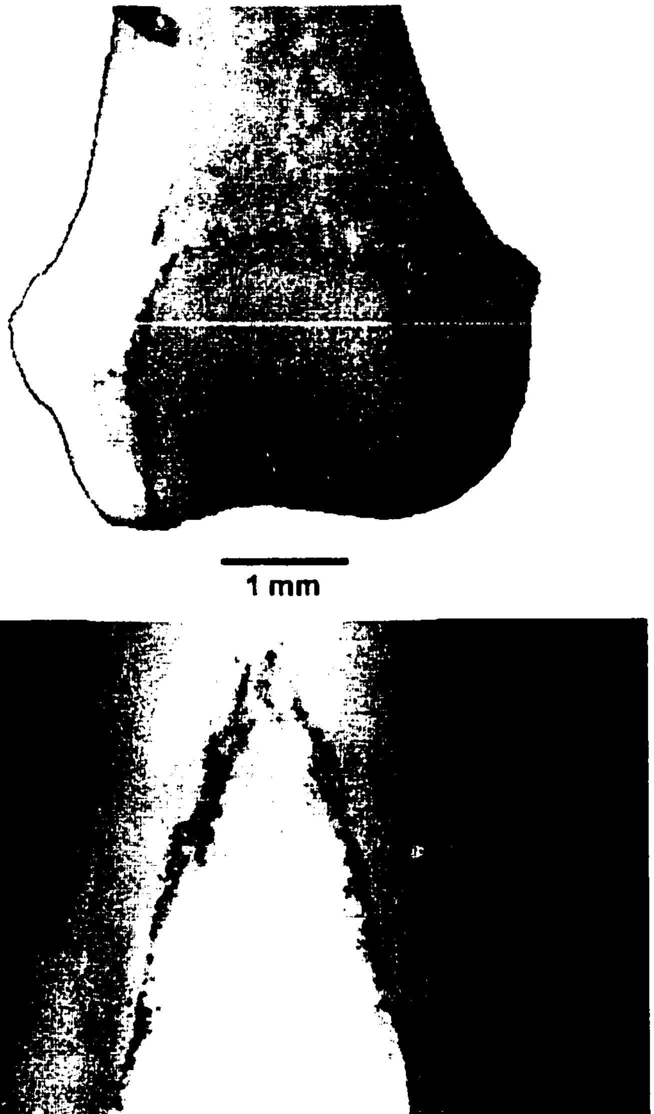


Figure 6.27. Distal femora of *Ptilocercus* (top) and *T. tana* (bottom). Note the short, wide patellar groove of *Ptilocercus*.

dermopterans and plesiadapiforms (Table 6.6; see Fig. 7.6; Beard, 1993b, fig. 10.11). The (derived) patellar groove of the ancestral euprimate, on the other hand, was likely elongated and deepened in response to graspleaping locomotion (see Szalay and Dagosto, 1980, 1988; Dagosto, 1988; Szalay and Lucas, 1996). This will be discussed further in the character analysis in chapter 7. A cluster analysis of the variables included in ten femoral indices shows that *Ptilocercus* is very different from tupaiines in its femoral morphology (Fig. 6.28).

Tibia

The length of the tibial crest is relatively longer in *Ptilocercus* and *D. melanura* than in other tupaiids (Fig. 6.29; Tables 6.19, 6.27). This feature is difficult to evaluate, especially in *D. melanura* because this species is represented by only a single specimen. The structure of the tibial crest is also different in these two taxa, as *Ptilocercus* has a poorly defined crest and *D. melanura* has a well defined, sharp crest like that of other tupaiines (Fig. 6.30). The increased length of the crest in *Ptilocercus* may provide a larger area of attachment for the tibialis anterior muscle, an invertor of the foot, but the interpretation of the length of the crest is confounded by its poor development in *Ptilocercus*.

The proximal tibia of *Ptilocercus* is relatively shallower (anteroposteriorly) than that of several tupaiines (Fig. 6.31, 6.33; Tables 6.20, 6.27). This difference is the result of the relatively large tibial tuberosity present in tupaiines (Fig. 6.33), which is certainly related to the large anterior inferior iliac spine present in these taxa (see above). The rectus femoris muscle, an extensor of the leg that originates from the anterior inferior iliac spine, inserts (with the rest of the quadriceps femoris muscles) directly into the

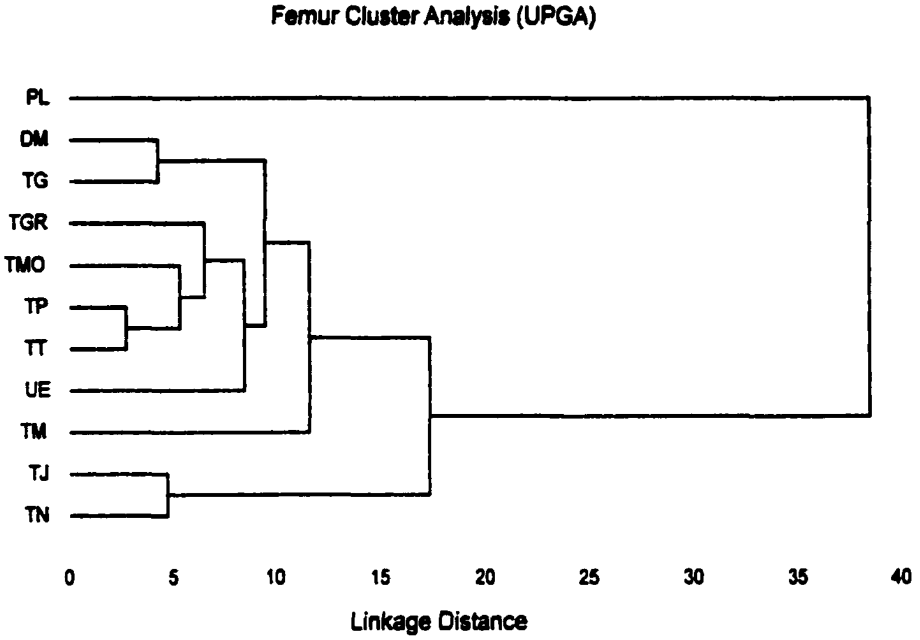


Figure 6.28. Cluster analysis of the variables included in ten femoral indices. Note the difference between *Ptilocercus* and the tupaiines.

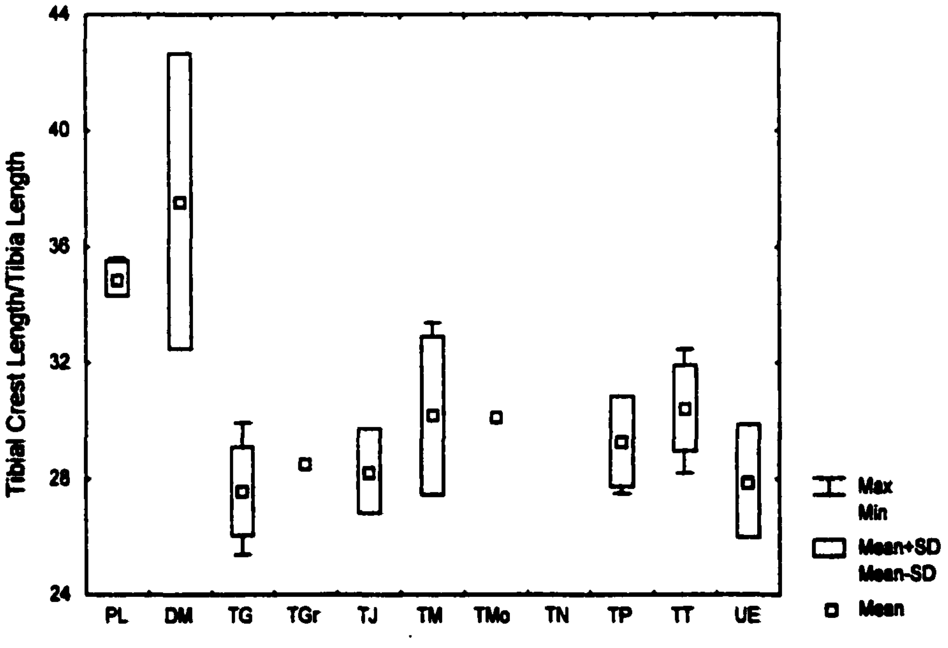


Figure 6.29. Box plot of tibial crest length index. Note the high indices of *Ptilocercus* and *Dendrogale*.

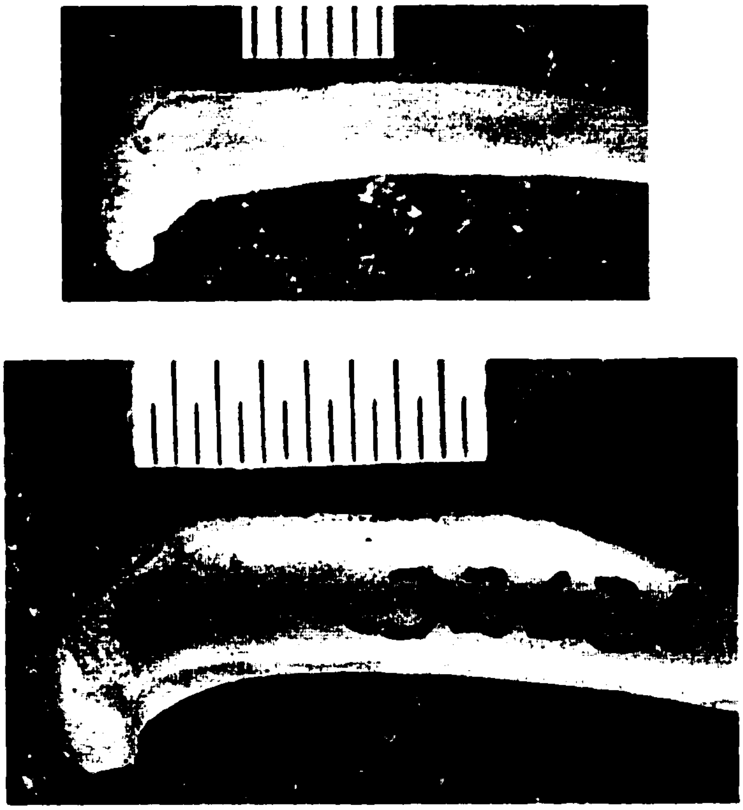


Figure 6.30. Proximal tibiae (lateral view) of *Ptilocercus* (top) and *T. tana* (bottom). Subdivisions on scale are 0.5 mm. Note the poorly defined tibial crest of *Ptilocercus*.

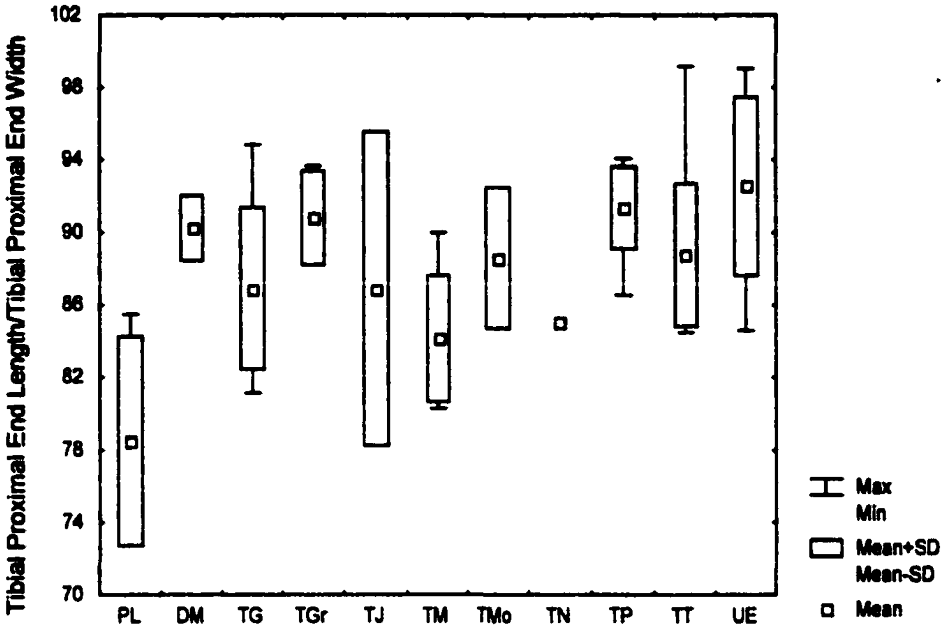


Figure 6.31. Box plot of tibial proximal end shape index. Note the low index of *Ptilocercus*.

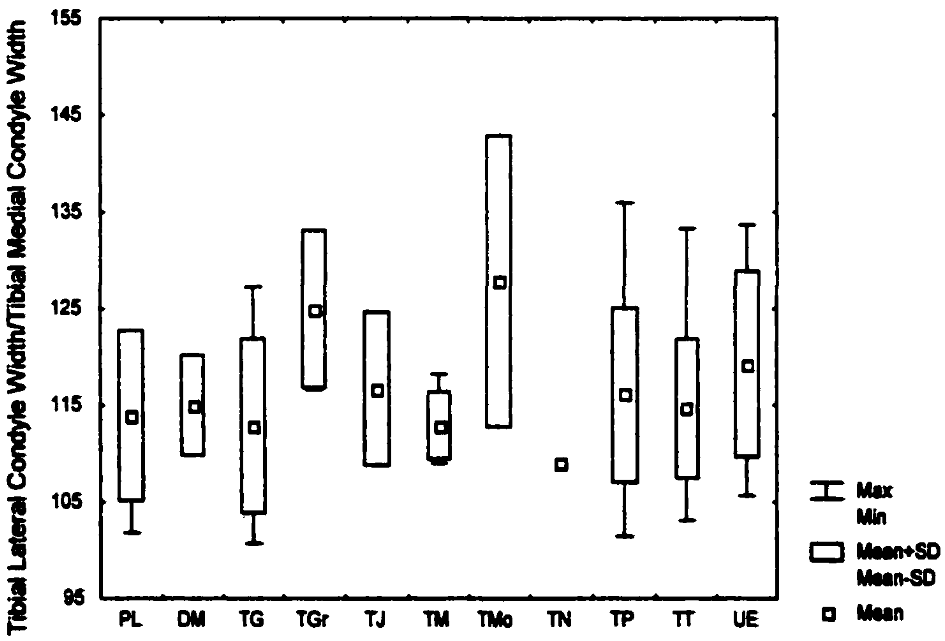


Figure 6.32. Box plot of tibial condyle width index.

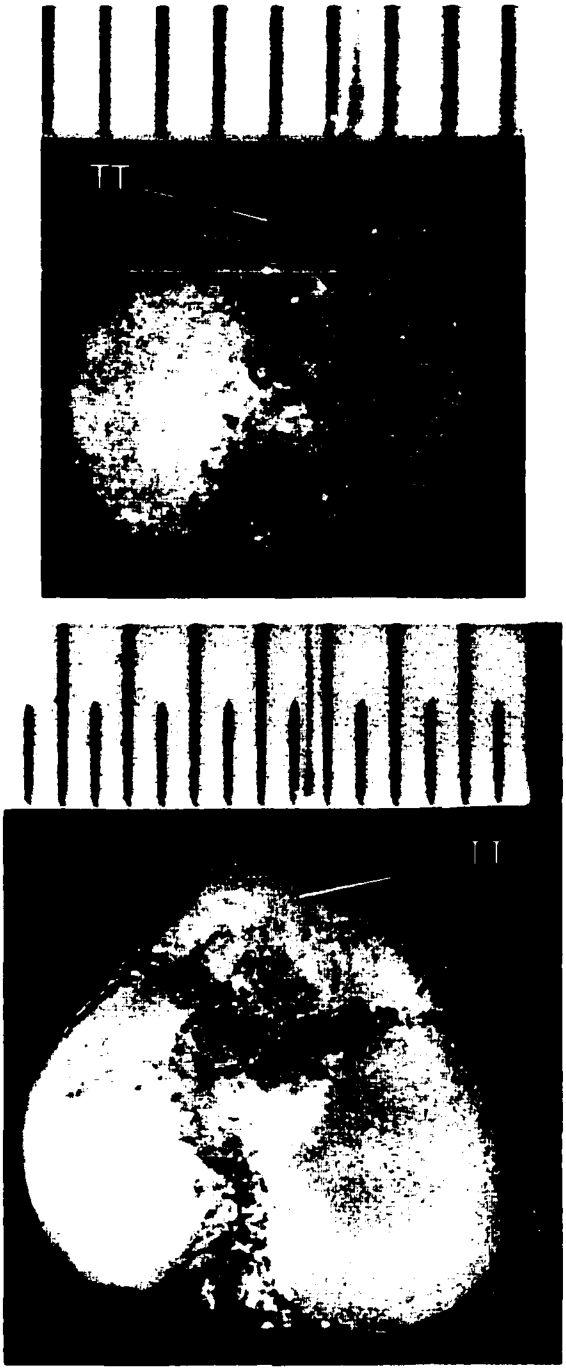


Figure 6.33. Proximal view of tibiae of *Ptilocercus* (top) and *T. tana* (bottom). TT: tibial tuberosity. Subdivisions on scale are 0.5 mm. Note the small tibial tuberosity of *Ptilocercus*.

Table 6.19: Probabilities* from Tukey Honest Significant Difference (HSD) post hoc test of tibial crest length index.

	Dendrogale melanura	*Dendrogale murina*	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
D. melanura		0.1480	0.1006	**0.0001**	**0.0007**	**0.0002**	**0.0003**	**0.0037**	**0.0002**	**0.0002**	**0.0002**
D. murina	0.1480		1.0000	**0.0428**	0.4850	0.2345	0.6693	0.8827	0.4163	0.6765	0.1716
P. lowii	0.1006	1.0000		**0.0002**	0.0837	**0.0076**	**0.0365**	0.3889	**0.0135**	**0.0157**	**0.0043**
T. glis	**0.0001**	**0.0428**	**0.0002**		1.0000	1.0000	0.3194	0.9380	0.9138	**0.0335**	1.0000
T. gracilis	**0.0007**	0.4850	0.0837	1.0000		1.0000	0.9984	0.9999	1.0000	0.9911	1.0000
T. javanica	**0.0002**	0.2345	**0.0076**	1.0000	1.0000		0.9646	0.9982	0.9999	0.8531	1.0000
T. minor	**0.0003**	0.6693	**0.0365**	0.3194	0.9984	0.9646		1.0000	0.9998	1.0000	0.8984
T. montana	**0.0037**	0.8827	0.3889	0.9380	0.9999	0.9982	1.0000		1.0000	1.0000	0.9921
T. palawanensis	**0.0002**	0.4163	**0.0135**	0.9138	1.0000	0.9999	0.9998	1.0000		0.9941	0.9984
T. tana	**0.0002**	0.6765	**0.0157**	**0.0335**	0.9911	0.8531	1.0000	1.0000	0.9941		0.7059
U. everetti	**0.0002**	0.1716	**0.0043**	1.0000	1.0000	1.0000	0.8984	0.9921	0.9984	0.7059	

*probabilities in bold are significant at the $p < .05$ level

Table 6.20: Probabilities* from Tukey Honest Significant Difference (HSD) post hoc test of tibial proximal end shape index.

	Dendrogale melanura	*Dendrogale murina*	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
D. melanura		1.0000	0.5444	1.0000	1.0000	1.0000	0.9955	1.0000	0.9999	1.0000	1.0000	0.9995
D. murina	1.0000		0.2185	0.9947	1.0000	0.9989	0.8918	1.0000	0.9936	1.0000	1.0000	1.0000
P. lowii	0.5444	0.2185		**0.0302**	**0.0150**	0.4847	0.6427	0.2230	0.9635	**0.0003**	**0.0029**	**0.0001**
T. glis	1.0000	0.9947	**0.0302**		0.9396	1.0000	0.9647	1.0000	1.0000	0.2720	0.9797	**0.0387**
T. gracilis	1.0000	1.0000	**0.0150**	0.9396		0.9969	0.5318	1.0000	0.9877	1.0000	0.9997	1.0000
T. javanica	1.0000	0.9989	0.4847	1.0000	0.9969		0.9996	1.0000	1.0000	0.9669	1.0000	0.8378
T. minor	0.9955	0.8918	0.6427	0.9647	0.5318	0.9996		0.9777	1.0000	0.0623	0.4968	**0.0103**
T. montana	1.0000	1.0000	0.2230	1.0000	1.0000	1.0000	0.9777		0.9999	0.9994	1.0000	0.9837
T. nicobarica	0.9999	0.9936	0.9635	1.0000	0.9877	1.0000	1.0000	0.9999		0.9511	0.9993	0.8507
T. palawanensis	1.0000	1.0000	**0.0003**	0.2720	1.0000	0.9669	0.0623	0.9994	0.9511		0.9269	0.9999
T. tana	1.0000	1.0000	**0.0029**	0.9797	0.9997	1.0000	0.4968	1.0000	0.9993	0.9269		0.4760
U. everetti	0.9995	1.0000	**0.0001**	**0.0387**	1.0000	0.8378	**0.0103**	0.9837	0.8507	0.9999	0.4760	

*probabilities in bold are significant at the $p < .05$ level

patella, as well as into the tibial tuberosity via the quadriceps tendon. Hence, the larger (more anteriorly projecting) tibial tuberosity of tupaiines increases the lever arm of the quadriceps tendon, which increases the mechanical advantage of the quadriceps femoris muscle for extension of the knee (see Muizon, 1998; Szalay and Sargis, submitted). As was discussed above, this is likely advantageous for tupaiines, which require powerful extension of the knee by the rectus femoris muscle for propulsion during terrestrial running. This is another feature that is likely related to the terrestrial ancestry of Tupaiinae. The small size of this feature in *Ptilocercus* is, again, probably indicative of a more habitually flexed hindlimb and a slower form of arboreal locomotion. The arboreal *Caluromys* also has a relatively small tibial tuberosity, while that of the terrestrial *Metachirus* is large (Muizon, 1998; Szalay and Sargis, submitted). A similar relationship between this feature and substrate preference also exists in macropodids (Muizon, 1998) and viverrids (Taylor, 1976).

As with the femoral condyles, the tibial condyles of tupaiids are relatively similar in width (Fig. 6.32; Table 6.27), unlike the unequal widths that characterize the tibial condyles of most marsupials (see above; Szalay and Sargis, submitted). In fact, there are no significant differences between any tupaiid species for the tibial condyle width index. As was discussed above, the condition found in tupaiids and other eutherians likely reflects the terrestrial ancestry of Eutheria (see Szalay, 1984, 1994; Szalay and Sargis, submitted). The lengths of the tibial condyles are not particularly informative either (Figs. 6.34-6.35; Table 6.27). There are no significant differences between any tupaiid species for the tibial lateral condyle length index, while *T. minor* and *T. palawanensis* are significantly different from a few other tupaiines for the tibial medial condyle length

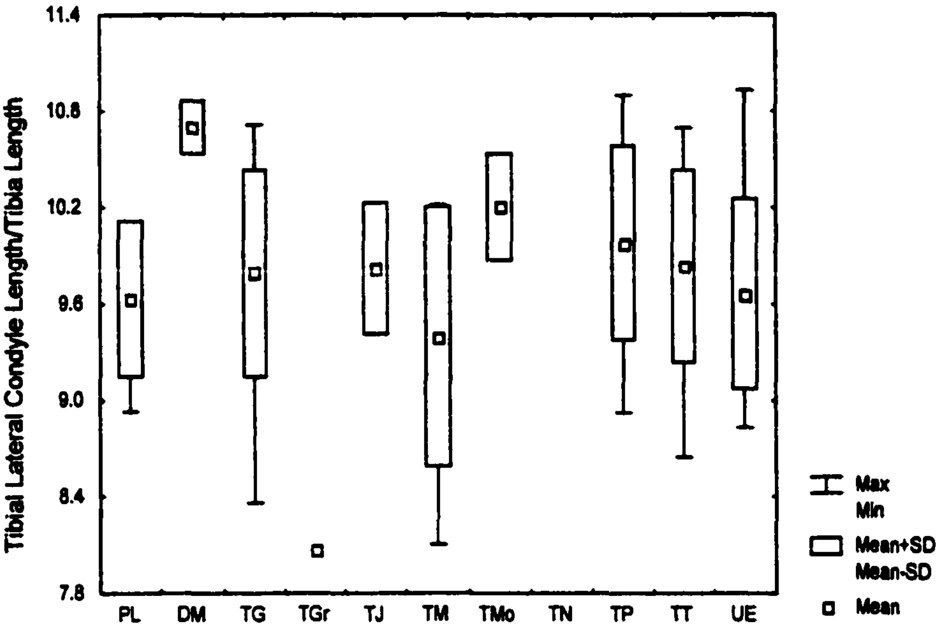


Figure 6.34. Box plot of tibial lateral condyle length index.

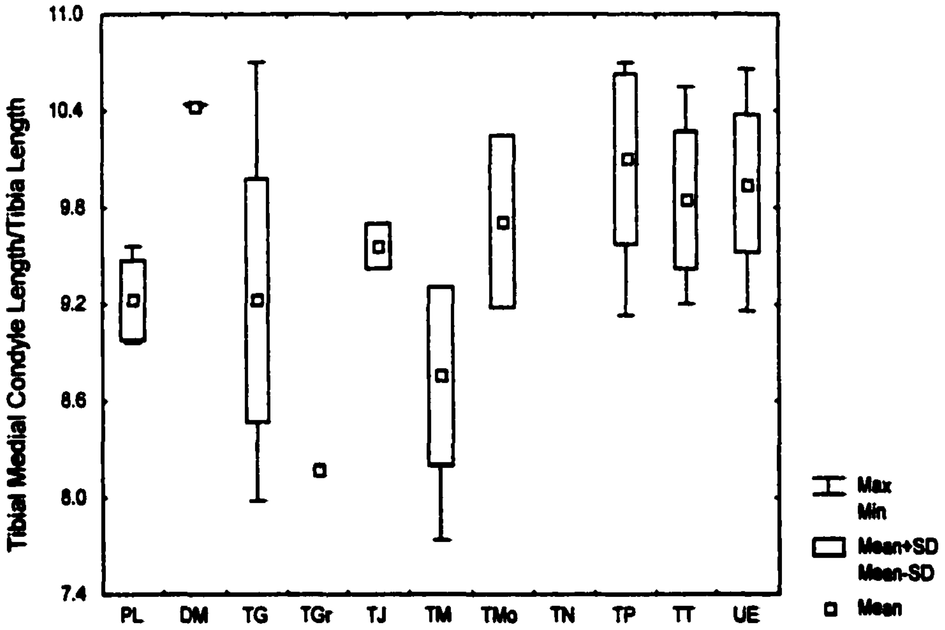


Figure 6.35. Box plot of tibial medial condyle length index.

index (Table 6.21). Hence, no clear relationship exists between these indices and substrate preference.

On the distal end of the tibia, the relative length of the medial malleolus is similar among all tupaiids (Figs. 6.36, 6.38; Table 6.27), and there are no significant differences between any tupaiid species for the tibial medial malleolus length index. This is in contrast to the condition seen in didelphid marsupials where, for instance, the medial malleolus of the arboreal *Caluromys* is relatively short, while that of the terrestrial *Metachirus* is longer (Szalay and Sargis, submitted). This is clearly related to efficiency in terrestrial locomotion because relatively long medial and lateral malleoli severely restrict mobility at the upper ankle joint so that only parasagittal movements are possible at this joint. Tupaiids and other eutherians are characterized by such a restricted upper ankle joint, and this feature, along with some discussed above, is likely retained from a terrestrial eutherian ancestor (Szalay, 1984, 1994; Szalay and Sargis, submitted).

The shape of the distal articular surface (lateral astragalar facet) is quite different in *Ptilocercus* and tupaiines (Figs. 6.37, 6.39; Table 6.27). That of *Ptilocercus* is longer than wide, while that of tupaiines is wider than long. The tibial distal articular surface shape index of *Ptilocercus* is significantly different from that of every tupaiine species except for the single specimens of *D. melanura*, *D. murina*, and *T. nicobarica*, as well as *T. javanica* (Table 6.22). *Ptilocercus* is significantly different from *Dendrogale* sp. for this index when the two *Dendrogale* species (specimens) are considered together (Table 6.23). It also seems likely that *Ptilocercus* would be significantly different from *T. nicobarica*, and possibly *T. javanica* (represented by two specimens for this index), if larger samples could be included because these taxa appear to be similar to other

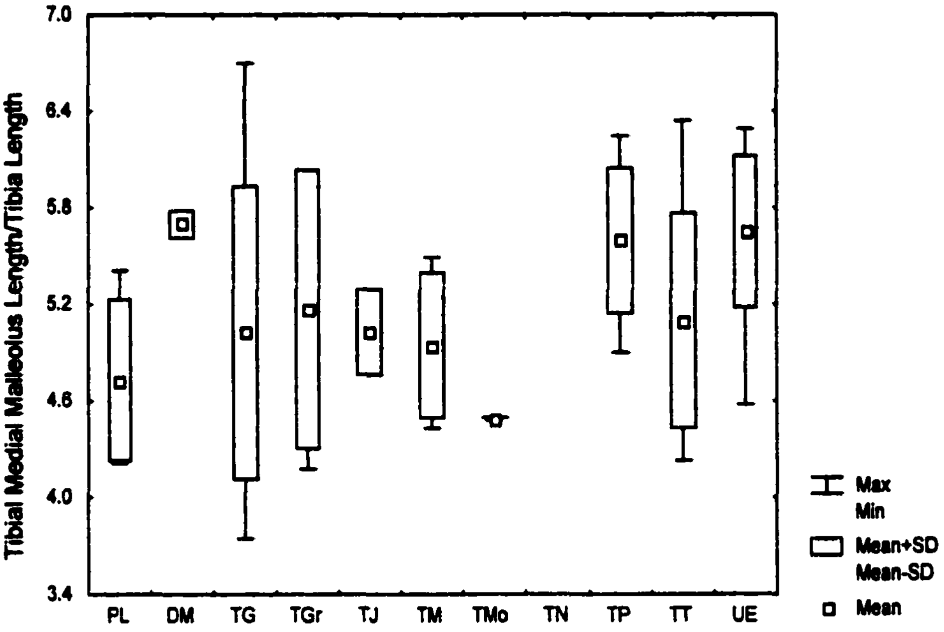


Figure 6.36. Box plot of tibial medial malleolus length index.

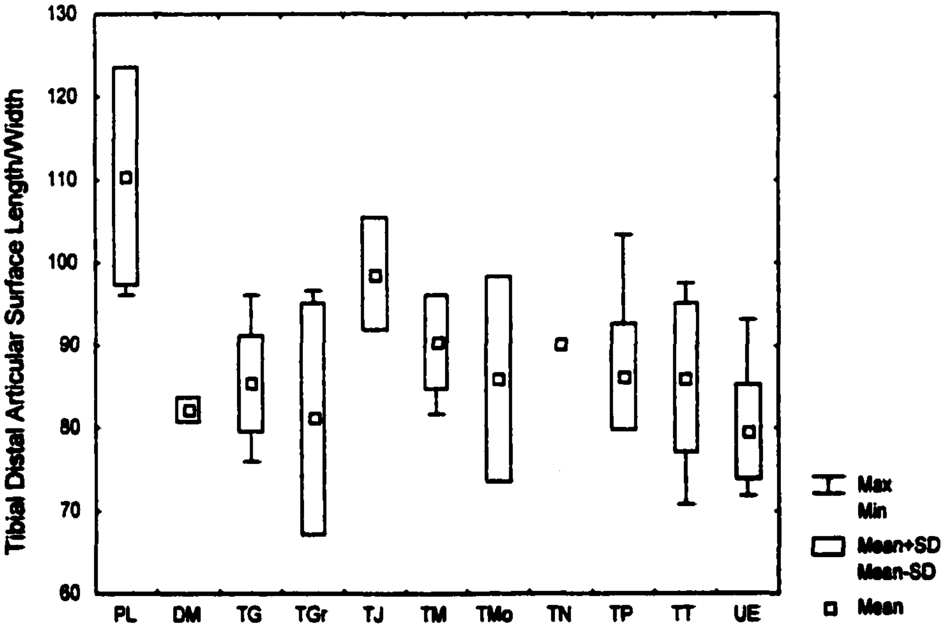


Figure 6.37. Box plot of tibial distal articular surface shape index. Note the high index of *Ptilocercus*.

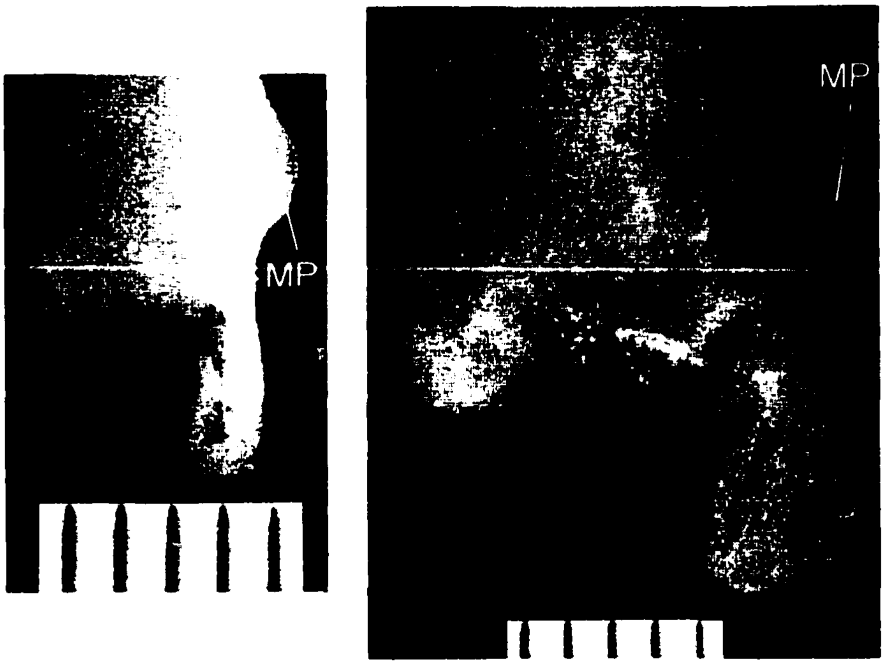


Figure 6.38. Distal tibiae of *Ptilocercus* (left) and *T. tana* (right). MP: medial protuberance. Subdivisions on scale are 0.5 mm. Note the large medial protuberance of *Ptilocercus*.

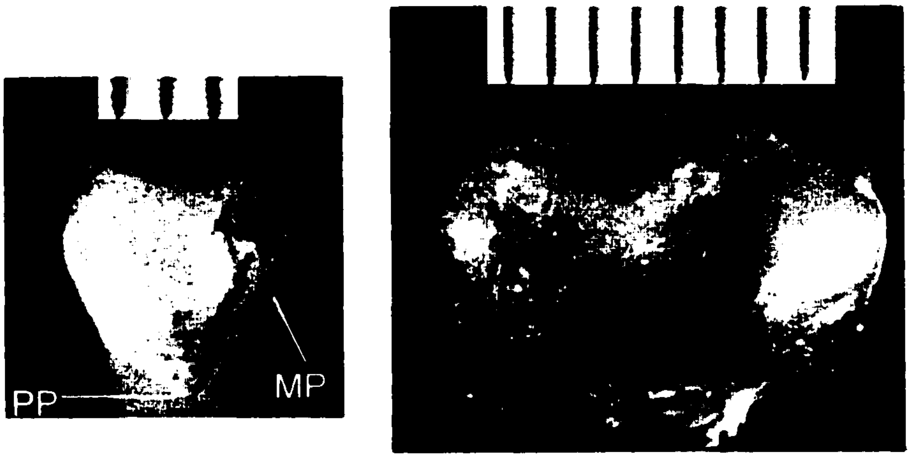


Figure 6.39. Distal view of tibiae of *Ptilocercus* (left) and *T. tana* (right). MP: medial protuberance, PP: posterior protuberance. Subdivisions on scale are 0.5 mm. Note the long, narrow distal articular surface of *Ptilocercus*. Also note the large medial and posterior protuberances of *Ptilocercus*.

Table 6.21: Probabilities* from Tukey Honest Significant Difference (HSD) post hoc test of tibial medial condyle length index

	Dendrogale melanura	*Dendrogale murina*	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
D. melanura		1.0000	0.6939	0.5894	0.1428	0.9745	0.1755	0.9944	1.0000	0.9959	0.9994
D. murina	1.0000		0.6895	0.5844	0.1412	0.9736	0.1729	0.9941	1.0000	0.9957	0.9993
P. lowii	0.6939	0.6895		1.0000	0.8252	0.9999	0.9648	0.9956	0.2199	0.6547	0.4868
T. glis	0.5894	0.5844	1.0000		0.7491	0.9995	0.8181	0.9869	**0.0126**	0.1199	0.0691
T. gracilis	0.1428	0.1412	0.8252	0.7491		0.6036	0.9967	0.4490	**0.0448**	0.1250	0.0887
T. javanica	0.9745	0.9736	0.9999	0.9995	0.6036		0.7824	1.0000	0.9747	0.9999	0.9985
T. minor	0.1755	0.1729	0.9648	0.8181	0.9967	0.7824		0.5599	**0.0006**	**0.0048**	**0.0029**
T. montana	0.9944	0.9941	0.9956	0.9869	0.4490	1.0000	0.5599		0.9983	1.0000	1.0000
T. palawanensis	1.0000	1.0000	0.2199	**0.0126**	**0.0448**	0.9747	**0.0006**	0.9983		0.9880	0.9999
T. tana	0.9959	0.9957	0.6547	0.1199	0.1250	0.9999	**0.0048**	1.0000	0.9880		1.0000
U. everetti	0.9994	0.9993	0.4868	0.0691	0.0887	0.9985	**0.0029**	1.0000	0.9999	1.0000	

*probabilities in bold are significant at the p < .05 level

Table 6.22: Probabilities* from Tukey Honest Significant Difference post hoc test of tibial distal articular surface shape index

	Dendrogale melanura	*Dendrogale murina*	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
D. melanura		1.0000	0.0585	1.0000	1.0000	0.8005	0.9938	1.0000	0.9996	1.0000	1.0000	1.0000
D. murina	1.0000		0.1054	1.0000	1.0000	0.9012	0.9994	1.0000	1.0000	1.0000	1.0000	1.0000
P. lowii	0.0585	0.1054		**0.0001**	**0.0006**	0.8379	**0.0103**	**0.0279**	0.4798	**0.0002**	**0.0002**	**0.0001**
T. glis	1.0000	1.0000	**0.0001**		0.9994	0.5370	0.9745	1.0000	1.0000	1.0000	1.0000	0.7926
T. gracilis	1.0000	1.0000	**0.0006**	0.9994		0.3922	0.8690	0.9999	0.9970	0.9977	0.9974	1.0000
T. javanica	0.8005	0.9012	0.8379	0.5370	0.3922		0.9783	0.8932	0.9992	0.6556	0.5993	0.0891
T. minor	0.9938	0.9994	**0.0103**	0.9745	0.8690	0.9783		0.9999	1.0000	0.9955	0.9896	0.2277
T. montana	1.0000	1.0000	**0.0279**	1.0000	0.9999	0.8932	0.9999		1.0000	1.0000	1.0000	0.9950
T. nicobarica	0.9996	1.0000	0.4798	1.0000	0.9970	0.9992	1.0000	1.0000		1.0000	1.0000	0.9740
T. palawanensis	1.0000	1.0000	**0.0002**	1.0000	0.9977	0.6556	0.9955	1.0000	1.0000		1.0000	0.7224
T. tana	1.0000	1.0000	**0.0002**	1.0000	0.9974	0.5993	0.9896	1.0000	1.0000	1.0000		0.6225
U. everetti	1.0000	1.0000	**0.0001**	0.7926	1.0000	0.0891	0.2277	0.9950	0.9740	0.7224	0.6225	

*probabilities in bold are significant at the p < .05 level

Table 6.23: Probabilities* from Tukey Honest Significant Difference post hoc test of tibial distal articular surface shape index with *Dendrogale* species combined.

	Dendrogale sp.	*Ptilocercus lowii*	*Tupaia glis*	*Tupaia gracilis*	*Tupaia javanica*	*Tupaia minor*	*Tupaia montana*	*Tupaia nicobarica*	*Tupaia palawanensis*	*Tupaia tana*	*Urogale everetti*
Dendrogale sp.		**0.0042**	1.0000	1.0000	0.5732	0.9660	1.0000	0.9988	0.9999	0.9999	1.0000
P. lowii	**0.0042**		**0.0002**	**0.0005**	0.7962	**0.0078**	**0.0218**	0.4269	**0.0003**	**0.0002**	**0.0002**
T. glis	1.0000	**0.0002**		0.9987	0.4825	0.9613	1.0000	0.9999	1.0000	1.0000	0.7461
T. gracilis	1.0000	**0.0005**	0.9987		0.3436	0.8316	0.9998	0.9943	0.9955	0.9951	1.0000
T. javanica	0.5732	0.7962	0.4825	0.3436		0.9666	0.8597	0.9982	0.6014	0.5443	0.0724
T. minor	0.9660	**0.0078**	0.9613	0.8316	0.9666		0.9997	1.0000	0.9918	0.9829	0.1929
T. montana	1.0000	**0.0218**	1.0000	0.9998	0.8597	0.9997		1.0000	1.0000	1.0000	0.9911
T. nicobarica	0.9988	0.4269	0.9999	0.9943	0.9982	1.0000	1.0000		1.0000	1.0000	0.9606
T. palawanensis	0.9999	**0.0003**	1.0000	0.9955	0.6014	0.9918	1.0000	1.0000		1.0000	0.6707
T. tana	0.9999	**0.0002**	1.0000	0.9951	0.5443	0.9829	1.0000	1.0000	1.0000		0.5677
U. everetti	1.0000	**0.0002**	0.7461	1.0000	0.0724	0.1929	0.9911	0.9606	0.6707	0.5677	

*probabilities in bold are significant at the $p < .05$ level

tupaiines in the morphology of their tibial distal articular surface (Fig. 6.37). Even if *T. javanica* is similar to *Ptilocercus* for this index, this is difficult to evaluate because of the current lack of information concerning the locomotion and substrate use of *T. javanica* (see Table 1.2). The longer-than-wide tibial distal articular surface of *Ptilocercus* is reflective of its long and narrow astragalar trochlea (see Szalay and Drawhorn, 1980; Dagosto, 1985). Most euprimates possess a tibial distal articular surface that is either as long as, or longer than, it is wide, and that of dermopterans and plesiadapiforms is as long as it is wide (Dagosto, 1985). Dagosto (1985) interpreted a longer-than-wide tibial distal articular surface as a derived feature of euprimates rather than archontans, but Szalay and Drawhorn (1980) implied that the tibial distal articular surface of the ancestral archontan was relatively long and narrow when they stated that a long, narrow astragalar trochlea is primitive for Archonta. The disparity between these studies may be due to the fact that Dagosto (1985) measured *Tupaia* (which has a wider-than-long tibial distal articular surface) for this feature, while Szalay and Drawhorn (1980) used the astragalus of *Ptilocercus* to represent the scandentian morphotype. If the condition found in *Ptilocercus* for this character is primitive for Scandentia, then the longer-than-wide tibial distal articular surface may represent a synapomorphy uniting scandentians and euprimates. However, this seems unlikely because this character is associated with several other derived features of the distal tibia in euprimates that are not present in *Ptilocercus* or other tupaiids (see Dagosto, 1985). It does seem likely, however, based on the distribution of this character discussed above, that a tibial distal articular surface that is as long as it is wide is primitive for Archonta.

The distal tibial morphology of *Ptilocercus* is further distinguished from that of tupaiines in that it possesses relatively large medial (proximal to the medial malleolus) and posterior protuberances (Figs. 6.38-6.39), which, by virtue of their relatively large size, create a relatively deep groove for the tendons of the flexor digitorum tibialis and tibialis posterior muscles. This deep groove is probably related to the size of the flexor digitorum tibialis muscle (Dagosto, 1983), which was described as large in *Ptilocercus* by Le Gros Clark (1926). This is significant because this muscle is important for grasping (Grand, 1967; Dagosto, 1983; Gebo, 1993), and *Ptilocercus* is capable of grasping (see chapter 3; Zitzmann, pers. comm.). This feature may also be related to the inversion of the foot required during arboreal locomotion because both the tibialis posterior and flexor digitorum tibialis are invertors of the foot (Grand, 1967). Once again, *Ptilocercus* is similar to the slow climbing (and powerfully grasping) lorisines in this feature as they also exhibit a deep groove for the tendons of these muscles, as well as a large posterior protuberance that separates the groove for these tendons from the groove for the flexor digitorum fibularis tendon (see Dagosto, 1983). Again, this does not imply that *Ptilocercus* is a specialized slow climber like lorisines, only that it likely uses a form of arboreal locomotion in which grasping is important.

Fibula

The morphology of the proximal fibula is relatively similar among tupaiids, except that *Ptilocercus* possesses a large sesamoid bone proximal to the fibula (Fig. 6.40). This is likely homologous with the parafibula of marsupials, and represents a primitive feature that was retained in *Ptilocercus* but not in tupaiines (Szalay and Sargis, submitted). Moving to the distal fibula, there are no significant differences between any

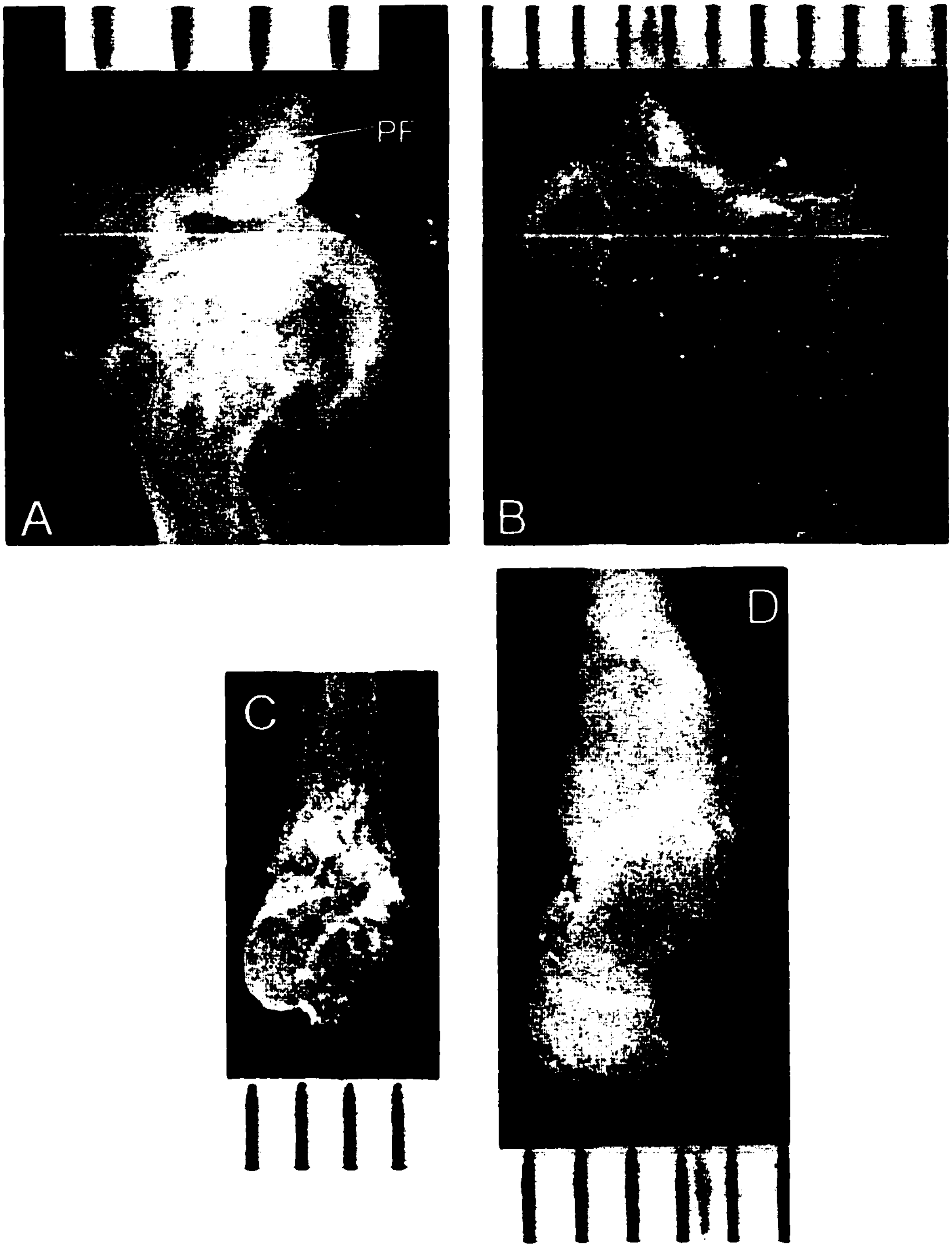


Figure 6.40. Proximal fibulae of *Ptilocercus* (A) and *T. tana* (B). Distal fibulae of *Ptilocercus* (C) and *T. tana* (D). PF: parafibula. Subdivisions on scale are 0.5 mm. Note the presence of a parafibula (sesamoid) in *Ptilocercus* (A).

tupaiid species for the fibular lateral malleolus length index (Fig. 6.41; Table 6.27). As discussed above, the terrestrial ancestry of eutherians is reflected by the bracketing of the astragalus between relatively long medial and lateral malleoli, which restricts movements at the upper ankle joint to the parasagittal plane (Szalay, 1984, 1994; Szalay and Sargis, submitted).

A cluster analysis of the variables included in eight tibial and fibular indices shows that *Ptilocercus* is quite different from tupaiines in its tibial and fibular morphology (Fig. 6.42). Similarly, a cluster analysis of the variables included in 25 hindlimb indices shows that *Ptilocercus* is very distinct from tupaiines in its hindlimb morphology (Fig. 6.43).

Forelimb and Hindlimb

Cluster Analysis. ·Cluster analyses of the variables included in 45 (including ten taxa; Fig. 6.44), 46 (including nine taxa; Fig. 6.45), and 47 (including eight taxa; Fig. 6.46) forelimb and hindlimb indices show that *Ptilocercus* is extremely different from tupaiines in its limb morphology. It is also interesting that when all the taxa are included (but only 45 of 47 indices are included), *Dendrogale*, *Urogale*, and *T. tana* (formerly *Lyonogale*) are all nested among species of *Tupaia* (Fig. 6.44). However, when one index is added, thereby removing *T. palawanensis* from the analysis (because this measurement was missing for this species), *Urogale* falls out from species of *Tupaia* (Fig. 6.45). Similarly, when an additional index is added (removing *T. gracilis* from the analysis), *Dendrogale* becomes separated (and *Urogale* remains separated) from the *Tupaia* species (Fig. 6.46). *T. tana*, on the other hand, remains nested among *Tupaia* species in all of these analyses, which shows how similar it is in its limb morphology to

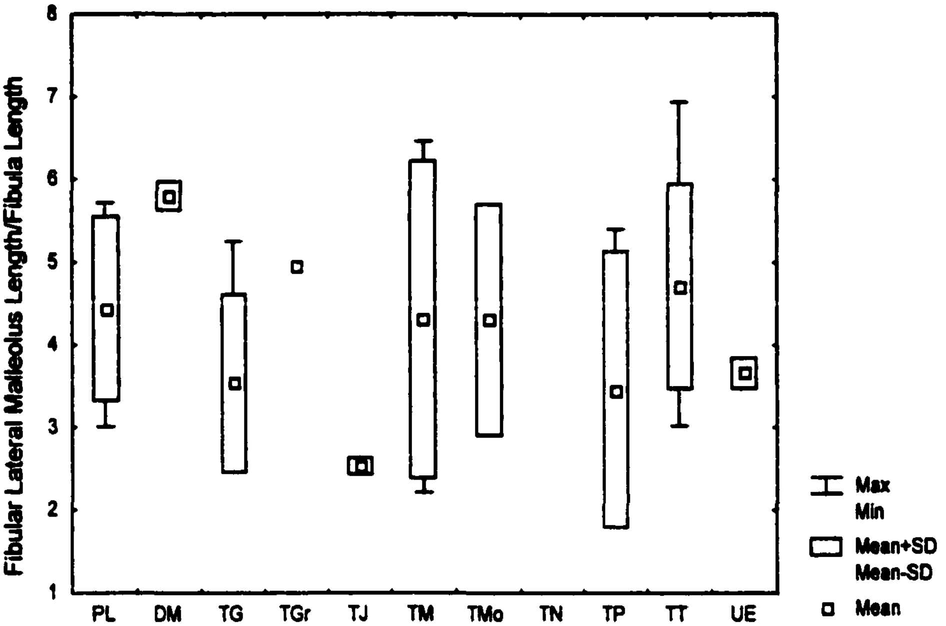


Figure 6.41. Box plot of fibular lateral malleolus length index.

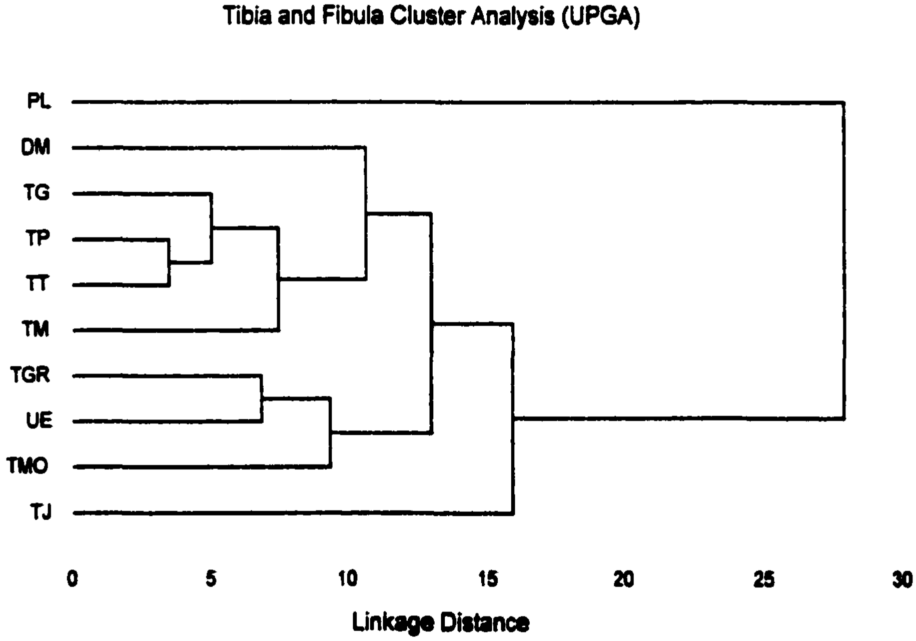


Figure 6.42. Cluster analysis of the variables included in eight tibial and fibular indices. Note the difference between *Ptilocercus* and the tupaiines.

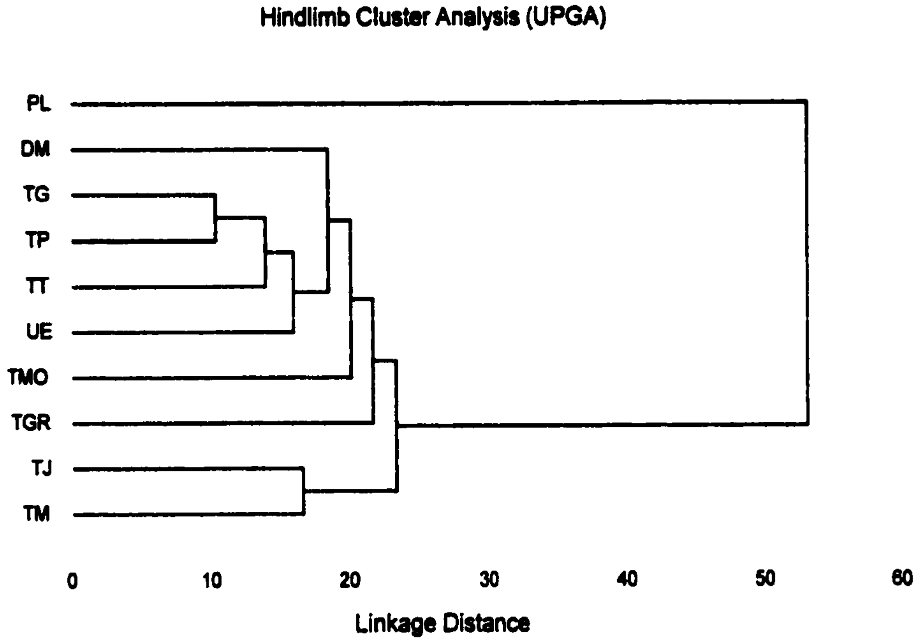


Figure 6.43. Cluster analysis of the variables included in 25 hindlimb indices. Note the difference between *Ptilocercus* and the tupaiines.

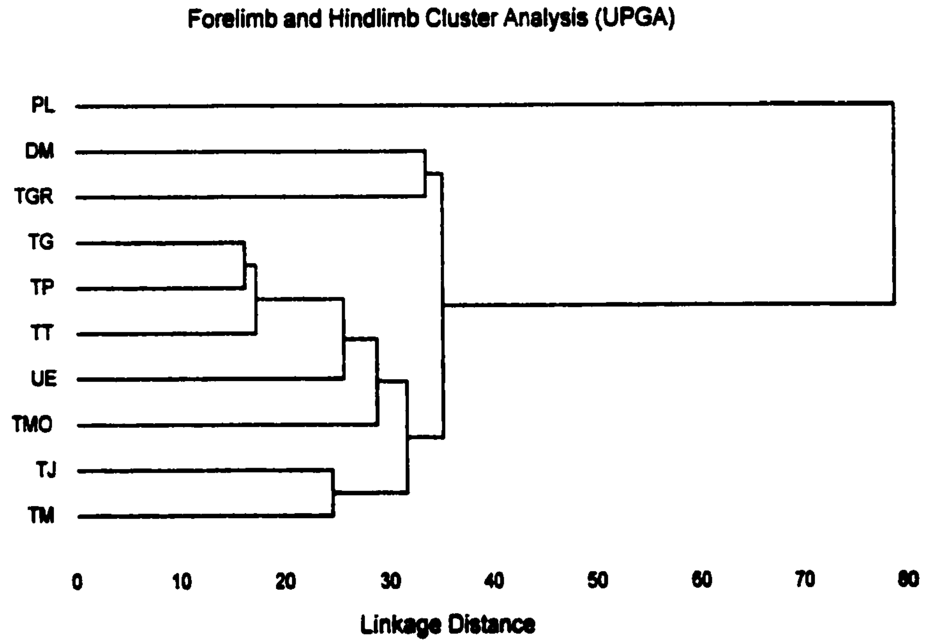


Figure 6.44. Cluster analysis of the variables included in 45 forelimb and hindlimb indices (does not include trochlea depth index or deltopectoral crest length index). Note the difference between *Ptilocercus* and the tupaiines.

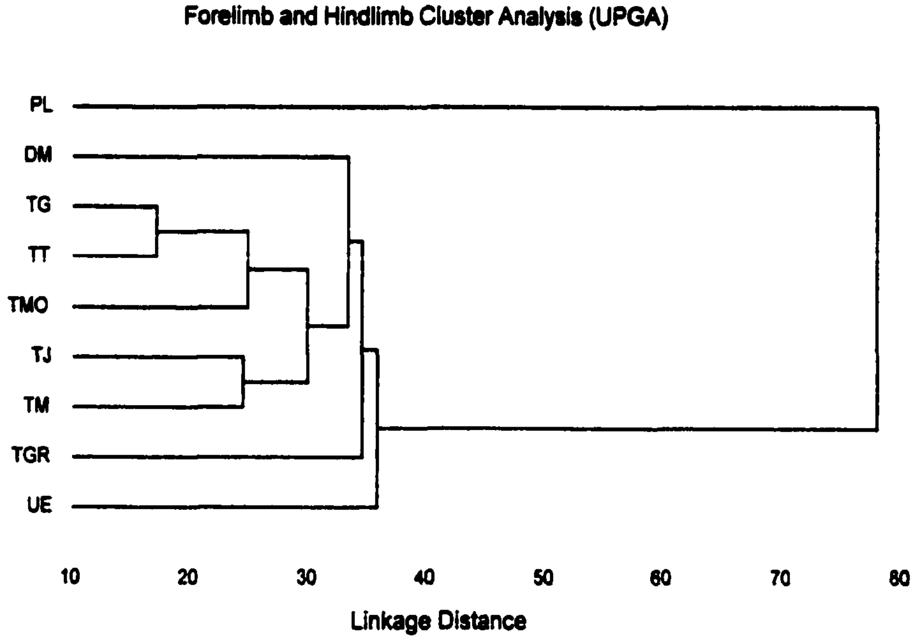


Figure 6.45. Cluster analysis of the variables included in 46 forelimb and hindlimb indices (does not include delto-pectoral crest length index). Note the difference between *Ptilocercus* and the tupaiines.

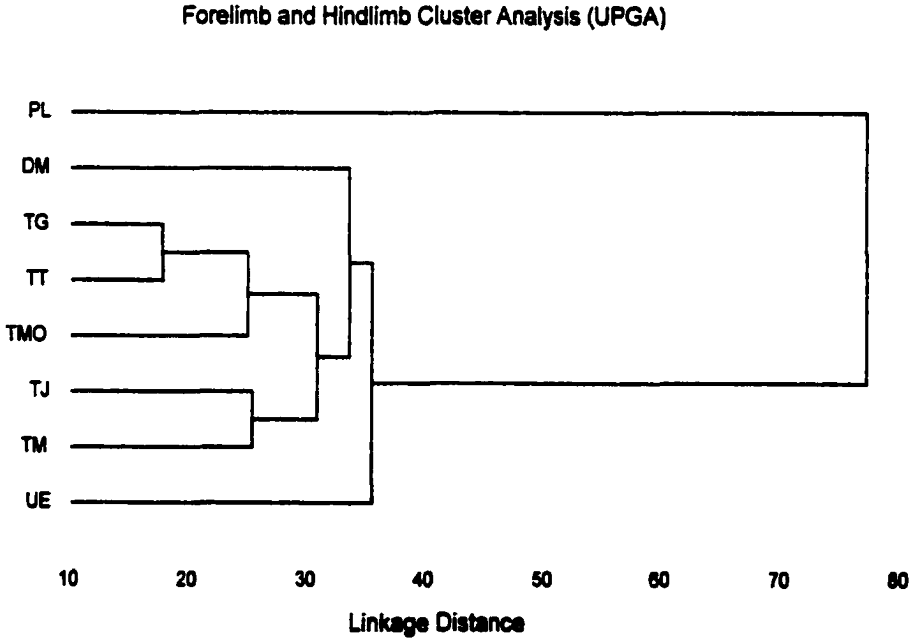


Figure 6.46. Cluster analysis of the variables included in 47 forelimb and hindlimb indices. Note the difference between *Ptilocercus* and the tupaiines. Also note the positions of *Urogale*, *Dendrogale*, and *T. tana*.

other species of *Tupaia* (Figs. 6.44-6.46). This is, perhaps, another reason to include *T. tana* in *Tupaia* rather than in the separate genus *Lyonogale*. *T. tana* is also similar to other species of *Tupaia* in its dentition (see figures in Butler, 1980; Szalay, pers. comm.), and is part of the *Tupaia* ingroup in molecular phylogenies of tupaiids (Dene *et al.*, 1978, 1980; Han *et al.*, 2000). This will be discussed further in chapter 7.

Principal Components Analysis. A PCA was performed on the species means of 70 measurements (see chapter 2). Figures 6.47-6.48 show bivariate plots of the first three factors from the principal components analysis (see Tables 6.24, 6.25, and 6.26 for eigenvalues, factor scores, and factor loadings, respectively). Factor 1, which accounts for 91.9 % of the total variance (Table 6.24), is likely a size vector as it separates large- (over 200 g), medium- (125-170 g), and small- (45-70 g) bodied tupaiids (see Fig. 6.47; Table 1.1). Factor 2, however, separates *Ptilocercus* from the tupaiines (Figs. 6.47-6.48). Factor 3 is difficult to interpret as it does not separate by body size, subfamily, or substrate preference (Fig. 6.48).

Pes

As stated above, due to the detailed studies conducted by Szalay and Drawhorn (1980) and Szalay and Dagosto (1988), the tarsus is the only well studied region of the tupaiid hindlimb. While I will not recount their entire analyses, I will expand and comment on some of their conclusions. First, I agree with Szalay and Drawhorn (1980) that the tupaiid foot, both in the way it is used in locomotion and in its morphology, provides strong evidence for the arboreal ancestry of tupaiids, in addition to some of the other features of the postcranium that also corroborate this hypothesis (see above). First,

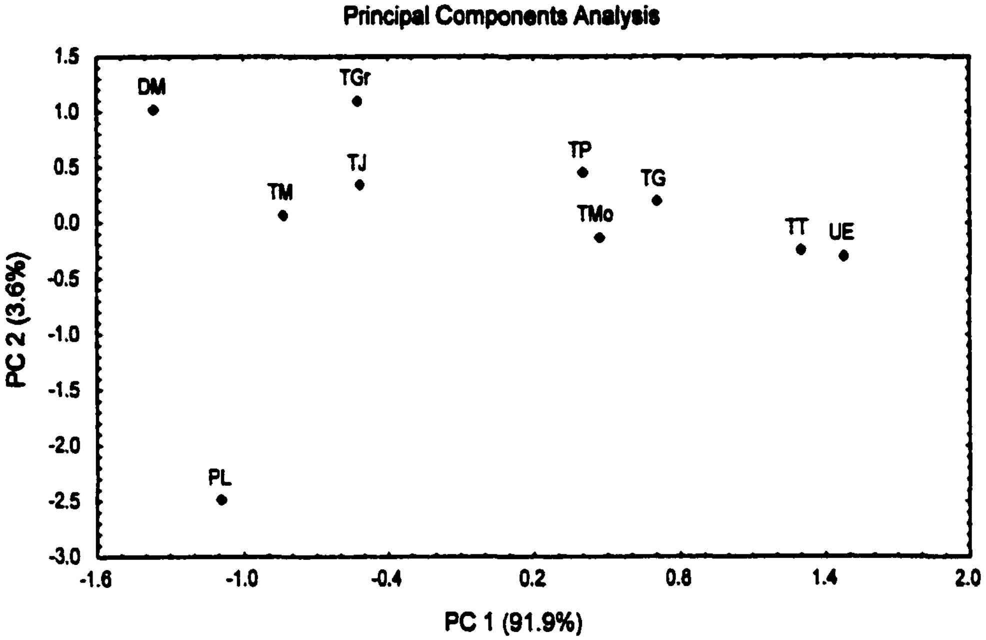


Figure 6.47. Bivariate plot of Factors 1 and 2 from the principal components analysis. Note that Factor 1 is likely a size vector and that Factor 2 separates *Ptilocercus* from all tupaiines.

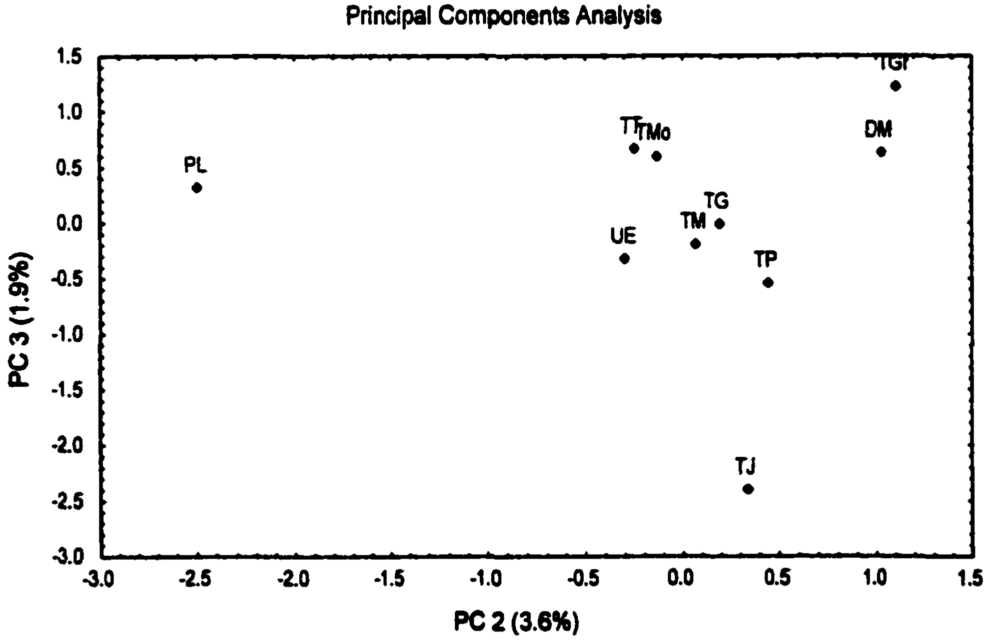


Figure 6.48. Bivariate plot of Factors 2 and 3 from the principal components analysis. Note that Factor 2 separates *Ptilocercus* from all tupaiines.

Table 6.24: Eigenvalues from principal components analysis.

Factors	Eigenvalues	% of Total Variance	Cumulative Eigenvalues	Cumulative % of Total Variance
1	64.3	91.9	64.3	91.9
2	2.5	3.6	66.8	95.5
3	1.3	1.9	68.1	97.3

Table 6.25: Factor scores from principal components analysis.

Taxon	Abbreviation	Factor 1	Factor 2	Factor 3
Ptilocercus lowii	PL	-1.0911	-2.4928	0.3205
Dendrogale sp.	DM	-1.3624	1.0243	0.6311
Tupaia glis	TG	0.7007	0.1891	-0.0099
T. gracilis	TGr	-0.5265	1.1042	1.2298
T. javanica	TJ	-0.5205	0.3346	-2.3971
T. minor	TM	-0.8345	0.0710	-0.1882
T. montana	TMo	0.4686	-0.1280	0.6070
T. palawanensis	TP	0.4010	0.4447	-0.5384
T. tana	TT	1.2946	-0.2498	0.6661
Urogale everetti	UE	1.4701	-0.2973	-0.3209

Table 6.26: Factor loadings from principal components analysis.[a]

Measurement[b]	Factor 1	Factor 2	Factor 3
SL	**0.985**	0.134	0.033
SW	**0.934**	-0.321	0.123
SGL	**0.986**	-0.003	0.075
SGW	**0.981**	-0.149	-0.001
HL	**0.980**	-0.009	0.056
HHW	**0.963**	-0.214	-0.082
HHL	**0.995**	-0.056	-0.013
HMSML	**0.932**	-0.293	0.119
HTW	**0.852**	-0.452	0.235
HCW	**0.976**	-0.081	-0.093
HTL	**0.996**	-0.041	0.040
HCL	**0.993**	-0.023	0.000
HDASW	**0.950**	-0.295	-0.029
HDEW	**0.934**	-0.333	-0.055
UL	**0.983**	-0.129	0.104
UOPL	**0.973**	0.040	-0.009
UTNW	**0.982**	0.050	-0.010
URFL	**0.910**	-0.335	-0.220
URFW	**0.916**	-0.346	-0.105
UTND	**0.975**	-0.003	0.088

Table 6.26 (con.)

Measurement[b]	Factor 1	Factor 2	Factor 3
UTNL	**0.989**	-0.066	-0.042
RL	**0.971**	-0.150	0.131
RNL	**0.955**	-0.196	0.053
RHW	**0.995**	-0.049	-0.036
RHRL	**0.941**	-0.247	0.121
RHL	**0.959**	-0.256	-0.054
INL	**0.990**	0.049	-0.009
ILL	**0.992**	-0.035	-0.002
ILW	**0.925**	0.365	-0.074
IAL	**0.982**	-0.155	0.017
IAW	**0.981**	-0.100	-0.014
IPL	**0.828**	0.061	-0.091
ISL	**0.954**	0.224	-0.015
ISW	**0.962**	0.122	-0.083
FEL	**0.976**	-0.004	0.090
FHL	**0.981**	-0.145	0.013
FHW	**0.994**	-0.045	-0.028
FGTL	**0.908**	0.358	-0.130
FLTL	**0.934**	0.135	-0.046
FTTL	**0.793**	0.581	-0.007
FMSML	**0.997**	0.010	0.011
FPGL	**0.922**	0.365	0.001
FPGW	**0.955**	-0.098	-0.220
FDEW	**0.993**	0.026	-0.099
FMCD	**0.978**	0.201	-0.015
FLCD	**0.965**	0.256	0.010
FMCW	**0.986**	-0.112	-0.089
FLCW	**0.983**	0.109	0.001
FMCL	**0.995**	0.093	0.017
FLCL	**0.990**	0.130	0.015
FICNW	**0.946**	0.172	-0.056
FLTLT	**0.986**	0.059	-0.114
FLTTT	**0.986**	0.100	0.000
TL	**0.969**	0.061	0.086
TLCL	**0.987**	0.052	0.024
TMCL	**0.988**	0.084	0.031
TLCW	**0.996**	0.007	0.035
TMCW	**0.991**	-0.036	-0.017
TPEW	**0.996**	0.028	-0.078
TPEL	**0.986**	0.149	-0.051
TDEW	**0.973**	0.208	-0.059
TMML	**0.938**	0.227	0.051
TMMW	**0.973**	0.092	-0.047

Table 6.26 (con.)

Measurement[b]	Factor 1	Factor 2	Factor 3
TDASW	**0.970**	0.201	-0.041
TDASL	**0.936**	-0.127	-0.238
TCL	**0.929**	0.010	0.357
FIL	**0.960**	0.097	0.107
FILML	0.527	0.135	**0.830**
FIHL	**0.974**	-0.134	-0.128
FILMW	**0.978**	0.143	0.001
Explained Variance	64.34	2.49	1.30
Proportion of Total Variance	0.919	0.036	0.019

[a]loadings in bold are > .700000
[b]see Table 2.3 for measurement abbreviations

it appears that all tupaiids, including terrestrial taxa like *T. tana*, are capable of some degree of hindfoot reversal, which they use when descending inclined substrates (see chapter 3; Sorenson, 1970; Jenkins, 1974; Szalay and Drawhorn, 1980; Jenkins and McClearn, 1984). Terrestrial tupaiids like *T. tana*, however, do not perform this behavior as frequently as arboreal tupaiids (see chapter 3), and are also not capable of the same degree of hindfoot reversal as the latter (Sorenson, 1970). The capacity for hindfoot reversal in the terrestrial species is likely retained from the arboreal ancestral tupaiid. The morphology of the tarsus also indicates an arboreal ancestor of the family because even terrestrial taxa, such as *T. tana* and *Urogale*, are characterized by a relatively mobile tarsus that facilitates inversion of the foot (Szalay and Drawhorn, 1980). For instance, all tupaiids have 1) a calcaneal astragalar facet that is largely anteroposteriorly oriented (which is longest and most helical in *Ptilocercus*), 2) a calcaneal sustentacular facet that retains a small distal articular surface (that is larger in the arboreal *T. minor* and is actually completely continuous in *Ptilocercus*), and 3) a navicular facet that is continuous with the sustentacular facet on the astragalus (and dominates the plantar surface of the astragalus in the arboreal *T. minor* and *Ptilocercus*; Szalay and Drawhorn, 1980; fig. 2). All of these features, and especially the extreme conditions found in *Ptilocercus*, facilitate inversion of the foot, an extremely important movement for arboreal locomotion, particularly on small branches. Hence, the ancestral tupaiid was likely arboreal and had a tarsus like that of *Ptilocercus*, and terrestrial tupaiines likely retain the less extreme versions of these features due to this arboreal ancestry (Szalay and Drawhorn, 1980). It also appears that some of the capacity for inversion, and hence some tarsal mobility, was lost in the transition to tupaiine terrestriality.

In addition to the features that distinguish *Ptilocercus* from tupaiines discussed above, *Ptilocercus* also has a more circular and concave cuboid facet on the calcaneus than do tupaiines (Szalay and Drawhorn, 1980, fig. 9). This deeper and more circular calcaneocuboid pivot of *Ptilocercus* allows for more rotation at the transverse tarsal joint than is possible in tupaiines. The calcaneocuboid pivot is also deeper in arboreal guenons than in terrestrial guenons (Gebo and Sargis, 1994). The condition of the calcaneocuboid joint found in *Ptilocercus* is also present in euprimates, plesiadapiforms, and dermopterans (see Szalay, 1977; Szalay and Drawhorn, 1980; Beard, 1993b), and may be primitive for Archonta (Szalay, 1977; Szalay and Drawhorn, 1980; contra Beard, 1993b). This will be discussed further in the character analysis in chapter 7.

While Szalay and Drawhorn (1980) were mistaken concerning the lack of a grasping hallux in tupaiids, Szalay and Dagosto (1988) correctly noted *Ptilocercus'* capacity for pedal grasping (see chapter 3). In *Ptilocercus*, the distal facet of the entocuneiform for articulation with the first metatarsal is more mediolaterally expanded dorsally than that of tupaiines (Fig. 6.49). This allows a greater range of abduction in the

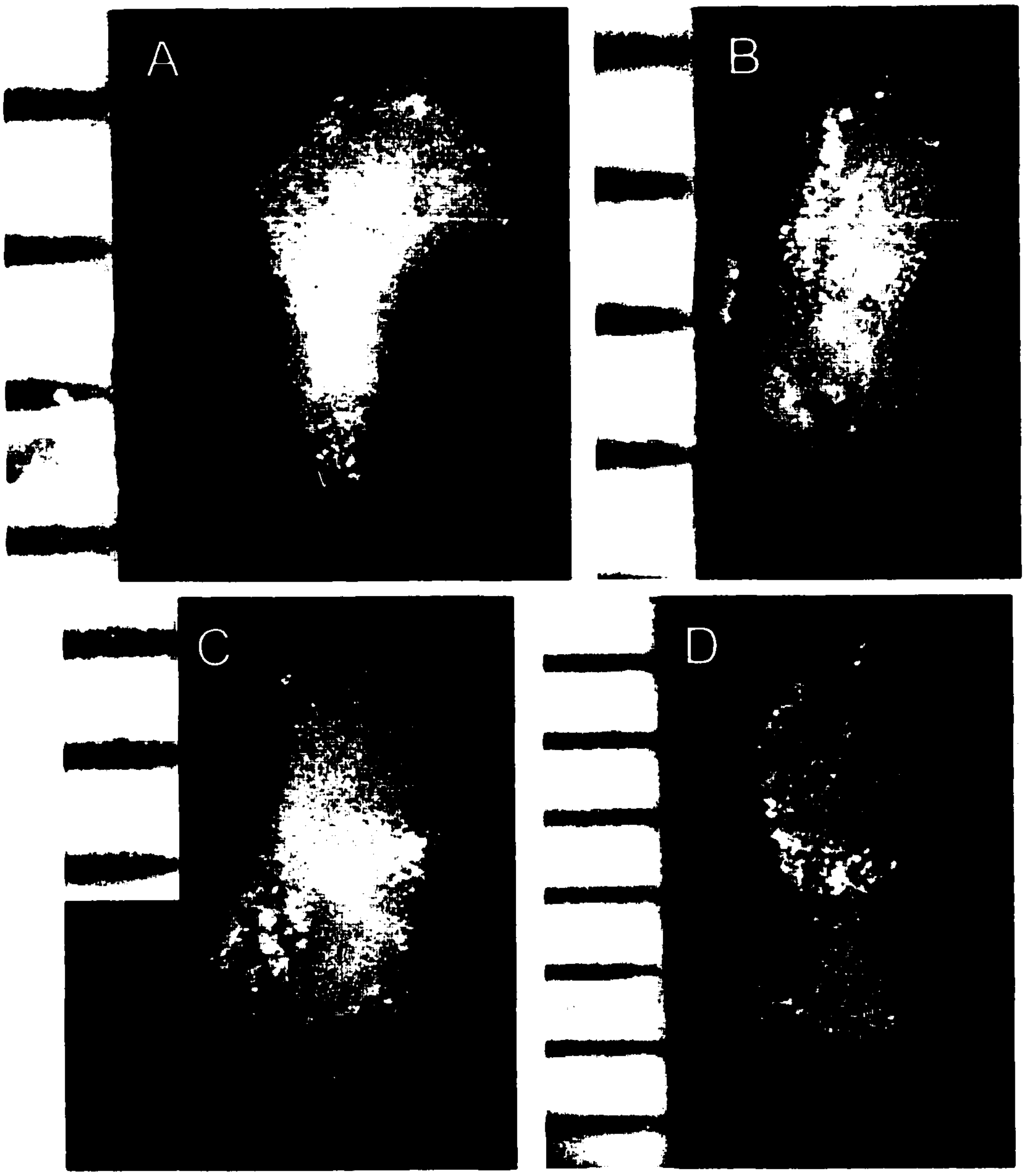


Figure 6.49. Entocuneiforms (distal view) of *Ptilocercus* (A), *Dendrogale melanura* (B), *T. minor* (C), and *T. tana* (D). Subdivisions on scale are 0.5 mm. Note the mediolateral expansion (dorsally) of the distal entocuneiform facet in *Ptilocercus* (A).

hallux of *Ptilocercus* for pedal grasping (Szalay and Dagosto, 1988). Lorisines, for instance, have a wide distal entocuneiform facet that has been reoriented to facilitate extreme abduction of the hallux for powerful grasping of large supports (Gebo, 1989). In tupaiines, on the other hand, the capacity for hallucial abduction is reduced by the restricted distal facet of the entocuneiform. This feature is also restricted in terrestrial cercopithecines, limiting their capacity for hallucial abduction as well (Jolly, 1967; Harrison, 1989). The condition of the distal facet of the entocuneiform (and grasping) seen in *Ptilocercus* may be primitive for tupaiids, and the condition found in tupaiines is likely related to their terrestrial ancestry as there is a reduced need for hallucial abduction during locomotion on the ground. The fact that *T. minor* is capable of grasping and habitually abducts its hallux (see chapter 3), yet is not capable of as great a range of abduction at the tarsometatarsal joint as *Ptilocercus*, may mean that *T. minor* achieves hallucial abduction at the metatarsophalangeal joint (see below). This form of abduction of the hallux has been described in *T. glis* by Jenkins (1974), and may indicate that *T. minor* and *Ptilocercus* grasp in different ways. Hence, it is unlikely that grasping is homologous in *Ptilocercus* and *T. minor*. It is likely, rather, that grasping is primitive for tupaiids and that the ancestral tupaiid was similar to *Ptilocercus* in its grasping behavior. That *T. minor's* grasping ability represents the primitive condition for the subfamily Tupaiinae is unlikely based on a host of postcranial features that reflect the likely terrestrial (and non-grasping) nature of the ancestral tupaiine (see above). Grasping, therefore, probably evolved secondarily in *T. minor*. It may have evolved first in a *Ptilocercus*-like ancestral tupaiid as an arboreal adaptation for moving on small, terminal branches. If the ancestral tupaiine was indeed terrestrial and had lost this ability to grasp, then grasping must have been evolved secondarily in *T. minor* when this species began exploiting fine branches as part of a return to an arboreal lifestyle (see chapter 3).

Alternatively, *Ptilocercus'* capacity for grasping may be retained from the ancestral archontan, which may have had the ability to grasp (see Szalay and Dagosto, 1988). Similarly, the condition of the distal facet of the entocuneiform found in *Ptilocercus* may be primitive for Archonta, as this condition is also found in plesiadapiforms (Fig. 7.7), dermopterans, and euprimates (see Szalay and Dagosto, 1988; Beard, 1993b). This will be discussed further in the character analysis in chapter 7.

The plantar process of the entocuneiform is relatively large in tupaiids (Szalay and Dagosto, 1988), and appears to be larger in *Ptilocercus* than in tupaiines (Fig. 6.50). This may be related to the increased demand for inversion of the foot during arboreal locomotion because the tibialis anterior, an invertor of the foot, typically inserts on this process in tupaiids (see George, 1977). However, Le Gros Clark (1926) reported that this muscle does not attach to the entocuneiform in *Ptilocercus*, but instead attaches to the first metatarsal. Hence, the large plantar process of the entocuneiform in *Ptilocercus* may "serve as a medial wall for the tunnel for powerful pedal flexors (flexor tibialis and flexor fibularis)" (Szalay and Dagosto, 1988, p. 9). This is a possibility in *Ptilocercus* because Le Gros Clark (1926) described these muscles as large and well developed, respectively, and *Ptilocercus* has a deep groove for the flexor tibialis tendon on its distal tibia (see above). This would also make sense functionally because both of these muscles are digital flexors and foot invertors (Gebo, 1993), which would be important in *Ptilocercus* for grasping small supports during arboreal locomotion. Finally, the large entocuneiform plantar process in *Ptilocercus* may provide a larger area of origin for the

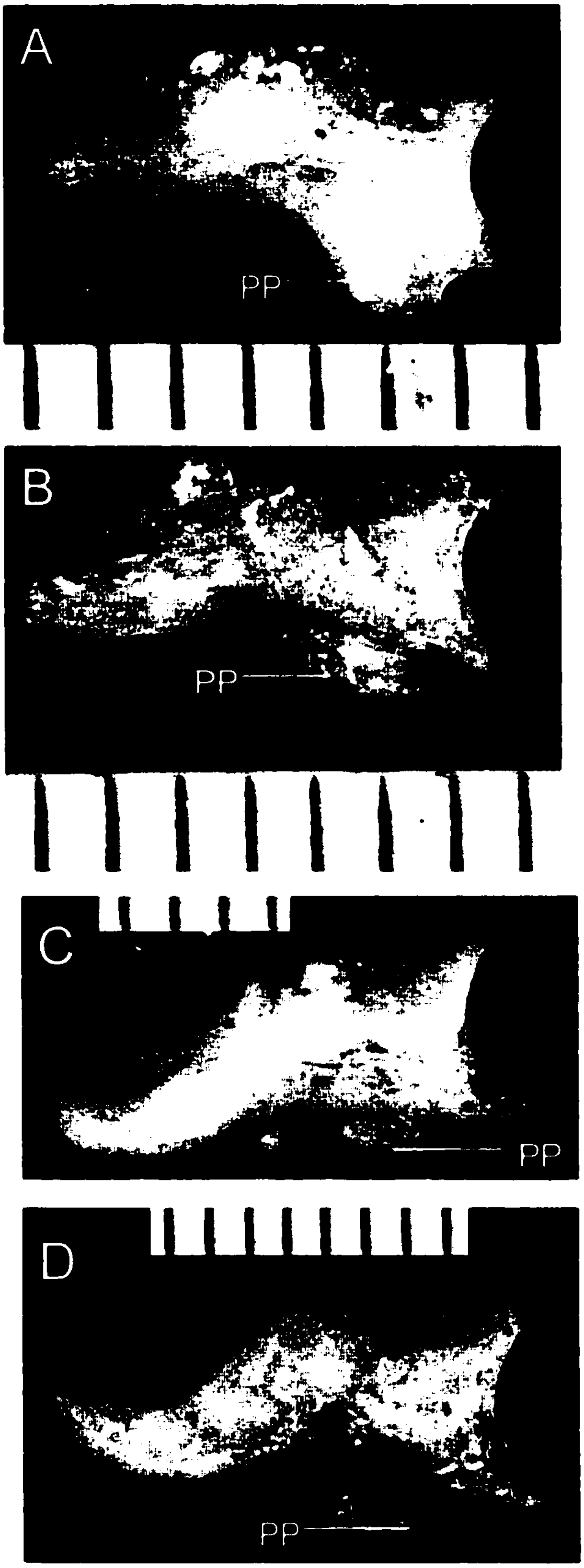


Figure 6.50. Entocuneiforms (lateral view) of *Ptilocercus* (A), *Dendrogale melanura* (B), *T. minor* (C), and *T. tana* (D). PP: plantar process. Subdivisions on scale are 0.5 mm. Note the large plantar process of *Ptilocercus* (A).

abductor hallucis and flexor hallucis brevis muscles, which may provide some advantage in abduction of the hallux and grasping of the hallux, respectively. It is interesting that *Ptilocercus* is the only tupaiid with two heads of the flexor hallucis brevis muscle (Le Gros Clark, 1926; George, 1977), perhaps indicating the importance of grasping in this taxon.

A large plantar process of the entocuneiform is clearly primitive for Scandentia, and may also be primitive for Archonta (Szalay and Dagosto, 1988). Plesiadapiforms also possess a large entocuneiform plantar process (Fig. 7.7; Szalay and Dagosto, 1988; contra Beard, 1993b), although this feature has been reduced in dermopterans and reduced or lost in euprimates (Szalay and Dagosto, 1988; Beard, 1993b; Szalay and Lucas, 1993, 1996). This will be discussed further in the character analysis in chapter 7.

The differences seen between *Ptilocercus* and tupaiines in the distal entocuneiform facet are, not surprisingly, reflected in the proximal facet of the first metatarsal (Fig. 6.51). In *Ptilocercus*, this facet is more globular and less restricted mediolaterally, while that of tupaiines is more restricted mediolaterally. The condition found in *Ptilocercus* allows greater mobility at the hallucial tarsometatarsal joint, which, in turn, increases the range of abduction of the hallux (see above). As noted above, this is advantageous for grasping branches with the foot. The proximal facet of the first metatarsal is also large in arboreal viverrids, and this allows the abduction of the hallux in these taxa (Taylor, 1976). The condition seen in tupaiines restricts the range of abduction of the hallux at the tarsometatarsal joint, but allows fore-and-aft flexion and extension at this joint. The reduction of mobility increases stability, especially for parasagittal movements on a relatively even substrate (*i.e.*, locomotion on the ground) in

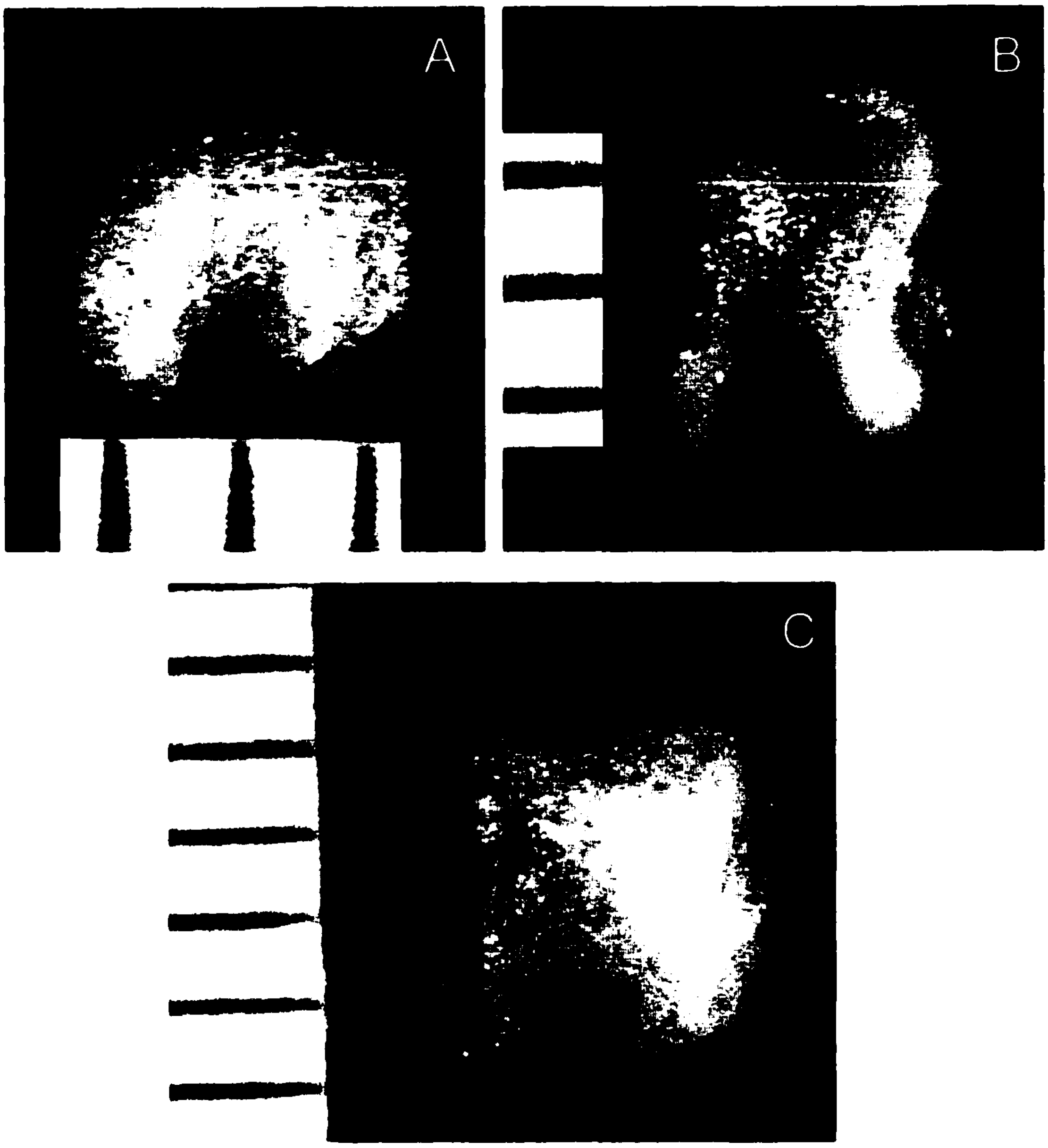


Figure 6.51. 1st metatarsals (proximal view) of *Ptilocercus* (A), *T. minor* (B), and *T. tana* (C). Subdivisions on scale are 0.5 mm. Note the globular (less mediolaterally restricted) proximal facet of the first metatarsal in *Ptilocercus* (A).

which the hallux is kept in line with the other digits. The fact that *T. minor* is characterized by the tupaiine condition (Fig. 6.51) further implies that grasping is achieved in this taxon through abduction of the hallux at the metatarsophalangeal joint, rather than at the tarsometatarsal joint as in *Ptilocercus* (see above). It also lends support to the proposal that both the type of grasping and the morphological adaptations for this behavior are not homologous in *Ptilocercus* and *T. minor*, which, in turn, supports the hypothesis that grasping evolved secondarily in *T. minor* (see discussion above on the evolution of tupaiid grasping). As with the condition of the distal entocuneiform facet, the proximal facet of the first metatarsal of *Ptilocercus* is similar to that of plesiadapiforms (Fig. 7.8) and may represent the primitive archontan condition. While this will be discussed further in chapter 7, it should be pointed out here that the similarity between *Ptilocercus* and plesiadapiforms in hallucial tarsometatarsal joint morphology implies that plesiadapiforms were capable of *Ptilocercus*-like (but not euprimate-like) grasping (see chapter 3; Szalay and Dagosto, 1988; contra Beard, 1993b).

In *Ptilocercus*, the first metatarsal is much shorter and more robust than the other metatarsals (Le Gros Clark, 1926), but this is not the case in tupaiines (Fig. 6.52). This may be related to habitual abduction of the hallux and grasping in *Ptilocercus* (see above), in that the shorter and more robust first metatarsal may be capable of incurring greater loads when the hallux is not in line with the other digits. In other words, a short, robust first metatarsal may provide some load-bearing advantage when the hallux is abducted and on one side of a branch, the other digits are on the other side of the branch, and the foot is grasping the branch. Alternatively, the longer first metatarsal found in tupaiines is more likely advantageous when the hallux is in line with the other digits and

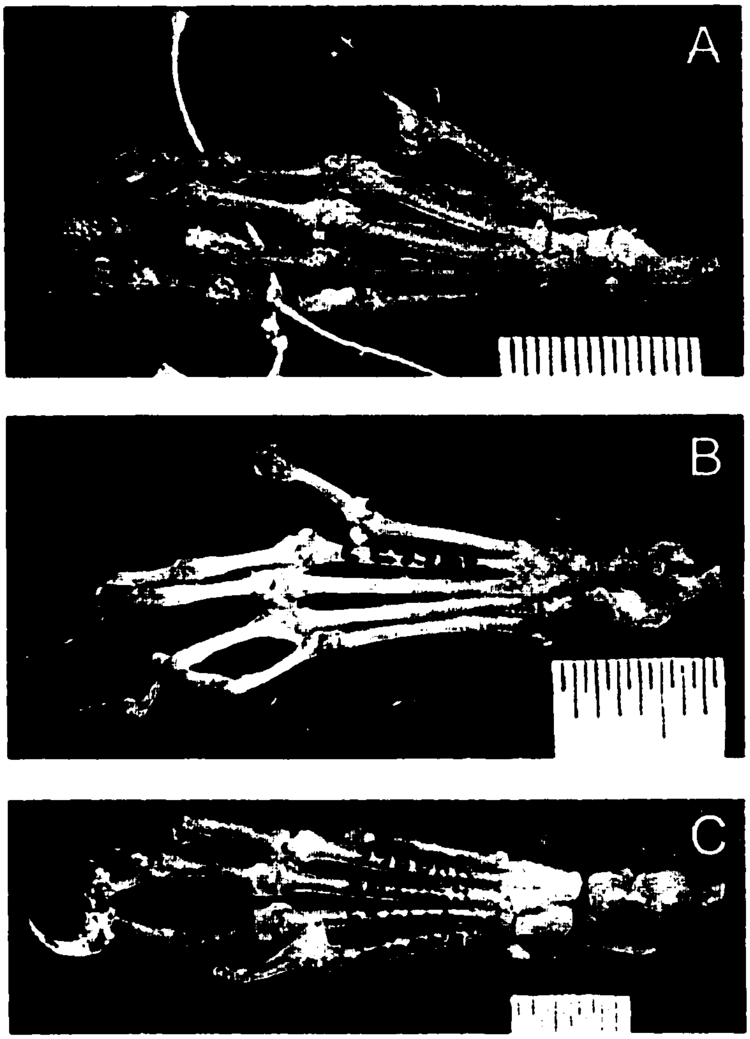


Figure 6.52. Left pes of *Ptilocercus* (A), *T. minor* (B), and *T. tana* (C). Subdivisions on scale are 0.5 mm. Note the short, robust first metatarsal of *Ptilocercus* (A).

the foot is involved in propulsion on a relatively even substrate like the ground. Again, the fact that *T. minor* exhibits the tupaiine condition for this feature likely reflects that hallucial abduction is achieved at the metatarsophalangeal joint in this species, that the capability for grasping was lost in the terrestrial ancestral tupaiine, that grasping (and the corresponding morphology) in *T. minor* and *Ptilocercus* is not homologous, and that grasping in *T. minor* evolved secondarily (see discussion above).

In tupaiids, the pedal ungual phalanges and claws are similar to those of the manus (Figs. 6.52-6.53). Hence, those of the pes will not be discussed here as those of the manus were discussed in detail above (see chapter 5). A further discussion of unguals will be included in the character analysis in chapter 7.

Summary

As with the forelimb, this analysis of the tupaiid hindlimb has clearly shown that *Ptilocercus* is adapted for arboreal locomotion, whereas tupaiines are adapted for terrestriality. The hindlimb of *Ptilocercus* appears to be habitually flexed and exhibits more joint mobility, a condition necessary for movement on uneven, discontinuous arboreal supports. The tarsus of *Ptilocercus* facilitates inversion of the foot, and its grasping hallux is capable of a great range of abduction. Tupaiines, on the other hand, are characterized by more extended hindlimbs and more stability in their joints. These joints restrict movements more to the parasagittal plane, which increases the efficiency of locomotion on a more even and continuous surface like the ground. The tupaiine hindlimb is more adapted for powerful flexion and extension and, consequently, for rapid terrestrial locomotion. Even the most arboreal tupaiines remain similar to their terrestrial relatives in their hindlimb morphology, which is a strong indication that the ancestor of

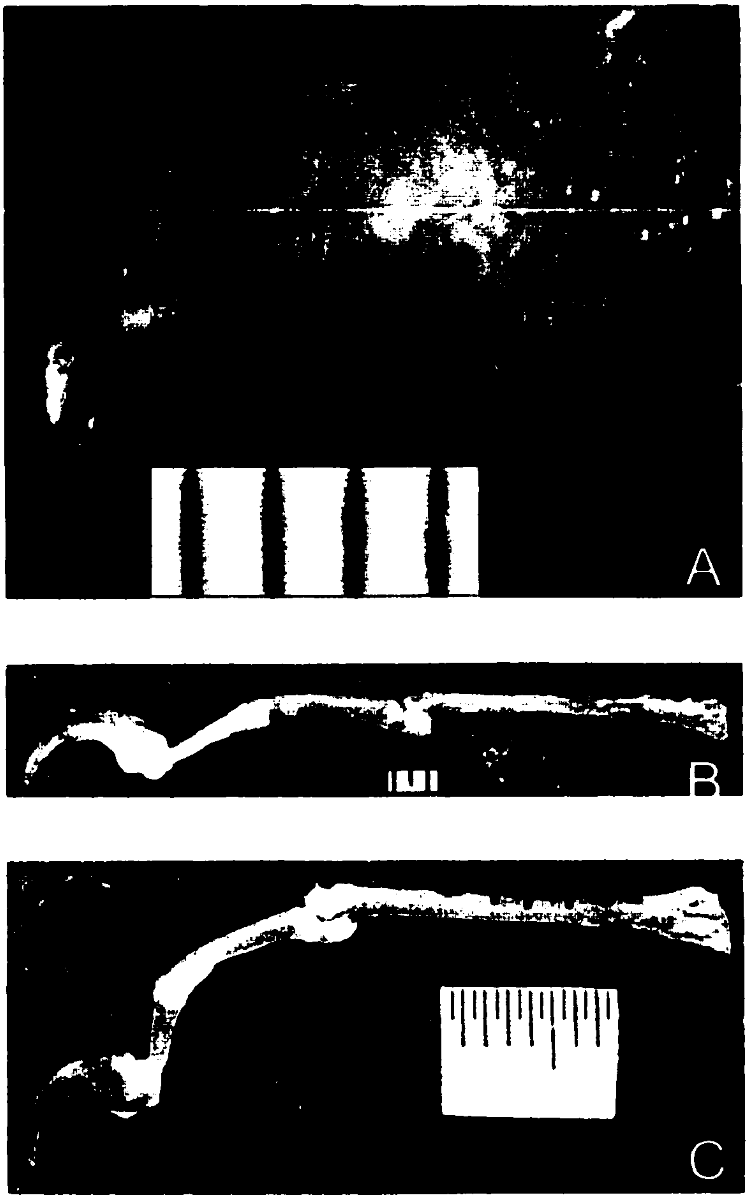


Figure 6.53. Claw of 3rd pedal digit of *Ptilocercus* (A). 3rd pedal digits of *Dendrogale melanura* (B) and *T. tana* (C). Subdivisions on scale are 0.5 mm. Note the short, deep claw of *Ptilocercus* (A).

the Tupaiinae was terrestrially adapted. Their hindlimb morphology appears to have been constrained by their terrestrial heritage. This also applies to their grasping capabilities, which were probably lost in their terrestrial ancestor. *Ptilocercus* and *T. minor* appear, based on their pedal morphology, to grasp in different (nonhomologous) ways, and grasping likely evolved secondarily in *T. minor*. Finally, the hindlimb character states of *Ptilocercus* are more similar to those of other archontans than are those of tupaiines. The implications of this will be discussed further in the character analysis in chapter 7.

Table 6.27: Hindlimb indices.
(see Table 2.4 for index descriptions)

Genus	Species	Subspecies	Museum	Number	4	24	25	26	27	28	29	30	31	32	33	34	35	36 (1)	36 (2)
Ptilocercus	*lowii*	*lowii*	FMNH	76855		60	19	86	29	27	88								79
Ptilocercus	*lowii*		MCZ	51736	104	61	21	87	32	26	76	88	2.8	7.1	1.9	17	25	11	73
Ptilocercus	*lowii*		NHM	1934.5.6.1	111	61	20		29	27									
Ptilocercus	*lowii*		NHM	67.1479	104	58	25	87	24	26	74	88	3.5	8.4	1.4	16	25	12	74
Ptilocercus	*lowii*		NHM	1960.8.4.6	105	56	23	92	22	27	77	91	3.8	7.2	2.2	14	26	11	71
Ptilocercus	*lowii*		NNM	a		63	23		30	29	74		4.0	8.8	1.7	15	26		
Ptilocercus	***lowii***	**Mean**			**106**	**60**	**22**	**88**	**28**	**27**	**78**	**89**	**3.5**	**7.9**	**1.8**	**16**	**25**	**11**	**74**
		SD			**3.59**	**2.36**	**2.27**	**2.51**	**3.83**	**0.93**	**5.89**	**1.55**	**0.51**	**0.84**	**0.37**	**1.17**	**0.48**	**0.24**	**3.45**
		n			**4**	**6**	**6**	**4**	**6**	**6**	**5**	**3**	**4**	**4**	**4**	**4**	**4**	**3**	**4**
Dendrogale	*melanura*		MCZ	36746	111	58	25	98	32	30	83	93	5.2	12.4	5.3	18	28	16	87
Dendrogale	*murina*	*frenata*	FMNH	46630	107	55	40	86	25	32	75	101	5.8	7.7	6.9	16	30	15	86
Dendrogale	**sp.**	**Mean**			**109**	**56**	**33**	**92**	**28**	**31**	**79**	**97**	**5.5**	**10.0**	**6.1**	**17**	**29**	**15**	**87**
		SD			**2.87**	**2.07**	**10.44**	**8.56**	**4.88**	**0.89**	**5.97**	**5.69**	**0.40**	**3.38**	**1.07**	**1.58**	**0.80**	**0.55**	**0.70**
		n			**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**
Tupaia	*glis*	*belangeri*	AMNH	113135	112	56	40	103	23	31	86	97	5.9	8.3	5.6	16	28	16	97
Tupaia	*glis*		AMNH	55561		57	43	96	21	30	79	94	5.8	6.0	6.0	16	29	15	99
Tupaia	*glis*		AMNH	55562		57	44	98	19	30	90	89	6.3	6.9	5.7	17	28	14	90
Tupaia	*glis*	*glis*	FMNH	98470	108	55	44	96	27	31	79	91	5.8	7.1	5.5	16	29	16	97
Tupaia	*glis*	*glis*	FMNH	98469	108	58	38	93	26	32	86	94	6.4	7.6	5.6	16	31	17	100
Tupaia	*glis*	*glis*	FMNH	98468	106	54	46	95	28	35	75	101						16	95
Tupaia	*glis*	*belangeri*	FMNH	46642	107	54	47	92	28	36	76	95	6.1	7.9	5.5	18	31	16	94
Tupaia	*glis*	*wilkinsoni*	FMNH	66019	106	55	43	91	25	35	70	91	6.5	7.4	5.1	17	27	17	104
Tupaia	*glis*	*longipes*	FMNH	76815		54	42	92	26	36	76	100	5.5	6.6	5.5	14	26	14	92
Tupaia	*glis*	*longipes*	FMNH	76819	112	53	44	94	27	35	68	94	5.5	5.0	6.5	15	28	14	92
Tupaia	*glis*	*longipes*	FMNH	76824		54	41	93	27	36	57	98	5.3	5.7	6.4	14	27	14	93
Tupaia	*glis*	*longipes*	FMNH	76825		55	40	91	25	35	65	97	5.4	6.2	6.4	14	29	14	97
Tupaia	*glis*	*demissa*	MHN	801.95	104	56	43	100	23	31	91	95	5.6	6.5	6.4	15	28	15	98
Tupaia	*glis*	*belangeri*	MNHN	1990-510								98	6.4					16	98
Tupaia	*glis*	*longipes*	USNM	198043	109	58	41	95	23	29	82	85	5.7	6.3	6.2	16	27	14	96
Tupaia	*glis*	*longipes*	USNM	396665	111	56	40	97	24	31	74	96	6.1	6.2	6.7	16	28	13	92
Tupaia	*glis*	*longipes*	USNM	396673	108	56	40	99	23	31	77	96	4.6	6.5	6.3	15	27	13	92
Tupaia	*glis*		SMNH	A620505	109	56	43	94	23	33	66	94	6.9	8.2	5.5	18	29	16	97

Genus	Species	Subspecies	Museum	Number	4	24	25	26	27	28	29	30	31	32	33	34	35	36 (1)	36 (2)
Tupaia	*glis*	*discolor*	ZS	1905/13	111							105	6.4	7.6	3.9	15	28	15	92
Tupaia	***glis***	**Mean**			**109**	**56**	**42**	**95**	**25**	**33**	**76**	**95**	**5.9**	**6.8**	**5.8**	**16**	**28**	**15**	**96**
		SD			**2.51**	**1.34**	**2.38**	**3.33**	**2.51**	**2.37**	**9.08**	**4.47**	**0.55**	**0.91**	**0.69**	**1.31**	**1.29**	**1.24**	**3.45**
		n			**13**	**17**	**17**	**17**	**17**	**17**	**17**	**19**	**18**	**17**	**17**	**17**	**17**	**19**	**19**
Tupaia	*gracilis*	*gracilis*	FMNH	140925	114	57	38	88	29	34	62	95						14	96
Tupaia	*gracilis*	*gracilis*	FMNH	140928	114	55	39	87	29	35	62	97						15	100
Tupaia	*gracilis*		USNM	449963	116	55	42	96	23	33	69	94	5.5	7.1	5.2	15	27	13	96
Tupaia	***gracilis***	**Mean**			**115**	**56**	**40**	**90**	**27**	**34**	**64**	**95**	**5.5**	**7.1**	**5.2**	**15**	**27**	**14**	**97**
		SD			**1.36**	**1.41**	**2.17**	**4.78**	**3.83**	**1.07**	**3.79**	**1.19**						**0.63**	**2.17**
		n			**3**	**3**	**3**	**3**	**3**	**3**	**3**	**3**	**1**	**1**	**1**	**1**	**1**	**3**	**3**
Tupaia	*javanica*	*occidentalis*	AMNH	106505		58	30	88	23	30	61								
Tupaia	*javanica*	*occidentalis*	AMNH	106506		57	42	85		30									
Tupaia	*javanica*	*occidentalis*	AMNH	106507		57	30	104		30									
Tupaia	*javanica*		MCZ	12949		53	41	98	22	32	92								
Tupaia	*javanica*		MHN	450.15	107	56	39	99	28	32		101	7.1	7.7	4.7	18	30	14	79
Tupaia	*javanica*		USNM	154593		60	40	94	29	30	76	97	6.8	8.9	6.8	20	32	16	90
Tupaia	*javanica*		SMNH	A630506	111	57	41	95	29	31	80	92	6.6	8.4	4.9	19	29	16	85
Tupaia	***javanica***	**Mean**			**109**	**57**	**38**	**95**	**26**	**31**	**77**	**96**	**6.8**	**8.3**	**5.4**	**19**	**30**	**15**	**85**
		SD			**2.60**	**1.98**	**5.24**	**6.41**	**3.48**	**1.01**	**12.52**	**4.54**	**0.24**	**0.60**	**1.14**	**0.87**	**1.48**	**1.00**	**5.64**
		n			**2**	**7**	**7**	**7**	**5**	**7**	**4**	**3**	**3**	**3**	**3**	**3**	**3**	**3**	**3**
Tupaia	*minor*	*caedis*	FMNH	140929		57	37	91	29	32	71	100						15	95
Tupaia	*minor*	*caedis*	FMNH	76865	107	57	37	85	29	33	76	105	4.4	8.1	5.2	16	29	14	90
Tupaia	*minor*	*malaccana*	MHN	801.94	110	58	32	97	22	29	65	91	5.5	6.7	5.8	18	30	14	82
Tupaia	*minor*		MNHN	1981-186	107							97	5.2	7.7	5.1	16	27	15	89
Tupaia	*minor*		USNM	396668	109	56	33	91	22	30	66	98	4.5	8.6	4.3	17	29	15	85
Tupaia	*minor*		USNM	396669	112	58	36	102	23	29	83	98	4.6	6.3	4.8	14	27	13	93
Tupaia	*minor*		USNM	396672	104	58	35	93	28	29	65	100	5.3	8.0	5.7	17	31	14	83
Tupaia	*minor*		NNM	36048(a)			35						5.5	8.5	5.8	16	27		
Tupaia	***minor***	**Mean**			**108**	**57**	**35**	**93**	**25**	**30**	**71**	**99**	**5.0**	**7.7**	**5.2**	**16**	**29**	**14**	**88**
		SD			**2.95**	**0.71**	**2.14**	**5.81**	**3.75**	**1.97**	**7.36**	**4.19**	**0.51**	**0.87**	**0.58**	**1.23**	**1.53**	**0.82**	**5.04**
		n			**6**	**6**	**7**	**6**	**6**	**6**	**6**	**7**	**7**	**7**	**7**	**7**	**7**	**7**	**7**
Tupaia	*montana*		USNM	449964	110	57	33	101	15	31	58	90	5.8	6.7	6.2	16	31	15	93
Tupaia	*montana*	*baluensis*	FS	82081	106	56	40	93	23	30	93	91	6.4	6.7	5.6	16	30	16	97
Tupaia	***montana***	**Mean**			**108**	**57**	**36**	**97**	**19**	**30**	**76**	**90**	**6.1**	**6.7**	**5.9**	**16**	**30**	**15**	**95**

Genus	Species	Subspecies	Museum	Number	4	24	25	26	27	28	29	30	31	32	33	34	35	36 (1)	36 (2)
		SD			**2.82**	**0.48**	**4.73**	**5.88**	**5.77**	**0.39**	**24.82**	**0.58**	**0.46**	**0.01**	**0.44**	**0.10**	**0.97**	**0.54**	**2.81**
		n			**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**
Tupaia	***nicobarica***	***nicobarica***	**USNM**	**111782**		**54**	**40**	**96**	**14**	**33**	**77**	**97**	**5.2**	**7.6**	**4.2**	**16**	**28**	**14**	**83**
Tupaia	*palawanensis*	*palawanensis*	FMNH	62950	108	55	44	97	22	32	75	95	5.3	8.3	6.2	17	32	17	95
Tupaia	*palawanensis*	*palawanensis*	FMNH	63018	106	55	46	94	24	32	79	97	5.3	8.4	6.2	16	29	16	96
Tupaia	*palawanensis*	*palawanensis*	FMNH	62976	107	56	44	87	28	35	65	93	6.4	7.2	6.3	16	29	16	100
Tupaia	*palawanensis*	*palawanensis*	FMNH	63020	109	55	43	95	24	35	74	99	6.3	8.5	5.9	18	29	17	99
Tupaia	*palawanensis*	*palawanensis*	FMNH	62977	108	55	43	89	27	35	81	97	6.1	8.7	6.0	18	29	16	93
Tupaia	*palawanensis*	*palawanensis*	FMNH	62978	110	54	44	90	26	34	73	98	6.1	7.3	5.7	16	29	16	91
Tupaia	*palawanensis*	*palawanensis*	FMNH	63019	109	55	45	93	27	36	73	90	6.0	7.7	5.5	17	29	16	92
Tupaia	*palawanensis*	*palawanensis*	FMNH	63017	108	54	46	92	27	35	73	95	4.7	6.9	6.3	16	29	16	99
Tupaia	*palawanensis*	*palawanensis*	FMNH	63016	108	57	44	92	27	33	72	85	5.3	8.2	5.4	17	29	17	97
Tupaia	*palawanensis*	*palawanensis*	FMNH	63011	111	55	44	92	26	34	72	90	4.6	7.6	6.2	17	28	17	97
Tupaia	*palawanensis*	*palawanensis*	FMNH	63010		56	41	91	26	33	68	92	6.3	8.2	4.0	17	30	15	92
Tupaia	***palawanensis***	**Mean**			**108**	**55**	**44**	**92**	**26**	**34**	**73**	**94**	**5.7**	**7.9**	**5.8**	**17**	**29**	**16**	**96**
		SD			**1.40**	**1.00**	**1.41**	**2.72**	**1.67**	**1.33**	**4.49**	**4.30**	**0.67**	**0.58**	**0.69**	**0.78**	**1.08**	**0.66**	**3.19**
		n			**10**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**
Tupaia	*tana*		AMNH	106483		59	39	96	23	27	88								
Tupaia	*tana*		AMNH	106485		57	45	92	22	30	82								
Tupaia	*tana*	*utara*	AMNH	35921	106	58	40	92	23	29	84	93	5.8	6.1	5.8	16	30	15	102
Tupaia	*tana*	*kretami*	FMNH	68793	103	55	41	94	22	31	97	94	6.2	6.8	7.1	17	30	15	88
Tupaia	*tana*	*paitana*	FMNH	76892	103	57	40	94	22	30	83	97	6.3	7.3	5.2	17	30	17	97
Tupaia	*tana*	*banguei*	FMNH	140935	103	55	40	90	25	33	66	102						16	92
Tupaia	*tana*	*banguei*	FMNH	140936	105	55	42	89	26	34	60	102						16	92
Tupaia	*tana*	*paitana*	FMNH	33031	107	55	48	89	24	34	71	97	5.1	6.8	6.5	15	30	17	97
Tupaia	*tana*	*kretami*	FMNH	68797		55	42	88	25	34	66	97	6.4	6.4	7.5	15	30	16	101
Tupaia	*tana*	*paitana*	FMNH	76813	103	55	44	92	24	34	70	94	5.7	6.4	6.1	15	31	16	101
Tupaia	*tana*		MHN	746.11	105	56	41	99	23	29	100	99	6.1	7.3	6.2	17	33	15	89
Tupaia	*tana*		MNHN	1977-361	103							96	6.4	6.6	7.8	17	30	16	101
Tupaia	*tana*	*tana*	USNM	174611		56	38	97	23	30	82								
Tupaia	*tana*	*paitana*	USNM	396660	102	57	42	101	21	29	94	83	6.3	7.9	7.4	16	32	15	90
Tupaia	*tana*		USNM	449965	104	57	46	97	24	28	101	85	5.9	7.7	5.9	17	30	16	96
Tupaia	*tana*		USNM	449966	104	57		99	25	31	102	87	5.3	6.9	8.4	16	30	15	96
Tupaia	*tana*		USNM	449968	103	58	44	100	24	29	104	88	5.5	7.3	7.7	17	31	15	87

Genus	Species	Subspecies	Museum	Number	4	24	25	26	27	28	29	30	31	32	33	34	35	36 (1)	36 (2)
Tupaia	*tana*		USNM	449969	103	56	43	94	24	30	94	87	5.9	7.2	6.4	17	31	15	89
Tupaia	*tana*	*utara*	USNM	83938															91
Tupaia	*tana*	*tana*	USNM	154341		58	46	96	24	30	85	88	4.8	7.3	7.2	17	28	15	92
Tupaia	*tana*		ZS	1910/1462		56	40	96	20	31	79								
Tupaia	***tana***	**Mean**			**104**	**57**	**42**	**95**	**23**	**31**	**85**	**93**	**5.8**	**7.0**	**6.8**	**16**	**30**	**16**	**94**
		SD			**1.36**	**1.33**	**2.62**	**3.96**	**1.59**	**2.06**	**13.55**	**6.03**	**0.50**	**0.52**	**0.93**	**0.74**	**1.15**	**0.70**	**5.13**
		n			**14**	**19**	**18**	**19**	**19**	**19**	**19**	**16**	**14**	**14**	**14**	**14**	**14**	**16**	**17**
Urogale	*everetti*		FMNH	57312	113	54	35	93	26	36	66	103	6.1	7.5	6.6	18	32	17	98
Urogale	*everetti*		FMNH	57148	114	56	40	94	27	35	78	92	6.9	8.0	6.6	19	34	18	98
Urogale	*everetti*		FMNH	57307	113	55	41	91	27	34	71	92	6.6	7.3	6.8	17	31	17	98
Urogale	*everetti*		FMNH	57308	113	57	41	89	26	35	74	95	6.3	8.5	7.4	16	26	17	100
Urogale	*everetti*		FMNH	61418	116	55	43	88	28	35	77	94	7.5	8.8	6.5	18	33	18	94
Urogale	*everetti*		FMNH	61419	118	54	48	90	29	35	74	95	6.3	7.1	8.1	17	31	18	100
Urogale	*everetti*		FMNH	61420	115	55	41	89	28	36	63	95	6.6	7.8	6.9	17	33	17	92
Urogale	*everetti*		FMNH	57329	115	56	39	91	26	36	72	96	7.9	7.9	6.6	18	30	18	98
Urogale	*everetti*		FMNH	57464	112	56	41	93	30	34	93	95	6.5	7.4	6.3	18	28	17	94
Urogale	*everetti*		FMNH	57465	113	56	41	97	28	35	79	92	7.9	7.0	7.0	17	32	18	97
Urogale	*everetti*		FMNH	57311	111	56	43	89	24	32	90	92	6.4	8.3	5.8	18	31	16	89
Urogale	***everetti***	**Mean**			**114**	**55**	**41**	**91**	**27**	**35**	**76**	**95**	**6.8**	**7.8**	**6.8**	**18**	**31**	**17**	**96**
		SD			**1.96**	**0.89**	**2.95**	**2.71**	**1.73**	**1.03**	**8.95**	**3.08**	**0.65**	**0.58**	**0.60**	**0.67**	**2.24**	**0.69**	**3.44**
		n			**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**
Tupaiinae		**Mean**			**109**	**56**	**39**	**94**	**24**	**32**	**75**	**95**	**5.8**	**7.7**	**5.7**	**17**	**29**	**15**	**92**
		n			**63**	**79**	**79**	**79**	**77**	**79**	**76**	**75**	**70**	**69**	**69**	**69**	**69**	**75**	**76**

Table 6.27: Hindlimb indices.
(see Table 2.4 for index descriptions)

Genus	Species	Subspecies	Museum	Number	37 (1)	37 (2)	38	39	40	41	42	43	44	45	46	47
Ptilocercus	*lowii*	*lowii*	FMNH	76855		70	87	97	34	74	102	8.9	9.2	5.4	120	5.7
Ptilocercus	*lowii*		MCZ	51736	10	65	84	78	36	81	123	10.0	9.6	4.2	103	3.0
Ptilocercus	*lowii*		NHM	1934.5.6.1												
Ptilocercus	*lowii*		NHM	67.1479	10	65	97	69		73	116	9.7	9.2	4.7	96	4.5
Ptilocercus	*lowii*		NHM	1960.8.4.6	11	67	95	65	35	85	115	9.9	9.0	4.6	123	4.5
Ptilocercus	*lowii*		NNM	a												
Ptilocercus	***lowii***	**Mean**			**10**	**67**	**91**	**77**	**35**	**78**	**114**	**9.6**	**9.2**	**4.7**	**111**	**4.4**
		SD			**0.35**	**2.09**	**6.30**	**14.47**	**0.63**	**5.75**	**8.77**	**0.48**	**0.25**	**0.50**	**13.12**	**1.11**
		n			**3**	**4**	**4**	**4**	**3**	**4**	**4**	**4**	**4**	**4**	**4**	**4**
Dendrogale	*melanura*		MCZ	36746	15	85	105	49	41	89	119	10.8	10.4	5.6	81	5.7
Dendrogale	*murina*	*frenata*	FMNH	46630	14	83	119	46	34	92	111	10.6	10.4	5.8	83	5.9
Dendrogale	**sp.**	**Mean**			**15**	**84**	**112**	**48**	**38**	**90**	**115**	**10.7**	**10.4**	**5.7**	**82**	**5.8**
		SD			**0.60**	**1.05**	**9.72**	**2.12**	**5.08**	**1.85**	**5.21**	**0.16**	**0.00**	**0.08**	**1.47**	**0.16**
		n			**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**
Tupaia	*glis*	*belangeri*	AMNH	113135	16	94	104	47	28	81	111	10.0	10.0	4.6	87	2.9
Tupaia	*glis*		AMNH	55561	15	98	106	39								
Tupaia	*glis*		AMNH	55562	14	89	118	47								
Tupaia	*glis*	*glis*	FMNH	98470	16	96	109	49	30	83	105	10.1	9.3	4.8	84	2.5
Tupaia	*glis*	*glis*	FMNH	98469	16	97	106	51	28	89	101	10.3	9.6	4.9	83	3.3
Tupaia	*glis*	*glis*	FMNH	98468	15	92	121			91	108	9.7	9.7	6.1	79	
Tupaia	*glis*	*belangeri*	FMNH	46642	16	90	109	37		93	107	10.5	10.7	6.6	81	
Tupaia	*glis*	*wilkinsoni*	FMNH	66019	16	100	115	42		91	127	10.7	9.0	6.7	82	
Tupaia	*glis*	*longipes*	FMNH	76815	13	91	115	43		84	107					
Tupaia	*glis*	*longipes*	FMNH	76819	14	91	124	42		95	127	9.2	8.5	5.4	91	
Tupaia	*glis*	*longipes*	FMNH	76824	13	90	113	48		83	106					
Tupaia	*glis*	*longipes*	FMNH	76825	14	91	108	52		85	121					
Tupaia	*glis*	*demissa*	MHN	801.95	15	95	120	50	27	83	103	9.5	9.4	4.5	82	2.7
Tupaia	*glis*	*belangeri*	MNHN	1990-510	16	98	113	47		83	104					
Tupaia	*glis*	*longipes*	USNM	198043	13	91	115	60	28	90	122	9.5	8.9	4.2	92	4.6
Tupaia	*glis*	*longipes*	USNM	396665	13	88	124	48	26	92	124	9.8	8.1	4.5	92	5.2
Tupaia	*glis*	*longipes*	USNM	396673	12	88	112	54	25	84	123	8.4	8.0	3.7	96	4.9
Tupaia	*glis*		SMNH	A620505	15	90	110	43	30	89	111	10.3	9.7	4.9	76	3.1

Genus	Species	Subspecies	Museum	Number	37 (1)	37 (2)	38	39	40	41	42	43	44	45	46	47
Tupaia	*glis*	*discolor*	ZS	1905/13	15	90	104	50	26	81	112	9.4	9.2	4.5	87	2.6
Tupaia	***glis***	**Mean**			**15**	**93**	**113**	**47**	**28**	**87**	**113**	**9.8**	**9.2**	**5.0**	**85**	**3.5**
		SD			**1.25**	**3.63**	**6.34**	**5.52**	**1.52**	**4.47**	**9.07**	**0.64**	**0.76**	**0.91**	**5.81**	**1.07**
		n			**19**	**19**	**19**	**18**	**9**	**17**	**17**	**13**	**13**	**13**	**13**	**9**
Tupaia	*gracilis*	*gracilis*	FMNH	140925	14	93	136			88	133			5.8	70	
Tupaia	*gracilis*	*gracilis*	FMNH	140928	14	95	116			94	125			5.5	77	
Tupaia	*gracilis*		USNM	449963	13	96	108	44	29	90	117	8.1	8.2	4.2	97	4.9
Tupaia	***gracilis***	**Mean**			**14**	**95**	**120**	**44**	**29**	**91**	**125**	**8.1**	**8.2**	**5.2**	**81**	**4.9**
		SD			**0.35**	**1.67**	**14.70**			**2.62**	**8.15**			**0.87**	**13.92**	
		n			**3**	**3**	**3**	**1**	**1**	**3**	**3**	**1**	**1**	**3**	**3**	**1**
Tupaia	*javanica*	*occidentalis*	AMNH	106505												
Tupaia	*javanica*	*occidentalis*	AMNH	106506												
Tupaia	*javanica*	*occidentalis*	AMNH	106507												
Tupaia	*javanica*		MCZ	12949												
Tupaia	*javanica*		MHN	450.15	13	75	103	49	29	93	111	9.5	9.5	5.2	94	2.6
Tupaia	*javanica*		USNM	154593	14	82	104	64								
Tupaia	*javanica*		SMNH	A630506	15	81	105	56	27	81	122	10.1	9.7	4.8	103	2.5
Tupaia	***javanica***	**Mean**			**14**	**79**	**104**	**57**	**28**	**87**	**117**	**9.8**	**9.6**	**5.0**	**99**	**2.5**
		SD			**0.76**	**3.41**	**1.12**	**7.47**	**1.45**	**8.66**	**8.02**	**0.41**	**0.14**	**0.27**	**6.73**	**0.09**
		n			**3**	**3**	**3**	**3**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**
Tupaia	*minor*	*caedis*	FMNH	140929	15	90	121									
Tupaia	*minor*	*caedis*	FMNH	76865	14	86	109	54		87	111	8.7	9.2	5.3	96	
Tupaia	*minor*	*malaccana*	MHN	801.94	14	82	115	53	28	82	109	10.2	9.0	4.6	86	2.2
Tupaia	*minor*		MNHN	1981-186	15	87	127	53		80	111	9.8	8.6	4.4	82	2.4
Tupaia	*minor*		USNM	396668	15	84	109	62	32	90	112	9.7	9.2	5.3	91	6.5
Tupaia	*minor*		USNM	396669	13	92	111	60	28	83	118	8.1	7.7	4.6	94	4.9
Tupaia	*minor*		USNM	396672	14	81	113	62	33	83	116	9.8	8.8	5.5	95	5.6
Tupaia	*minor*		NNM	36048(a)				48								
Tupaia	***minor***	**Mean**			**14**	**86**	**115**	**56**	**30**	**84**	**113**	**9.4**	**8.8**	**4.9**	**90**	**4.3**
		SD			**0.68**	**4.13**	**6.66**	**5.35**	**2.71**	**3.53**	**3.43**	**0.80**	**0.55**	**0.45**	**5.68**	**1.91**
		n			**7**	**7**	**7**	**7**	**4**	**6**	**6**	**6**	**6**	**6**	**6**	**5**
Tupaia	*montana*		USNM	449964	14	89	109	45	30	91	117	10.0	10.1	4.5	77	5.3
Tupaia	*montana*	*baluensis*	FS	82081	15	92	129	43		86	139	10.4	9.3	4.5	95	3.3
Tupaia	***montana***	**Mean**			**15**	**90**	**119**	**44**	**30**	**89**	**128**	**10.2**	**9.7**	**4.5**	**86**	**4.3**

Genus	Species	Subspecies	Museum	Number	37 (1)	37 (2)	38	39	40	41	42	43	44	45	46	47
		SD			**0.41**	**1.99**	**14.73**	**1.12**		**3.92**	**15.03**	**0.33**	**0.54**	**0.00**	**12.46**	**1.39**
		n			**2**	**2**	**2**	**2**	**1**	**2**	**2**	**2**	**2**	**2**	**2**	**2**
Tupaia	***nicobarica***	***nicobarica***	**USNM**	**111782**	**15**	**85**	**102**	**55**		**85**	**109**				**90**	
Tupaia	*palawanensis*	*palawanensis*	FMNH	62950	15	88	104	46	30	87	101	10.1	10.7	4.9	85	2.5
Tupaia	*palawanensis*	*palawanensis*	FMNH	63018	15	87	102	48	28	89	115	10.9	10.6	5.1	103	2.5
Tupaia	*palawanensis*	*palawanensis*	FMNH	62976	16	98	129	49	30	94	109	9.6	10.4	5.6	83	5.4
Tupaia	*palawanensis*	*palawanensis*	FMNH	63020	16	95	118	51		91	112	10.0	10.6	6.1	81	
Tupaia	*palawanensis*	*palawanensis*	FMNH	62977	16	91	130	46		93	136	10.6	9.8	5.4	87	
Tupaia	*palawanensis*	*palawanensis*	FMNH	62978	15	88	130	51		92	120	10.3	9.7	5.5	86	
Tupaia	*palawanensis*	*palawanensis*	FMNH	63019	15	87	116	47		90	113	10.1	10.0	6.2	83	
Tupaia	*palawanensis*	*palawanensis*	FMNH	63017	16	96	118	43		94	123	9.2	9.1	5.4	81	
Tupaia	*palawanensis*	*palawanensis*	FMNH	63016	16	93	121	46		91	117	8.9	9.7	5.7	86	
Tupaia	*palawanensis*	*palawanensis*	FMNH	63011	17	94	119	49		93	115	10.2	10.6	6.2	86	
Tupaia	*palawanensis*	*palawanensis*	FMNH	63010	15	90	123	45								
Tupaia	***palawanensis***	**Mean**			**16**	**91**	**119**	**47**	**29**	**91**	**116**	**10.0**	**10.1**	**5.6**	**86**	**3.5**
		SD			**0.69**	**3.97**	**9.35**	**2.49**	**1.57**	**2.26**	**9.09**	**0.60**	**0.53**	**0.45**	**6.42**	**1.67**
		n			**11**	**11**	**11**	**11**	**3**	**10**	**10**	**10**	**10**	**10**	**10**	**3**
Tupaia	*tana*		AMNH	106483												
Tupaia	*tana*		AMNH	106485												
Tupaia	*tana*	*utara*	AMNH	35921	15	98	117	47	31	87	111	9.5	9.3	4.9	97	6.9
Tupaia	*tana*	*kretami*	FMNH	68793	15	87	108	48	31	90	112	10.2	9.9	5.1	97	3.2
Tupaia	*tana*	*paitana*	FMNH	76892	17	94	110	45	28	90	111	10.5	10.3	5.1	95	3.6
Tupaia	*tana*	*banguei*	FMNH	140935	16	92	124			85	109	9.5	9.6	6.3	71	
Tupaia	*tana*	*banguei*	FMNH	140936	16	91	124			84	133	9.5	10.2	6.3	74	
Tupaia	*tana*	*paitana*	FMNH	33031	16	94	123	46		99	114	9.4	10.1	5.5	89	
Tupaia	*tana*	*kretami*	FMNH	68797	16	99	121	45		94	110					
Tupaia	*tana*	*paitana*	FMNH	76813	16	98	135	42		87	119	10.6	9.9	5.9	80	
Tupaia	*tana*		MHN	746.11	15	87	116	59	31	86	103	10.7	10.2	4.2	87	3.0
Tupaia	*tana*		MNHN	1977-361	15	97	122	52		87	115	10.1	9.3	5.1	98	3.4
Tupaia	*tana*	*tana*	USNM	174611												
Tupaia	*tana*	*paitana*	USNM	396660	14	86	125	60	29	86	111	9.7	9.8	5.1	83	5.1
Tupaia	*tana*		USNM	449965	15	93	121	48	31	87	115	9.3	9.4	4.8	74	5.1
Tupaia	*tana*		USNM	449966	15	94	120	46	31	94	119	10.5	10.5	4.7	83	5.4
Tupaia	*tana*		USNM	449968	14	83	132	41	32	86	127	10.1	10.3	4.6	88	5.3

Genus	Species	Subspecies	Museum	Number	37 (1)	37 (2)	38	39	40	41	42	43	44	45	46	47
Tupaia	*tana*		USNM	449969	14	87	119	41	32	88	113	9.3	9.2	4.4	93	5.2
Tupaia	*tana*	*utara*	USNM	83938		84	115	55	28	88	112	8.6	9.8	4.4	83	5.7
Tupaia	*tana*	*tana*	USNM	154341	14	90	114	51								
Tupaia	*tana*		ZS	1910/1462												
Tupaia	***tana***	**Mean**			**15**	**91**	**120**	**48**	**30**	**89**	**115**	**9.8**	**9.8**	**5.1**	**86**	**4.7**
		SD			**0.72**	**5.10**	**6.77**	**6.00**	**1.47**	**3.93**	**7.21**	**0.59**	**0.42**	**0.66**	**8.91**	**1.23**
		n			**16**	**17**	**17**	**15**	**10**	**16**	**16**	**15**	**15**	**15**	**15**	**11**
Urogale	*everetti*		FMNH	57312	17	96	117	72	29	95	123	9.9	10.2	5.9	79	3.8
Urogale	*everetti*		FMNH	57148	18	97	135	42		92	110	9.4	10.0	5.6	76	
Urogale	*everetti*		FMNH	57307	17	96	131	50		89	117	9.5	9.8	5.7	77	
Urogale	*everetti*		FMNH	57308	17	99	122	45		91	124	10.0	10.3	5.8	82	
Urogale	*everetti*		FMNH	61418	17	92	122	45		99	134	10.3	10.2	5.8	73	
Urogale	*everetti*		FMNH	61419	18	97	126	51		93	130	9.5	9.2	5.2	72	
Urogale	*everetti*		FMNH	61420	16	91	123	50		99	107	8.8	9.5	5.5	77	
Urogale	*everetti*		FMNH	57329	18	95	132	50		92	116	9.2	10.2	5.7	82	
Urogale	*everetti*		FMNH	57464	17	93	108	51		98	114	9.4	9.6	6.2	83	
Urogale	*everetti*		FMNH	57465	17	87	120	65		85	130	9.3	10.0	6.3	81	
Urogale	*everetti*		FMNH	57311	16	84	109	52	27	85	106	10.9	10.7	4.6	93	3.5
Urogale	***everetti***	**Mean**			**17**	**94**	**122**	**52**	**28**	**93**	**119**	**9.7**	**9.9**	**5.6**	**80**	**3.7**
		SD			**0.65**	**4.55**	**8.74**	**8.91**	**1.96**	**4.94**	**9.68**	**0.59**	**0.42**	**0.47**	**5.74**	**0.19**
		n			**11**	**11**	**11**	**11**	**2**	**11**	**11**	**11**	**11**	**11**	**11**	**2**
Tupaiinae		**Mean**			**15**	**89**	**115**	**50**	**30**	**89**	**117**	**9.7**	**9.5**	**5.2**	**87**	**4.1**
		n			**75**	**76**	**76**	**71**	**34**	**70**	**70**	**62**	**62**	**64**	**65**	**37**

Table 6.28: Hindlimb measurements.
(see Table 2.3 for measurement descriptions)

Genus	Species	Subspecies	Museum	Number	INL	ILL	ILW	IAL	IAW	IPL	ISL	ISW	FEL	FHL	FHW	FGTL	FLTL
Ptilocercus	*lowii*	*lowii*	FMNH	76855	20.33	12.17	2.28	2.98	2.56	5.89	5.50	4.84					
Ptilocercus	*lowii*		MCZ	51736	22.15	13.50	2.82	3.26	2.83	7.17	5.84	4.44	28.78	2.61	2.30	0.81	2.05
Ptilocercus	*lowii*		NHM	1934.5.6.1	21.43	13.10	2.58			6.23	5.74		26.79				
Ptilocercus	*lowii*		NHM	67.1479	21.06	12.24	3.00	3.06	2.67	5.02	5.57	4.12	27.65	2.59	2.29	0.97	2.32
Ptilocercus	*lowii*		NHM	1960.8.4.6	21.61	12.11	2.84	2.84	2.60	4.85	5.85	4.53	26.81	2.54	2.31	1.02	1.94
Ptilocercus	*lowii*		NNM	a	20.14	12.61	2.88			6.06	5.82	4.29	25.76			1.02	2.27
Ptilocercus	***lowii***	**Mean**			**21.12**	**12.62**	**2.73**	**3.04**	**2.67**	**5.87**	**5.72**	**4.44**	**27.16**	**2.58**	**2.30**	**0.96**	**2.15**
		SD			**0.77**	**0.57**	**0.26**	**0.18**	**0.12**	**0.85**	**0.15**	**0.27**	**1.13**	**0.04**	**0.01**	**0.10**	**0.18**
		n			**6**	**6**	**6**	**4**	**4**	**6**	**6**	**5**	**5**	**3**	**3**	**4**	**4**
Dendrogale	*melanura*		MCZ	36746	22.17	12.75	3.23	2.36	2.32	7.08	6.75	5.61	23.18	2.27	2.12	1.21	2.88
Dendrogale	*murina*	*frenata*	FMNH	46630	21.29	11.62	4.66	2.68	2.31	5.33	6.75	5.04	24.05	2.08	2.11	1.39	1.84
Dendrogale	**sp.**	**Mean**			**21.73**	**12.19**	**3.95**	**2.52**	**2.32**	**6.21**	**6.75**	**5.33**	**23.62**	**2.18**	**2.12**	**1.30**	**2.36**
		SD			**0.62**	**0.80**	**1.01**	**0.23**	**0.01**	**1.24**	**0.00**	**0.40**	**0.62**	**0.13**	**0.01**	**0.13**	**0.74**
		n			**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**
Tupaia	*glis*	*belangeri*	AMNH	113135	32.42	18.17	7.24	4.22	4.36	7.54	9.96	8.55	39.28	3.54	3.44	2.32	3.25
Tupaia	*glis*		AMNH	55561	29.45	16.89	7.20	3.44	3.29	6.32	8.92	7.02	35.08	3.05	2.86	2.02	2.11
Tupaia	*glis*		AMNH	55562	30.80	17.54	7.80	4.05	3.96	5.76	9.39	8.46	37.76	3.32	2.95	2.36	2.59
Tupaia	*glis*	*glis*	FMNH	98470	32.24	17.85	7.94	4.37	4.18	8.60	10.03	7.97	39.14	3.54	3.21	2.27	2.77
Tupaia	*glis*	*glis*	FMNH	98469	31.04	17.91	6.89	4.09	3.81	8.11	9.87	8.45	37.45	3.41	3.19	2.41	2.84
Tupaia	*glis*	*glis*	FMNH	98468	31.54	17.14	7.80	3.96	3.75	8.73	10.94	8.20	37.97	3.19	3.22		
Tupaia	*glis*	*belangeri*	FMNH	46642	33.77	18.21	8.52	4.21	3.86	9.55	12.08	9.13	39.27	3.50	3.34	2.41	3.11
Tupaia	*glis*	*wilkinsoni*	FMNH	66019	30.55	16.92	7.31	3.79	3.43	7.71	10.60	7.41	36.33	3.19	2.90	2.36	2.70
Tupaia	*glis*	*longipes*	FMNH	76815	33.65	18.31	7.60	4.11	3.80	8.83	12.14	9.17	45.92	3.40	3.40	2.53	3.02
Tupaia	*glis*	*longipes*	FMNH	76819	32.66	17.45	7.70	4.53	4.28	8.69	11.57	7.91	43.03	3.56	3.36	2.37	2.17
Tupaia	*glis*	*longipes*	FMNH	76824	34.12	18.38	7.50	4.34	4.04	9.17	12.22	7.01	46.33	3.62	3.56	2.47	2.65
Tupaia	*glis*	*longipes*	FMNH	76825	35.52	19.70	7.88	4.43	4.05	8.94	12.47	8.16	46.16	3.62	3.52	2.48	2.88
Tupaia	*glis*	*demissa*	MHN	801.95	32.36	17.99	7.82	4.26	4.24	7.40	9.99	9.06	41.55	3.31	3.13	2.31	2.68
Tupaia	*glis*	*belangeri*	MNHN	1990-510									39.50	3.52	3.44	2.53	
Tupaia	*glis*	*longipes*	USNM	198043	33.94	19.58	7.96	4.51	4.30	7.80	10.01	8.18	45.17	3.88	3.30	2.57	2.86
Tupaia	*glis*	*longipes*	USNM	396665	34.36	19.36	7.71	4.22	4.08	8.09	10.64	7.86	47.43	3.80	3.65	2.90	2.95
Tupaia	*glis*	*longipes*	USNM	396673	34.16	19.23	7.62	4.15	4.11	7.75	10.55	8.14	46.33	3.68	3.53	2.12	3.02
Tupaia	*glis*		SMNH	A620505	30.10	16.82	7.21	3.88	3.63	6.97	9.98	6.57	36.59	3.09	2.90	2.52	3.00

Genus	Species	Subspecies	Museum	Number	INL	ILL	ILW	IAL	IAW	IPL	ISL	ISW	FEL	FHL	FHW	FGTL	FLTL
Tupaia	*glis*	*discolor*	ZS	1905/13									41.91	3.27	3.42	2.67	3.19
Tupaia	***glis***	**Mean**			**32.51**	**18.09**	**7.63**	**4.15**	**3.95**	**8.00**	**10.67**	**8.07**	**41.17**	**3.45**	**3.28**	**2.42**	**2.81**
		SD			**1.73**	**0.94**	**0.38**	**0.28**	**0.31**	**1.01**	**1.07**	**0.74**	**4.02**	**0.23**	**0.24**	**0.20**	**0.31**
		n			**17**	**17**	**17**	**17**	**17**	**17**	**17**	**17**	**19**	**19**	**19**	**18**	**17**
Tupaia	*gracilis*	*gracilis*	FMNH	140925	23.74	13.62	5.22	3.06	2.70	6.96	8.17	5.04	32.27	2.59	2.46		
Tupaia	*gracilis*	*gracilis*	FMNH	140928	24.18	13.38	5.24	3.08	2.68	7.07	8.35	5.20	31.99	2.65	2.56		
Tupaia	*gracilis*		USNM	449963	24.15	13.20	5.60	2.88	2.76	5.47	7.88	5.40	33.35	2.62	2.47	1.83	2.37
Tupaia	***gracilis***	**Mean**			**24.02**	**13.40**	**5.35**	**3.01**	**2.71**	**6.50**	**8.13**	**5.21**	**32.54**	**2.62**	**2.50**	**1.83**	**2.37**
		SD			**0.25**	**0.21**	**0.21**	**0.11**	**0.04**	**0.89**	**0.24**	**0.18**	**0.72**	**0.03**	**0.06**		
		n			**3**	**3**	**3**	**3**	**3**	**3**	**3**	**3**	**3**	**3**	**3**	**1**	**1**
Tupaia	*javanica*	*occidentalis*	AMNH	106505	21.67	12.49	3.78	2.97	2.61	5.02	6.43	3.94					
Tupaia	*javanica*	*occidentalis*	AMNH	106506	25.17	14.34	6.05	3.36	2.87		7.66						
Tupaia	*javanica*	*occidentalis*	AMNH	106507	23.86	13.50	4.03	2.99	3.10		7.16						
Tupaia	*javanica*		MCZ	12949	27.37	14.53	5.90	3.33	3.27	5.89	8.84	8.10					
Tupaia	*javanica*		MHN	450.15	23.38	12.99	5.08	2.91	2.89	6.57	7.47		28.31	2.55	2.57	2.01	2.18
Tupaia	*javanica*		USNM	154593	24.98	14.88	5.92	2.87	2.71	7.23	7.51	5.70	28.88	2.76	2.67	1.95	2.57
Tupaia	*javanica*		SMNH	A630506	25.18	14.31	5.91	3.21	3.05	7.23	7.70	6.14	30.63	2.90	2.66	2.03	2.56
Tupaia	***javanica***	**Mean**			**24.52**	**13.86**	**5.24**	**3.09**	**2.93**	**6.39**	**7.54**	**5.97**	**29.27**	**2.74**	**2.63**	**2.00**	**2.44**
		SD			**1.78**	**0.88**	**0.97**	**0.20**	**0.23**	**0.94**	**0.72**	**1.71**	**1.21**	**0.18**	**0.06**	**0.04**	**0.22**
		n			**7**	**7**	**7**	**7**	**7**	**5**	**7**	**4**	**3**	**3**	**3**	**3**	**3**
Tupaia	*minor*	*caedis*	FMNH	140929	21.93	12.51	4.69	3.11	2.82	6.41	7.09	5.05	25.52	2.29	2.30		
Tupaia	*minor*	*caedis*	FMNH	76865	22.07	12.55	4.64	3.30	2.81	6.39	7.37	5.62	27.24	2.26	2.38	1.19	2.21
Tupaia	*minor*	*malaccana*	MHN	801.94	23.71	13.70	4.32	3.18	3.09	5.18	6.81	4.40	28.12	2.54	2.32	1.56	1.89
Tupaia	*minor*		MNHN	1981-186									27.67	2.49	2.42	1.45	2.12
Tupaia	*minor*		USNM	396668	22.87	12.91	4.28	3.16	2.89	4.98	6.92	4.58	26.73	2.60	2.56	1.20	2.30
Tupaia	*minor*		USNM	396669	24.10	13.93	5.06	2.90	2.96	5.45	7.07	5.87	34.50	2.60	2.55	1.58	2.18
Tupaia	*minor*		USNM	396672	22.98	13.41	4.72	2.75	2.55	6.54	6.60	4.30	27.37	2.48	2.48	1.44	2.20
Tupaia	*minor*		NNM	36048(a)		13.65	4.74						27.58			1.53	2.34
Tupaia	***minor***	**Mean**			**22.94**	**13.24**	**4.64**	**3.07**	**2.85**	**5.83**	**6.98**	**4.97**	**28.09**	**2.47**	**2.43**	**1.42**	**2.18**
		SD			**0.86**	**0.58**	**0.27**	**0.20**	**0.18**	**0.70**	**0.26**	**0.66**	**2.71**	**0.14**	**0.10**	**0.16**	**0.15**
		n			**6**	**7**	**7**	**6**	**6**	**6**	**6**	**6**	**8**	**7**	**7**	**7**	**7**
Tupaia	*montana*		USNM	449964	31.66	18.05	5.97	3.56	3.59	4.62	9.67	5.63	36.78	3.34	3.00	2.13	2.47
Tupaia	*montana*	*baluensis*	FS	82081	31.47	17.73	7.05	4.42	4.09	7.16	9.44	8.81	39.25	3.74	3.39	2.53	2.63
Tupaia	***montana***	**Mean**			**31.57**	**17.89**	**6.51**	**3.99**	**3.84**	**5.89**	**9.56**	**7.22**	**38.02**	**3.54**	**3.20**	**2.33**	**2.55**

Genus	Species	Subspecies	Museum	Number	INL	ILL	ILW	IAL	IAW	IPL	ISL	ISW	FEL	FHL	FHW	FGTL	FLTL
		SD			**0.13**	**0.23**	**0.76**	**0.61**	**0.35**	**1.80**	**0.16**	**2.25**	**1.75**	**0.28**	**0.28**	**0.28**	**0.11**
		n			**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**
Tupaia	***nicobarica***	***nicobarica***	**USNM**	**111782**	**31.86**	**17.29**	**6.95**	**3.92**	**3.76**	**4.56**	**10.39**	**7.96**	**37.88**	**3.65**	**3.55**	**1.96**	**2.89**
Tupaia	*palawanensis*	*palawanensis*	FMNH	62950	32.21	17.85	7.85	4.31	4.16	7.21	10.18	7.62	37.85	3.61	3.44	2.02	3.14
Tupaia	*palawanensis*	*palawanensis*	FMNH	63018	30.99	17.13	7.82	4.14	3.88	7.38	10.01	7.94	37.43	3.11	3.02	2.00	3.14
Tupaia	*palawanensis*	*palawanensis*	FMNH	62976	30.64	17.15	7.59	3.60	3.13	8.49	10.61	6.91	36.96	3.18	2.95	2.38	2.67
Tupaia	*palawanensis*	*palawanensis*	FMNH	63020	30.39	16.77	7.23	3.82	3.64	7.43	10.66	7.88	35.99	3.04	3.00	2.27	3.05
Tupaia	*palawanensis*	*palawanensis*	FMNH	62977	30.07	16.60	7.14	3.84	3.42	8.16	10.51	8.55	35.62	3.05	2.95	2.16	3.09
Tupaia	*palawanensis*	*palawanensis*	FMNH	62978	29.92	16.05	7.06	3.91	3.53	7.85	10.14	7.39	35.85	2.95	2.90	2.18	2.61
Tupaia	*palawanensis*	*palawanensis*	FMNH	63019	30.82	16.84	7.64	3.73	3.48	8.28	11.02	7.99	35.76	3.00	2.70	2.16	2.75
Tupaia	*palawanensis*	*palawanensis*	FMNH	63017	31.42	16.82	7.78	3.94	3.61	8.47	11.13	8.12	36.90	2.95	2.80	1.72	2.56
Tupaia	*palawanensis*	*palawanensis*	FMNH	63016	31.30	17.82	7.80	3.93	3.60	8.53	10.32	7.41	36.76	3.31	2.80	1.93	3.00
Tupaia	*palawanensis*	*palawanensis*	FMNH	63011	31.91	17.69	7.78	4.06	3.74	8.20	10.84	7.85	36.16	3.45	3.10	1.65	2.75
Tupaia	*palawanensis*	*palawanensis*	FMNH	63010	30.38	17.03	7.00	3.83	3.49	8.03	10.12	6.89	37.18	3.25	3.00	2.34	3.05
Tupaia	***palawanensis***	**Mean**			**30.91**	**17.07**	**7.52**	**3.92**	**3.61**	**8.00**	**10.50**	**7.69**	**36.59**	**3.17**	**2.97**	**2.07**	**2.89**
		SD			**0.74**	**0.55**	**0.34**	**0.20**	**0.26**	**0.47**	**0.38**	**0.51**	**0.75**	**0.21**	**0.19**	**0.24**	**0.22**
		n			**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**
Tupaia	*tana*		AMNH	106483	34.09	20.18	7.97	4.97	4.79	7.73	9.36	8.20					
Tupaia	*tana*		AMNH	106485	36.39	20.68	9.21	5.23	4.83	8.10	10.83	8.83					
Tupaia	*tana*	*utara*	AMNH	35921	30.77	17.99	7.21	4.24	3.92	7.16	8.95	7.49	38.89	3.38	3.14	2.25	2.39
Tupaia	*tana*	*kretami*	FMNH	68793	37.44	20.52	8.46	5.55	5.23	8.22	11.55	11.24	47.65	4.25	3.99	2.95	3.22
Tupaia	*tana*	*paitana*	FMNH	76892	36.33	20.82	8.27	5.50	5.17	7.85	10.86	9.00	45.42	4.24	4.13	2.87	3.33
Tupaia	*tana*	*banguei*	FMNH	140935	33.62	18.64	7.48	4.87	4.38	8.38	10.97	7.28	41.06	3.69	3.76		
Tupaia	*tana*	*banguei*	FMNH	140936	34.24	18.71	7.94	4.64	4.15	8.79	11.60	6.93	41.27	3.69	3.77		
Tupaia	*tana*	*paitana*	FMNH	33031	37.83	20.94	9.98	5.85	5.18	9.18	12.99	9.25	45.76	4.06	3.92	2.34	3.09
Tupaia	*tana*	*kretami*	FMNH	68797	35.46	19.66	8.28	4.91	4.30	9.00	11.94	7.88	44.19	4.06	3.94	2.81	2.81
Tupaia	*tana*	*paitana*	FMNH	76813	37.81	20.83	9.16	5.41	4.99	9.15	12.80	8.94	46.69	4.04	3.79	2.65	2.99
Tupaia	*tana*		MHN	746.11	38.52	21.74	8.84	5.82	5.74	8.98	11.19	11.14	49.05	4.71	4.65	3.00	3.59
Tupaia	*tana*		MNHN	1977-361									46.66	4.09	3.93	2.98	3.08
Tupaia	*tana*	*tana*	USNM	174611	35.65	20.12	7.69	5.16	5.03	8.12	10.71	8.80					
Tupaia	*tana*	*paitana*	USNM	396660	37.30	21.31	8.95	4.75	4.81	7.84	10.76	10.13	47.92	4.46	3.72	3.04	3.78
Tupaia	*tana*		USNM	449965	36.29	20.77	9.49	4.70	4.56	8.80	10.25	10.40	44.50	4.31	3.65	2.62	3.44
Tupaia	*tana*		USNM	449966	34.82	19.89		4.20	4.16	8.72	10.66	10.90	43.66	3.98	3.45	2.32	3.02
Tupaia	*tana*		USNM	449968	36.05	21.00	9.33	4.49	4.49	8.82	10.55	11.00	42.69	4.22	3.72	2.33	3.11

Genus	Species	Subspecies	Museum	Number	INL	ILL	ILW	IAL	IAW	IPL	ISL	ISW	FEL	FHL	FHW	FGTL	FLTL
Tupaia	*tana*		USNM	449969	36.88	20.68	8.92	4.71	4.42	8.98	11.02	10.35	46.24	4.38	3.81	2.75	3.31
Tupaia	*tana*	*utara*	USNM	83938													
Tupaia	*tana*	*tana*	USNM	154341	36.18	21.10	9.74	4.53	4.35	8.58	10.75	9.16	46.00	4.25	3.72	2.23	3.35
Tupaia	*tana*		ZS	1910/1462	36.36	20.30	8.21	5.34	5.14	7.15	11.15	8.76					
Tupaia	***tana***	**Mean**			**35.90**	**20.31**	**8.62**	**4.99**	**4.72**	**8.40**	**10.99**	**9.25**	**44.85**	**4.11**	**3.82**	**2.65**	**3.18**
		SD			**1.82**	**0.97**	**0.79**	**0.49**	**0.47**	**0.63**	**0.97**	**1.35**	**2.77**	**0.32**	**0.32**	**0.30**	**0.34**
		n			**19**	**19**	**18**	**19**	**19**	**19**	**19**	**19**	**16**	**16**	**16**	**14**	**14**
Urogale	*everetti*		FMNH	57312	39.61	21.37	7.57	4.86	4.53	10.49	14.13	9.33	43.57	3.85	3.96	2.66	3.28
Urogale	*everetti*		FMNH	57148	39.89	22.51	9.10	4.38	4.12	10.89	13.86	10.88	40.96	3.91	3.59	2.84	3.28
Urogale	*everetti*		FMNH	57307	41.61	22.89	9.45	4.85	4.40	11.30	14.17	10.00	43.04	4.04	3.73	2.84	3.16
Urogale	*everetti*		FMNH	57308	40.28	22.92	9.29	4.88	4.36	10.49	13.97	10.30	44.33	4.09	3.90	2.79	3.78
Urogale	*everetti*		FMNH	61418	40.64	22.45	9.62	4.94	4.33	11.26	14.16	10.94	42.74	3.99	3.75	3.19	3.75
Urogale	*everetti*		FMNH	61419	40.16	21.88	10.43	4.85	4.35	11.53	13.96	10.39	41.11	3.85	3.66	2.59	2.90
Urogale	*everetti*		FMNH	61420	43.63	23.78	9.66	4.75	4.24	12.02	15.62	9.84	42.71	3.91	3.72	2.84	3.34
Urogale	*everetti*		FMNH	57329	40.14	22.51	8.86	4.67	4.24	10.47	14.32	10.33	41.72	4.06	3.88	3.31	3.31
Urogale	*everetti*		FMNH	57464	41.25	22.97	9.50	5.11	4.77	12.55	14.22	13.17	43.32	4.13	3.94	2.81	3.19
Urogale	*everetti*		FMNH	57465	40.21	22.32	9.14	4.57	4.42	11.30	14.02	11.09	43.10	4.04	3.72	3.41	3.03
Urogale	*everetti*		FMNH	57311	38.45	21.47	9.30	4.85	4.33	9.07	12.33	11.06	42.94	4.24	3.92	2.76	3.55
Urogale	***everetti***	**Mean**			**40.53**	**22.46**	**9.27**	**4.79**	**4.37**	**11.03**	**14.07**	**10.67**	**42.69**	**4.01**	**3.80**	**2.91**	**3.32**
		SD			**1.32**	**0.70**	**0.69**	**0.20**	**0.17**	**0.92**	**0.75**	**1.00**	**1.03**	**0.12**	**0.13**	**0.27**	**0.27**
		n			**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**

Table 6.28: Hindlimb measurements.
(see Table 2.3 for measurement descriptions)

Genus	Species	Subspecies	Museum	Number	FTTL	FMSML	FMSAP	FPGL	FPGW	FDEW	FMCD	FLCD	FMCW	FLCW	FMCL	FLCL
Ptilocercus	*lowii*	*lowii*	FMNH	76855				2.17	2.11	4.20	3.32	2.92	1.43	1.24	2.15	1.97
Ptilocercus	*lowii*		MCZ	51736	0.56	2.25		2.89	2.26	4.44	3.23	2.89	1.50	1.26	2.25	2.18
Ptilocercus	*lowii*		NHM	1934.5.6.1			1.97									
Ptilocercus	*lowii*		NHM	67.1479	0.38	1.96		3.29	2.27	4.37	3.23	2.85	1.59	1.54	1.99	1.95
Ptilocercus	*lowii*		NHM	1960.8.4.6	0.60	1.83		3.39	2.19	4.28	3.04	2.88	1.46	1.39	1.97	1.97
Ptilocercus	*lowii*		NNM	a	0.44	1.90	1.79			3.95						
Ptilocercus	***lowii***	**Mean**			**0.50**	**1.99**	**1.88**	**2.94**	**2.21**	**4.25**	**3.21**	**2.89**	**1.50**	**1.36**	**2.09**	**2.02**
		SD			**0.10**	**0.18**	**0.13**	**0.55**	**0.07**	**0.19**	**0.12**	**0.03**	**0.07**	**0.14**	**0.13**	**0.11**
		n			**4**	**4**	**2**	**4**	**4**	**5**	**4**	**4**	**4**	**4**	**4**	**4**
Dendrogale	*melanura*		MCZ	36746	1.24	1.96		4.06	1.99	4.17	3.63	3.53	1.29	1.36	2.09	2.17
Dendrogale	*murina*	*frenata*	FMNH	46630	1.65	1.86	1.80	3.52	1.62	4.16	3.58	3.46	1.20	1.43	2.11	2.13
Dendrogale	**sp.**	**Mean**			**1.45**	**1.91**	**1.80**	**3.79**	**1.81**	**4.17**	**3.61**	**3.50**	**1.25**	**1.40**	**2.10**	**2.15**
		SD			**0.29**	**0.07**		**0.38**	**0.26**	**0.01**	**0.04**	**0.05**	**0.06**	**0.05**	**0.01**	**0.03**
		n			**2**	**2**	**1**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**
Tupaia	*glis*	*belangeri*	AMNH	113135	2.20	3.25	3.10	6.30	2.95	6.65	6.48	6.22	2.24	2.34	3.45	3.56
Tupaia	*glis*		AMNH	55561	2.11	2.44		6.86	2.70	5.43	5.40	5.30	1.79	1.89	3.21	3.19
Tupaia	*glis*		AMNH	55562	2.14	2.79		5.69	2.69	6.00	5.40	5.31	1.95	2.30	3.18	3.13
Tupaia	*glis*	*glis*	FMNH	98470	2.16	2.85	2.73	6.33	3.12	6.65	6.44	6.36	2.10	2.29	3.41	3.59
Tupaia	*glis*	*glis*	FMNH	98469	2.08	2.80	2.60	5.76	2.91	6.19	6.19	6.03	2.00	2.12	3.28	3.39
Tupaia	*glis*	*glis*	FMNH	98468		2.91	2.55		3.07	6.31	6.01	5.79	2.09	2.52	3.34	3.48
Tupaia	*glis*	*belangeri*	FMNH	46642	2.17	2.89	3.15	7.43	2.76	6.84	6.40	6.14	2.33	2.54	3.49	3.56
Tupaia	*glis*	*wilkinsoni*	FMNH	66019	1.87	2.88	2.65	6.38	2.68	5.95	6.16	5.93	2.12	2.44	3.34	3.08
Tupaia	*glis*	*longipes*	FMNH	76815	2.53	3.05	3.02	7.48	3.25	6.73	6.20	6.13	2.23	2.57	3.48	3.56
Tupaia	*glis*	*longipes*	FMNH	76819	2.81	2.90	2.79	7.25	3.03	6.68	6.17	6.07	2.13	2.65	3.34	3.45
Tupaia	*glis*	*longipes*	FMNH	76824	2.98	3.15	2.71	7.03	3.38	6.89	6.43	6.21	2.30	2.60	3.57	3.70
Tupaia	*glis*	*longipes*	FMNH	76825	2.97	3.30	2.88	6.79	3.54	6.90	6.67	6.31	2.41	2.61	3.57	3.70
Tupaia	*glis*	*demissa*	MHN	801.95	2.67	3.11	2.59	6.46	3.20	6.40	6.24	6.10	2.06	2.48	3.45	3.71
Tupaia	*glis*	*belangeri*	MNHN	1990-510		2.85	3.05	6.94	3.24	6.42	6.29	6.29	2.20	2.48	3.51	3.72
Tupaia	*glis*	*longipes*	USNM	198043	2.80	3.17		5.25	3.17	6.61	6.32	5.99	2.27	2.60	3.75	3.65
Tupaia	*glis*	*longipes*	USNM	396665	3.20	3.29		7.51	3.61	6.97	6.39	6.14	2.31	2.87	3.74	3.69
Tupaia	*glis*	*longipes*	USNM	396673	2.92	3.21		6.24	3.34	6.38	5.89	5.63	2.34	2.61	3.45	3.34
Tupaia	*glis*		SMNH	A620505	2.00	2.87	2.73	6.28	2.71	5.98	5.80	5.38	1.82	2.01	3.24	3.20

Genus	Species	Subspecies	Museum	Number	FTTL	FMSML	FMSAP	FPGL	FPGW	FDEW	FMCD	FLCD	FMCW	FLCW	FMCL	FLCL
Tupaia	*glis*	*discolor*	ZS	1905/13	1.62	2.96	2.78	6.37	3.19	6.77	6.25	6.12	2.21	2.30	3.53	3.60
Tupaia	***glis***	**Mean**			**2.43**	**2.98**	**2.81**	**6.58**	**3.08**	**6.46**	**6.16**	**5.97**	**2.15**	**2.43**	**3.44**	**3.49**
		SD			**0.46**	**0.22**	**0.20**	**0.64**	**0.29**	**0.41**	**0.34**	**0.33**	**0.17**	**0.24**	**0.16**	**0.21**
		n			**17**	**19**	**14**	**18**	**19**	**19**	**19**	**19**	**19**	**19**	**19**	**19**
Tupaia	*gracilis*	*gracilis*	FMNH	140925		2.21	2.13		2.46	4.72	4.52	4.38	1.41	1.92	2.63	2.56
Tupaia	*gracilis*	*gracilis*	FMNH	140928		2.42	2.20		2.28	4.73	4.72	4.51	1.59	1.84	2.60	2.56
Tupaia	*gracilis*		USNM	449963	1.73	2.15		5.28	2.30	4.67	4.50	4.48	1.57	1.69	2.65	2.67
Tupaia	***gracilis***	**Mean**			**1.73**	**2.26**	**2.17**	**5.28**	**2.35**	**4.71**	**4.58**	**4.46**	**1.52**	**1.82**	**2.63**	**2.60**
		SD				**0.14**	**0.05**		**0.10**	**0.03**	**0.12**	**0.07**	**0.10**	**0.12**	**0.03**	**0.06**
		n			**1**	**3**	**2**	**1**	**3**	**3**	**3**	**3**	**3**	**3**	**3**	**3**
Tupaia	*javanica*	*occidentalis*	AMNH	106505												
Tupaia	*javanica*	*occidentalis*	AMNH	106506												
Tupaia	*javanica*	*occidentalis*	AMNH	106507												
Tupaia	*javanica*		MCZ	12949												
Tupaia	*javanica*		MHN	450.15	1.32	2.18	1.88	4.90	2.41	5.01	3.96	3.78	1.55	1.60	2.40	2.30
Tupaia	*javanica*		USNM	154593	1.95	2.40		4.32	2.77	5.05	4.56	4.12	1.56	1.63	2.47	2.51
Tupaia	*javanica*		SMNH	A630506	1.51	2.24	2.11	5.28	2.98	5.61	4.79	4.55	1.83	1.93	2.72	2.72
Tupaia	***javanica***	**Mean**			**1.59**	**2.27**	**2.00**	**4.83**	**2.72**	**5.22**	**4.44**	**4.15**	**1.65**	**1.72**	**2.53**	**2.51**
		SD			**0.32**	**0.11**	**0.16**	**0.48**	**0.29**	**0.34**	**0.43**	**0.39**	**0.16**	**0.18**	**0.17**	**0.21**
		n			**3**	**3**	**2**	**3**	**3**	**3**	**3**	**3**	**3**	**3**	**3**	**3**
Tupaia	*minor*	*caedis*	FMNH	140929		1.92	1.83		2.22	4.13	3.94	3.72	1.46	1.77	2.28	2.31
Tupaia	*minor*	*caedis*	FMNH	76865	1.41	1.93	1.90	4.07	2.19	4.34	3.90	3.73	1.63	1.78	2.19	2.22
Tupaia	*minor*	*malaccana*	MHN	801.94	1.64	2.25	1.83	4.34	2.29	4.92	4.05	4.01	1.49	1.71	2.39	2.49
Tupaia	*minor*		MNHN	1981-186	1.40	1.93	1.71	4.49	2.40	4.76	4.24	4.12	1.47	1.86	2.36	2.38
Tupaia	*minor*		USNM	396668	1.15	2.27		4.11	2.53	4.60	3.92	3.88	1.63	1.77	2.38	2.40
Tupaia	*minor*		USNM	396669	1.67	2.40		4.02	2.41	4.85	4.50	4.46	1.64	1.82	2.68	2.75
Tupaia	*minor*		USNM	396672	1.56	2.21		3.71	2.29	4.63	3.82	3.74	1.53	1.73	2.33	2.24
Tupaia	*minor*		NNM	36048(a)	1.61	2.18		4.92	2.34	4.60						
Tupaia	***minor***	**Mean**			**1.49**	**2.14**	**1.82**	**4.24**	**2.33**	**4.60**	**4.05**	**3.95**	**1.55**	**1.78**	**2.37**	**2.40**
		SD			**0.18**	**0.19**	**0.08**	**0.39**	**0.11**	**0.26**	**0.24**	**0.27**	**0.08**	**0.05**	**0.15**	**0.18**
		n			**7**	**8**	**4**	**7**	**8**	**8**	**7**	**7**	**7**	**7**	**7**	**7**
Tupaia	*montana*		USNM	449964	2.27	2.96		5.90	2.65	5.92	5.48	5.27	1.87	2.03	3.25	3.12
Tupaia	*montana*	*baluensis*	FS	82081	2.18	3.06	3.26	6.67	2.89	6.37	6.15	5.85	2.11	2.73	3.35	3.34
Tupaia	***montana***	**Mean**			**2.23**	**3.01**	**3.26**	**6.29**	**2.77**	**6.15**	**5.82**	**5.56**	**1.99**	**2.38**	**3.30**	**3.23**

Genus	Species	Subspecies	Museum	Number	FTTL	FMSML	FMSAP	FPGL	FPGW	FDEW	FMCD	FLCD	FMCW	FLCW	FMCL	FLCL
		SD			**0.06**	**0.07**		**0.54**	**0.17**	**0.32**	**0.47**	**0.41**	**0.17**	**0.49**	**0.07**	**0.16**
		n			**2**	**2**	**1**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**
Tupaia	***nicobarica***	***nicobarica***	**USNM**	**111782**	**1.58**	**2.88**		**6.28**	**3.47**	**6.53**	**5.39**	**5.53**	**2.15**	**2.20**	**3.44**	**3.41**
Tupaia	*palawanensis*	*palawanensis*	FMNH	62950	2.36	3.20	2.79	6.26	2.91	6.67	6.33	5.84	2.18	2.27	3.28	3.28
Tupaia	*palawanensis*	*palawanensis*	FMNH	63018	2.33	3.05	2.78	5.86	2.81	6.32	6.09	5.51	2.26	2.30	3.22	3.19
Tupaia	*palawanensis*	*palawanensis*	FMNH	62976	2.33	2.82	2.66	5.29	2.60	6.11	6.09	6.01	2.02	2.60	3.21	3.36
Tupaia	*palawanensis*	*palawanensis*	FMNH	63020	2.13	2.92	2.71	5.61	2.85	6.14	6.10	5.83	2.06	2.43	3.33	3.19
Tupaia	*palawanensis*	*palawanensis*	FMNH	62977	2.12	2.84	2.67	6.26	2.85	6.09	5.64	5.53	2.05	2.66	3.30	3.44
Tupaia	*palawanensis*	*palawanensis*	FMNH	62978	2.03	2.80	2.52	5.37	2.72	6.26	5.71	5.50	2.04	2.65	3.21	3.29
Tupaia	*palawanensis*	*palawanensis*	FMNH	63019	1.97	2.69	2.46	5.80	2.74	6.13	5.64	5.32	2.08	2.42	3.28	3.30
Tupaia	*palawanensis*	*palawanensis*	FMNH	63017	2.32	2.71	2.54	6.64	2.84	6.02	5.96	5.76	2.02	2.38	3.21	3.26
Tupaia	*palawanensis*	*palawanensis*	FMNH	63016	1.98	2.84	2.51	6.20	2.86	6.32	6.16	5.90	2.15	2.61	3.19	3.31
Tupaia	*palawanensis*	*palawanensis*	FMNH	63011	2.25	3.18	2.86	5.70	2.81	6.45	6.26	6.05	2.22	2.64	3.46	3.34
Tupaia	*palawanensis*	*palawanensis*	FMNH	63010	1.47	2.54	2.50	6.08	2.74	6.02	5.55	5.42	1.95	2.39	3.35	3.20
Tupaia	***palawanensis***	**Mean**			**2.12**	**2.87**	**2.64**	**5.92**	**2.79**	**6.23**	**5.96**	**5.70**	**2.09**	**2.49**	**3.28**	**3.29**
		SD			**0.26**	**0.20**	**0.14**	**0.41**	**0.09**	**0.20**	**0.27**	**0.25**	**0.10**	**0.15**	**0.08**	**0.08**
		n			**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**
Tupaia	*tana*		AMNH	106483												
Tupaia	*tana*		AMNH	106485												
Tupaia	*tana*	*utara*	AMNH	35921	2.25	2.76		5.45	2.55	5.90	6.00	5.79	1.96	2.29	3.53	3.69
Tupaia	*tana*	*kretami*	FMNH	68793	3.38	3.97	3.48	8.07	3.88	8.32	7.32	7.26	2.83	3.07	4.25	4.42
Tupaia	*tana*	*paitana*	FMNH	76892	2.34	3.52	3.38	8.30	3.70	7.95	7.75	7.50	2.69	2.97	4.08	4.21
Tupaia	*tana*	*banguei*	FMNH	140935		3.24	3.18		3.28	7.02	6.46	6.44	2.30	2.85	3.63	3.86
Tupaia	*tana*	*banguei*	FMNH	140936		3.23	3.18		3.34	7.18	6.57	6.50	2.23	2.77	3.58	3.80
Tupaia	*tana*	*paitana*	FMNH	33031	2.97	3.62	3.24	7.58	3.47	7.89	7.63	7.43	2.74	3.38	4.10	4.15
Tupaia	*tana*	*kretami*	FMNH	68797	3.31	3.46	3.35	7.11	3.17	6.99	7.03	6.89	2.48	3.01	3.88	4.01
Tupaia	*tana*	*paitana*	FMNH	76813	2.84	3.81	3.68	7.97	3.35	7.53	7.61	7.40	2.57	3.47	4.24	4.33
Tupaia	*tana*		MHN	746.11	3.02	4.25	3.87	7.17	4.26	8.47	7.50	7.39	2.79	3.25	4.20	4.28
Tupaia	*tana*		MNHN	1977-361	3.65	3.33	3.37	6.99	3.60	7.42	7.52	7.20	2.46	2.99	4.09	4.12
Tupaia	*tana*	*tana*	USNM	174611												
Tupaia	*tana*	*paitana*	USNM	396660	3.53	3.50		6.08	3.63	7.89	7.10	6.76	2.57	3.20	4.04	4.04
Tupaia	*tana*		USNM	449965	2.62	3.38		7.23	3.44	7.23	6.97	6.71	2.32	2.80	3.91	3.91
Tupaia	*tana*		USNM	449966	3.66	3.19		6.91	3.20	6.94	6.64	6.55	2.23	2.68	3.71	3.66
Tupaia	*tana*		USNM	449968	3.28	3.44		7.83	3.22	7.31	6.33	6.06	2.34	3.08	3.97	3.95

Genus	Species	Subspecies	Museum	Number	FTTL	FMSML	FMSAP	FPGL	FPGW	FDEW	FMCD	FLCD	FMCW	FLCW	FMCL	FLCL
Tupaia	*tana*		USNM	449969	2.94	3.50		8.10	3.33	7.67	6.82	6.65	2.39	2.85	3.74	3.69
Tupaia	*tana*	*utara*	USNM	83938				6.57	3.63	7.55	6.86	6.37	2.50	2.87	4.03	4.00
Tupaia	*tana*	*tana*	USNM	154341	3.29	3.38		6.43	3.29	7.33	6.74	6.59	2.50	2.86	3.96	4.01
Tupaia	*tana*		ZS	1910/1462												
Tupaia	***tana***	**Mean**			**3.08**	**3.47**	**3.41**	**7.19**	**3.43**	**7.45**	**6.99**	**6.79**	**2.46**	**2.96**	**3.94**	**4.01**
		SD			**0.45**	**0.34**	**0.23**	**0.82**	**0.36**	**0.60**	**0.51**	**0.51**	**0.23**	**0.28**	**0.23**	**0.23**
		n			**14**	**16**	**9**	**15**	**17**	**17**	**17**	**17**	**17**	**17**	**17**	**17**
Urogale	*everetti*		FMNH	57312	2.89	3.87	3.53	5.03	3.64	7.60	7.46	7.33	2.71	3.16	4.45	4.44
Urogale	*everetti*		FMNH	57148	2.71	3.32	3.18	8.14	3.42	7.48	7.36	7.24	2.40	3.25	3.96	4.01
Urogale	*everetti*		FMNH	57307	2.91	3.72	3.63	7.47	3.70	7.58	7.46	7.31	2.72	3.55	4.04	4.12
Urogale	*everetti*		FMNH	57308	3.28	3.48	3.46	8.18	3.68	7.61	7.61	7.55	2.84	3.47	4.37	4.40
Urogale	*everetti*		FMNH	61418	2.76	3.87	3.43	8.05	3.64	8.05	7.60	7.44	2.91	3.55	4.40	4.55
Urogale	*everetti*		FMNH	61419	3.34	3.74	3.40	6.61	3.39	7.42	7.39	7.20	2.58	3.25	3.83	4.03
Urogale	*everetti*		FMNH	61420	2.96	3.73	3.40	7.20	3.63	7.69	7.09	7.02	2.77	3.40	4.00	4.08
Urogale	*everetti*		FMNH	57329	2.75	3.71	3.41	7.48	3.73	7.77	7.63	7.38	2.58	3.40	3.95	4.18
Urogale	*everetti*		FMNH	57464	2.75	3.66	3.53	8.02	4.07	7.69	7.26	7.16	2.70	2.92	4.03	4.07
Urogale	*everetti*		FMNH	57465	3.03	3.84	3.31	6.09	3.96	8.21	7.93	7.15	2.85	3.43	4.17	4.26
Urogale	*everetti*		FMNH	57311	2.49	3.34	3.27	7.49	3.88	7.90	7.03	6.66	2.52	2.74	3.88	4.04
Urogale	***everetti***	**Mean**			**2.90**	**3.66**	**3.41**	**7.25**	**3.70**	**7.73**	**7.44**	**7.22**	**2.69**	**3.28**	**4.10**	**4.20**
		SD			**0.25**	**0.20**	**0.13**	**0.99**	**0.21**	**0.24**	**0.26**	**0.24**	**0.16**	**0.26**	**0.22**	**0.19**
		n			**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**

Table 6.28: Hindlimb measurements.
(see Table 2.3 for measurement descriptions)

Genus	Species	Subspecies	Museum	Number	FICNW	FLTLT	FLTTT	TL	TLCL	TMCL	TLCW	TMCW	TPEW	TPEL	TDEW	TMML
Ptilocercus	*lowii*	*lowii*	FMNH	76855	1.30			26.99	2.41	2.48	1.67	1.64	3.91	2.91	2.41	1.46
Ptilocercus	*lowii*		MCZ	51736	1.19	4.79	7.15	29.91	2.99	2.86	2.05	1.67	4.23	3.42	2.60	1.26
Ptilocercus	*lowii*		NHM	1934.5.6.1				29.83								
Ptilocercus	*lowii*		NHM	67.1479	1.25	4.46	7.05	28.67	2.79	2.64	1.93	1.66	4.06	2.97	2.56	1.35
Ptilocercus	*lowii*		NHM	1960.8.4.6	1.27	3.74	6.97	28.23	2.79	2.53	1.99	1.73	3.99	3.41	2.54	1.29
Ptilocercus	*lowii*		NNM	a		3.95	6.59							3.44		
Ptilocercus	***lowii***	**Mean**			**1.25**	**4.24**	**6.94**	**28.73**	**2.75**	**2.63**	**1.91**	**1.68**	**4.05**	**3.23**	**2.53**	**1.34**
		SD			**0.05**	**0.48**	**0.24**	**1.21**	**0.24**	**0.17**	**0.17**	**0.04**	**0.14**	**0.27**	**0.08**	**0.09**
		n			**4**	**4**	**4**	**5**	**4**	**4**	**4**	**4**	**4**	**5**	**4**	**4**
Dendrogale	*melanura*		MCZ	36746	1.39	4.21	6.58	25.71	2.78	2.68	1.91	1.61	3.89	3.46	2.88	1.45
Dendrogale	*murina*	*frenata*	FMNH	46630	1.26	3.83	7.10	25.70	2.72	2.68	1.58	1.42	3.91	3.58	2.88	1.48
Dendrogale	**sp.**	**Mean**			**1.33**	**4.02**	**6.84**	**25.71**	**2.75**	**2.68**	**1.75**	**1.52**	**3.90**	**3.52**	**2.88**	**1.47**
		SD			**0.09**	**0.27**	**0.37**	**0.01**	**0.04**	**0.00**	**0.23**	**0.13**	**0.01**	**0.08**	**0.00**	**0.02**
		n			**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**
Tupaia	*glis*	*belangeri*	AMNH	113135	1.72	6.27	10.88	43.90	4.41	4.39	3.01	2.70	6.69	5.44	4.28	2.03
Tupaia	*glis*		AMNH	55561	1.74	5.77	10.22									
Tupaia	*glis*		AMNH	55562	1.64	6.55	10.45									
Tupaia	*glis*	*glis*	FMNH	98470	1.85	6.38	11.29	42.10	4.25	3.92	2.92	2.79	6.48	5.37	4.19	2.01
Tupaia	*glis*	*glis*	FMNH	98469	1.79	6.17	11.49	40.52	4.19	3.89	2.84	2.82	5.93	5.26	4.14	1.97
Tupaia	*glis*	*glis*	FMNH	98468	1.97			40.20	3.90	3.88	2.82	2.62	6.01	5.45	4.61	2.45
Tupaia	*glis*	*belangeri*	FMNH	46642		7.17	12.11	42.14	4.43	4.51	2.62	2.46	6.49	6.02	4.70	2.77
Tupaia	*glis*	*wilkinsoni*	FMNH	66019		6.30	9.98	38.36	4.11	3.44	2.66	2.09	5.93	5.42	4.35	2.57
Tupaia	*glis*	*longipes*	FMNH	76815		6.36	12.02		4.17	4.43	2.97	2.77	6.48	5.42		
Tupaia	*glis*	*longipes*	FMNH	76819		6.46	12.04	48.34	4.43	4.12	2.72	2.15	6.17	5.85	4.67	2.59
Tupaia	*glis*	*longipes*	FMNH	76824		6.54	12.34		4.36	4.22	2.69	2.53	6.73	5.60		
Tupaia	*glis*	*longipes*	FMNH	76825		6.55	13.21		4.43	4.30	2.95	2.44	6.64	5.64		
Tupaia	*glis*	*demissa*	MHN	801.95	2.16	6.35	11.69	43.41	4.12	4.10	2.87	2.79	6.47	5.38	4.18	1.97
Tupaia	*glis*	*belangeri*	MNHN	1990-510	2.11				4.14	3.57	2.81	2.70	6.77	5.64		
Tupaia	*glis*	*longipes*	USNM	198043	2.10	7.20	12.07	49.40	4.68	4.40	3.11	2.55	6.87	6.17	4.97	2.06
Tupaia	*glis*	*longipes*	USNM	396665	2.01	7.45	13.20	52.71	5.14	4.25	3.11	2.50	7.00	6.47	5.15	2.36
Tupaia	*glis*	*longipes*	USNM	396673	1.79	6.75	12.64	50.23	4.20	4.01	2.99	2.43	6.66	5.61	4.77	1.88
Tupaia	*glis*		SMNH	A620505	1.70	6.43	10.72	39.83	4.10	3.85	2.64	2.37	5.87	5.20	4.30	1.94

Genus	Species	Subspecies	Museum	Number	FICNW	FLTLT	FLTTT	TL	TLCL	TMCL	TLCW	TMCW	TPEW	TPEL	TDEW	TMML
Tupaia	*glis*	*discolor*	ZS	1905/13	2.18	6.23	11.67	46.72	4.37	4.28	3.13	2.79	6.78	5.50	4.34	2.11
Tupaia	***glis***	**Mean**			**1.90**	**6.53**	**11.65**	**44.45**	**4.32**	**4.09**	**2.87**	**2.56**	**6.47**	**5.61**	**4.51**	**2.21**
		SD			**0.19**	**0.42**	**0.96**	**4.57**	**0.28**	**0.30**	**0.17**	**0.22**	**0.36**	**0.34**	**0.32**	**0.30**
		n			**13**	**17**	**17**	**13**	**17**	**17**	**17**	**17**	**17**	**17**	**13**	**13**
Tupaia	*gracilis*	*gracilis*	FMNH	140925	1.53			36.71			2.38	1.79	4.60	4.07	3.28	2.13
Tupaia	*gracilis*	*gracilis*	FMNH	140928	1.50			36.56			2.28	1.82	4.56	4.27	3.33	2.02
Tupaia	*gracilis*		USNM	449963	1.48	5.04	8.99	38.80	3.13	3.17	2.24	1.92	4.64	4.19	3.47	1.62
Tupaia	***gracilis***	**Mean**			**1.50**	**5.04**	**8.99**	**37.36**	**3.13**	**3.17**	**2.30**	**1.84**	**4.60**	**4.18**	**3.36**	**1.92**
		SD			**0.03**			**1.25**			**0.07**	**0.07**	**0.04**	**0.10**	**0.10**	**0.27**
		n			**3**	**1**	**1**	**3**	**1**	**1**	**3**	**3**	**3**	**3**	**3**	**3**
Tupaia	*javanica*	*occidentalis*	AMNH	106505												
Tupaia	*javanica*	*occidentalis*	AMNH	106506												
Tupaia	*javanica*	*occidentalis*	AMNH	106507												
Tupaia	*javanica*		MCZ	12949												
Tupaia	*javanica*		MHN	450.15	1.55	5.06	8.49	30.32	2.89	2.87	2.01	1.81	4.59	4.27	3.38	1.58
Tupaia	*javanica*		USNM	154593	1.56	5.66	9.28									
Tupaia	*javanica*		SMNH	A630506	1.70	5.69	8.97	33.93	3.43	3.28	2.35	1.92	5.36	4.33	3.55	1.64
Tupaia	***javanica***	**Mean**			**1.60**	**5.47**	**8.91**	**32.13**	**3.16**	**3.08**	**2.18**	**1.87**	**4.98**	**4.30**	**3.47**	**1.61**
		SD			**0.08**	**0.36**	**0.40**	**2.55**	**0.38**	**0.29**	**0.24**	**0.08**	**0.54**	**0.04**	**0.12**	**0.04**
		n			**3**	**3**	**3**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**
Tupaia	*minor*	*caedis*	FMNH	140929	1.34											
Tupaia	*minor*	*caedis*	FMNH	76865		4.41	7.94	29.09	2.54	2.68	1.95	1.76	4.08	3.53	2.65	1.53
Tupaia	*minor*	*malaccana*	MHN	801.94	1.56	4.96	8.45	30.84	3.15	2.77	1.94	1.78	4.67	3.82	3.19	1.43
Tupaia	*minor*		MNHN	1981-186	1.36	4.40	7.60	29.58	2.91	2.54	1.87	1.68	4.51	3.62	3.18	1.31
Tupaia	*minor*		USNM	396668	1.20	4.61	7.85	29.17	2.82	2.69	2.00	1.78	4.29	3.86	3.32	1.54
Tupaia	*minor*		USNM	396669	1.50	4.77	9.23	38.76	3.14	3.00	2.27	1.92	4.97	4.14	3.65	1.77
Tupaia	*minor*		USNM	396672	1.49	4.56	8.40	28.40	2.79	2.50	2.06	1.78	4.33	3.59	3.24	1.56
Tupaia	*minor*		NNM	36048(a)		4.52	7.50									
Tupaia	***minor***	**Mean**			**1.41**	**4.60**	**8.14**	**30.97**	**2.89**	**2.70**	**2.02**	**1.78**	**4.48**	**3.76**	**3.21**	**1.52**
		SD			**0.13**	**0.20**	**0.60**	**3.90**	**0.23**	**0.18**	**0.14**	**0.08**	**0.31**	**0.23**	**0.32**	**0.15**
		n			**6**	**7**	**7**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**
Tupaia	*montana*		USNM	449964	1.75	6.00	11.42	40.61	4.05	4.10	2.58	2.20	5.66	5.17	4.14	1.82
Tupaia	*montana*	*baluensis*	FS	82081	2.01	6.46	11.65	41.77	4.36	3.90	3.02	2.18	6.34	5.44	4.00	1.87
Tupaia	***montana***	**Mean**			**1.88**	**6.23**	**11.54**	**41.19**	**4.21**	**4.00**	**2.80**	**2.19**	**6.00**	**5.31**	**4.07**	**1.85**

Genus	Species	Subspecies	Museum	Number	FICNW	FLTLT	FLTTT	TL	TLCL	TMCL	TLCW	TMCW	TPEW	TPEL	TDEW	TMML
		SD			**0.18**	**0.33**	**0.16**	**0.82**	**0.22**	**0.14**	**0.31**	**0.01**	**0.48**	**0.19**	**0.10**	**0.04**
		n			**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**
Tupaia	***nicobarica***	***nicobarica***	**USNM**	**111782**	**1.99**	**6.22**	**10.75**		**3.97**	**4.06**	**3.17**	**2.91**	**6.46**	**5.49**	**4.64**	**1.91**
Tupaia	*palawanensis*	*palawanensis*	FMNH	62950	2.03	6.27	12.18	41.03	4.14	4.39	2.80	2.76	6.24	5.40	4.19	2.01
Tupaia	*palawanensis*	*palawanensis*	FMNH	63018	1.77	6.13	10.96	39.73	4.33	4.22	2.67	2.33	6.08	5.43	4.10	2.01
Tupaia	*palawanensis*	*palawanensis*	FMNH	62976		6.00	10.57	39.51	3.79	4.09	2.51	2.30	5.86	5.51	4.49	2.20
Tupaia	*palawanensis*	*palawanensis*	FMNH	63020		6.34	10.50	39.36	3.93	4.16	2.56	2.28	5.93	5.42	4.32	2.39
Tupaia	*palawanensis*	*palawanensis*	FMNH	62977		6.58	10.45	38.31	4.05	3.74	2.72	2.00	5.74	5.31	4.00	2.07
Tupaia	*palawanensis*	*palawanensis*	FMNH	62978		5.81	10.45	39.41	4.05	3.84	2.57	2.15	5.69	5.22	3.93	2.15
Tupaia	*palawanensis*	*palawanensis*	FMNH	63019		6.10	10.38	39.00	3.92	3.89	2.66	2.36	5.91	5.34	4.42	2.41
Tupaia	*palawanensis*	*palawanensis*	FMNH	63017		5.73	10.60	39.96	3.67	3.65	2.71	2.21	5.90	5.55	4.01	2.17
Tupaia	*palawanensis*	*palawanensis*	FMNH	63016		6.21	10.48	39.56	3.53	3.82	2.76	2.35	6.04	5.50	3.80	2.24
Tupaia	*palawanensis*	*palawanensis*	FMNH	63011		6.06	10.21	40.03	4.09	4.23	2.71	2.35	6.18	5.72	4.21	2.50
Tupaia	*palawanensis*	*palawanensis*	FMNH	63010		6.20	11.19									
Tupaia	***palawanensis***	**Mean**			**1.90**	**6.13**	**10.72**	**39.59**	**3.95**	**4.00**	**2.67**	**2.31**	**5.96**	**5.44**	**4.15**	**2.22**
		SD			**0.18**	**0.24**	**0.55**	**0.71**	**0.24**	**0.25**	**0.09**	**0.19**	**0.18**	**0.14**	**0.22**	**0.17**
		n			**2**	**11**	**11**	**10**	**10**	**10**	**10**	**10**	**10**	**10**	**10**	**10**
Tupaia	*tana*		AMNH	106483												
Tupaia	*tana*		AMNH	106485												
Tupaia	*tana*	*utara*	AMNH	35921	1.81	6.14	11.53	41.30	3.94	3.84	3.02	2.73	6.12	5.33	4.65	2.02
Tupaia	*tana*	*kretami*	FMNH	68793	2.08	7.93	14.45	49.13	5.01	4.84	3.58	3.19	7.89	7.09	4.98	2.52
Tupaia	*tana*	*paitana*	FMNH	76892	2.27	7.70	13.66	46.97	4.93	4.82	3.63	3.28	7.73	6.95	4.95	2.41
Tupaia	*tana*	*banguei*	FMNH	140935	2.16			42.38	4.02	4.07	3.08	2.83	6.90	5.89	4.55	2.66
Tupaia	*tana*	*banguei*	FMNH	140936	2.31			43.21	4.12	4.39	3.60	2.70	6.96	5.88	4.94	2.74
Tupaia	*tana*	*paitana*	FMNH	33031		6.95	13.64	48.92	4.62	4.95	3.66	3.21	7.29	7.23	5.11	2.71
Tupaia	*tana*	*kretami*	FMNH	68797		6.81	13.19		4.67	4.64	3.19	2.89	6.78	6.35		
Tupaia	*tana*	*paitana*	FMNH	76813		7.07	14.46	48.00	5.09	4.76	3.45	2.91	7.33	6.39	4.56	2.83
Tupaia	*tana*		MHN	746.11	2.51	8.17	16.12	51.33	5.49	5.24	3.66	3.55	8.40	7.21	5.45	2.17
Tupaia	*tana*		MNHN	1977-361	2.18	7.83	14.23	47.98	4.83	4.45	3.64	3.16	7.36	6.41	5.04	2.46
Tupaia	*tana*	*tana*	USNM	174611												
Tupaia	*tana*	*paitana*	USNM	396660	2.67	7.87	15.36	48.87	4.74	4.77	3.11	2.79	7.47	6.43	5.16	2.48
Tupaia	*tana*		USNM	449965	2.35	7.58	13.15	46.38	4.31	4.37	3.36	2.91	7.28	6.33	5.01	2.23
Tupaia	*tana*		USNM	449966	1.96	6.78	13.25	45.50	4.77	4.80	3.19	2.68	6.72	6.35	5.01	2.15
Tupaia	*tana*		USNM	449968	2.03	7.28	13.44	43.99	4.43	4.54	3.39	2.67	7.05	6.08	5.30	2.01

Genus	Species	Subspecies	Museum	Number	FICNW	FLTLT	FLTTT	TL	TLCL	TMCL	TLCW	TMCW	TPEW	TPEL	TDEW	TMML
Tupaia	*tana*		USNM	449969	2.17	7.69	14.31	47.80	4.43	4.40	3.08	2.72	6.91	6.11	5.19	2.08
Tupaia	*tana*	*utara*	USNM	83938	2.26			51.00	4.41	4.99	3.15	2.82	7.56	6.67	5.50	2.22
Tupaia	*tana*	*tana*	USNM	154341	2.16	7.91	13.01									
Tupaia	*tana*		ZS	1910/1462												
Tupaia	***tana***	**Mean**			**2.21**	**7.41**	**13.84**	**46.85**	**4.61**	**4.62**	**3.36**	**2.94**	**7.23**	**6.42**	**5.03**	**2.38**
		SD			**0.22**	**0.58**	**1.11**	**3.03**	**0.42**	**0.36**	**0.24**	**0.26**	**0.53**	**0.52**	**0.28**	**0.27**
		n			**14**	**14**	**14**	**15**	**16**	**16**	**16**	**16**	**16**	**16**	**15**	**15**
Urogale	*everetti*		FMNH	57312	1.75	7.70	13.75	49.02	4.83	4.98	3.71	3.01	7.75	7.35	5.64	2.87
Urogale	*everetti*		FMNH	57148		7.63	14.13	46.63	4.39	4.66	3.23	2.94	7.40	6.82	5.01	2.61
Urogale	*everetti*		FMNH	57307		7.26	13.52	48.83	4.66	4.77	3.51	3.00	7.69	6.88	5.40	2.78
Urogale	*everetti*		FMNH	57308		7.25	11.65	49.98	5.00	5.15	3.53	2.85	7.76	7.10	5.05	2.89
Urogale	*everetti*		FMNH	61418		7.68	14.06	49.45	5.11	5.02	3.73	2.79	7.32	7.25	5.66	2.86
Urogale	*everetti*		FMNH	61419		7.13	12.80	48.37	4.61	4.43	3.68	2.83	7.57	7.07	4.93	2.51
Urogale	*everetti*		FMNH	61420		7.38	14.06	49.26	4.35	4.68	3.09	2.88	7.22	7.13	5.31	2.69
Urogale	*everetti*		FMNH	57329		7.69	12.56	48.16	4.43	4.89	3.27	2.81	7.37	6.79	5.23	2.76
Urogale	*everetti*		FMNH	57464		7.69	12.31	48.36	4.53	4.62	3.43	3.00	7.62	7.44	5.29	2.99
Urogale	*everetti*		FMNH	57465		7.38	13.68	48.49	4.50	4.87	3.83	2.94	7.92	6.70	5.51	3.05
Urogale	*everetti*		FMNH	57311	2.09	7.72	13.19	47.85	5.23	5.10	3.54	3.35	7.38	6.27	4.78	2.19
Urogale	***everetti***	**Mean**			**1.92**	**7.50**	**13.25**	**48.58**	**4.69**	**4.83**	**3.50**	**2.95**	**7.55**	**6.98**	**5.26**	**2.75**
		SD			**0.24**	**0.22**	**0.82**	**0.90**	**0.30**	**0.22**	**0.23**	**0.16**	**0.22**	**0.33**	**0.29**	**0.24**
		n			**2**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**

Table 6.28: Hindlimb measurements.
(see Table 2.3 for measurement descriptions)

Genus	Species	Subspecies	Museum	Number	TMMW	TDASW	TDASL	TCL	FIL	FILML	FIHL	FILMW
Ptilocercus	*lowii*	*lowii*	FMNH	76855	0.80	1.72	2.07	9.28	25.56	1.46	2.34	1.82
Ptilocercus	*lowii*		MCZ	51736	0.84	1.80	1.85	10.65	27.26	0.82	2.89	1.92
Ptilocercus	*lowii*		NHM	1934.5.6.1					27.22			
Ptilocercus	*lowii*		NHM	67.1479	0.80	1.79	1.72		27.25	1.22	2.87	1.76
Ptilocercus	*lowii*		NHM	1960.8.4.6	0.96	1.49	1.83	9.81	26.42	1.20	2.67	1.92
Ptilocercus	*lowii*		NNM	a				9.17	25.33			
Ptilocercus	***lowii***	**Mean**			**0.85**	**1.70**	**1.87**	**9.73**	**26.51**	**1.18**	**2.69**	**1.86**
		SD			**0.08**	**0.14**	**0.15**	**0.68**	**0.89**	**0.26**	**0.26**	**0.08**
		n			**4**	**4**	**4**	**4**	**6**	**4**	**4**	**4**
Dendrogale	*melanura*		MCZ	36746	0.80	2.08	1.69	10.58	24.45	1.39	2.38	1.92
Dendrogale	*murina*	*frenata*	FMNH	46630	0.75	1.92	1.60	8.73	24.00	1.42	1.92	1.89
Dendrogale	**sp.**	**Mean**			**0.78**	**2.00**	**1.65**	**9.66**	**24.23**	**1.41**	**2.15**	**1.91**
		SD			**0.04**	**0.11**	**0.06**	**1.31**	**0.32**	**0.02**	**0.33**	**0.02**
		n			**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**
Tupaia	*glis*	*belangeri*	AMNH	113135	1.11	3.04	2.63	12.12	41.56	1.20	3.56	2.48
Tupaia	*glis*		AMNH	55561								
Tupaia	*glis*		AMNH	55562								
Tupaia	*glis*	*glis*	FMNH	98470	1.38	3.04	2.54	12.60	39.38	1.00	3.22	2.35
Tupaia	*glis*	*glis*	FMNH	98469	1.25	2.87	2.38	11.17	37.83	1.26	3.49	2.61
Tupaia	*glis*	*glis*	FMNH	98468	1.21	2.82	2.23		37.56		3.34	2.31
Tupaia	*glis*	*belangeri*	FMNH	46642	1.53	3.15	2.55		38.51		4.37	2.72
Tupaia	*glis*	*wilkinsoni*	FMNH	66019	1.11	2.76	2.26		36.19		3.61	2.53
Tupaia	*glis*	*longipes*	FMNH	76815							3.65	
Tupaia	*glis*	*longipes*	FMNH	76819	1.44	2.90	2.63		45.78		3.49	2.47
Tupaia	*glis*	*longipes*	FMNH	76824							3.46	
Tupaia	*glis*	*longipes*	FMNH	76825								
Tupaia	*glis*	*demissa*	MHN	801.95	1.34	3.14	2.59	11.85	40.62	1.08	3.82	2.61
Tupaia	*glis*	*belangeri*	MNHN	1990-510								
Tupaia	*glis*	*longipes*	USNM	198043	1.48	3.04	2.79	13.68	48.00	2.20	4.13	2.66
Tupaia	*glis*	*longipes*	USNM	396665	1.69	3.18	2.91	13.91	49.94	2.62	3.70	2.98
Tupaia	*glis*	*longipes*	USNM	396673	1.61	2.82	2.71	12.75	47.92	2.33	3.44	2.85
Tupaia	*glis*		SMNH	A620505	1.32	2.99	2.27	11.91	37.56	1.18	3.55	2.76

Genus	Species	Subspecies	Museum	Number	TMMW	TDASW	TDASL	TCL	FIL	FILML	FIHL	FILMW
Tupaia	*glis*	*discolor*	ZS	1905/13	1.34	3.08	2.69	12.35	42.28	1.09		2.68
Tupaia	***glis***	**Mean**			**1.37**	**2.99**	**2.55**	**12.48**	**41.78**	**1.55**	**3.63**	**2.62**
		SD			**0.18**	**0.14**	**0.21**	**0.88**	**4.65**	**0.64**	**0.30**	**0.19**
		n			**13**	**13**	**13**	**9**	**13**	**9**	**14**	**13**
Tupaia	*gracilis*	*gracilis*	FMNH	140925	1.16	2.20	1.53		34.88		2.65	2.17
Tupaia	*gracilis*	*gracilis*	FMNH	140928	1.11	2.26	1.75					
Tupaia	*gracilis*		USNM	449963	1.22	2.07	2.00	11.06	37.58	1.86	2.96	2.36
Tupaia	***gracilis***	**Mean**			**1.16**	**2.18**	**1.76**	**11.06**	**36.23**	**1.86**	**2.81**	**2.27**
		SD			**0.06**	**0.10**	**0.24**		**1.91**		**0.22**	**0.13**
		n			**3**	**3**	**3**	**1**	**2**	**1**	**2**	**2**
Tupaia	*javanica*	*occidentalis*	AMNH	106505								
Tupaia	*javanica*	*occidentalis*	AMNH	106506								
Tupaia	*javanica*	*occidentalis*	AMNH	106507								
Tupaia	*javanica*		MCZ	12949								
Tupaia	*javanica*		MHN	450.15	1.04	2.30	2.16	8.88	28.52	0.74	2.81	1.93
Tupaia	*javanica*		USNM	154593								
Tupaia	*javanica*		SMNH	A630506	1.16	2.33	2.41	9.24	32.08	0.79	3.36	2.45
Tupaia	***javanica***	**Mean**			**1.10**	**2.32**	**2.29**	**9.06**	**30.30**	**0.77**	**3.09**	**2.19**
		SD			**0.08**	**0.02**	**0.18**	**0.25**	**2.52**	**0.04**	**0.39**	**0.37**
		n			**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**
Tupaia	*minor*	*caedis*	FMNH	140929								
Tupaia	*minor*	*caedis*	FMNH	76865	0.75	2.02	1.93		27.61		2.47	1.81
Tupaia	*minor*	*malaccana*	MHN	801.94	1.09	2.24	1.92	8.61	28.95	0.64	2.87	1.94
Tupaia	*minor*		MNHN	1981-186	0.95	2.13	1.74		27.91	0.67	2.56	1.69
Tupaia	*minor*		USNM	396668	0.95	2.14	1.94	9.19	27.25	1.76	2.88	1.91
Tupaia	*minor*		USNM	396669	1.20	2.08	1.96	10.84	36.87	1.80	3.17	2.28
Tupaia	*minor*		USNM	396672	1.06	1.85	1.76	9.48	27.31	1.52	2.80	1.93
Tupaia	*minor*		NNM	36048(a)					27.60			
Tupaia	***minor***	**Mean**			**1.00**	**2.08**	**1.88**	**9.53**	**29.07**	**1.28**	**2.79**	**1.93**
		SD			**0.15**	**0.13**	**0.10**	**0.95**	**3.49**	**0.58**	**0.25**	**0.20**
		n			**6**	**6**	**6**	**4**	**7**	**5**	**6**	**6**
Tupaia	*montana*		USNM	449964	1.34	2.76	2.13	12.24	39.32	2.08	3.27	2.35
Tupaia	*montana*	*baluensis*	FS	82081	1.28	2.88	2.73		39.77	1.32	3.92	2.50
Tupaia	***montana***	**Mean**			**1.31**	**2.82**	**2.43**	**12.24**	**39.55**	**1.70**	**3.60**	**2.43**

Genus	Species	Subspecies	Museum	Number	TMMW	TDASW	TDASL	TCL	FIL	FILML	FIHL	FILMW
		SD			**0.04**	**0.08**	**0.42**		**0.32**	**0.54**	**0.46**	**0.11**
		n			**2**	**2**	**2**	**1**	**2**	**2**	**2**	**2**
Tupaia	***nicobarica***	***nicobarica***	**USNM**	**111782**	**1.58**	**3.09**	**2.79**	**12.10**		**2.22**	**2.83**	**2.75**
Tupaia	*palawanensis*	*palawanensis*	FMNH	62950	1.32	2.81	2.40	12.26	38.35	0.96	3.76	2.80
Tupaia	*palawanensis*	*palawanensis*	FMNH	63018	1.41	2.37	2.45	10.93	37.41	0.93	3.92	2.69
Tupaia	*palawanensis*	*palawanensis*	FMNH	62976	1.46	2.77	2.29	12.04	36.89	1.99	2.82	2.50
Tupaia	*palawanensis*	*palawanensis*	FMNH	63020	1.32	2.88	2.33		36.97		3.58	2.56
Tupaia	*palawanensis*	*palawanensis*	FMNH	62977	1.32	2.62	2.29		36.02		3.47	2.53
Tupaia	*palawanensis*	*palawanensis*	FMNH	62978	1.19	2.77	2.38		35.96		3.56	2.43
Tupaia	*palawanensis*	*palawanensis*	FMNH	63019	1.42	2.74	2.28		36.85		3.46	2.41
Tupaia	*palawanensis*	*palawanensis*	FMNH	63017	1.13	2.77	2.25		37.58		3.00	2.40
Tupaia	*palawanensis*	*palawanensis*	FMNH	63016	1.06	2.73	2.35		37.44		3.53	2.39
Tupaia	*palawanensis*	*palawanensis*	FMNH	63011	1.39	2.74	2.36		37.71		3.67	2.64
Tupaia	*palawanensis*	*palawanensis*	FMNH	63010								
Tupaia	***palawanensis***	**Mean**			**1.30**	**2.72**	**2.34**	**11.74**	**37.12**	**1.29**	**3.48**	**2.54**
		SD			**0.13**	**0.14**	**0.06**	**0.71**	**0.74**	**0.60**	**0.33**	**0.14**
		n			**10**	**10**	**10**	**3**	**10**	**3**	**10**	**10**
Tupaia	*tana*		AMNH	106483								
Tupaia	*tana*		AMNH	106485								
Tupaia	*tana*	*utara*	AMNH	35921	1.58	2.94	2.85	12.83	38.90	2.70		2.34
Tupaia	*tana*	*kretami*	FMNH	68793	1.61	3.63	3.53	15.03	46.88	1.51	4.43	3.18
Tupaia	*tana*	*paitana*	FMNH	76892	1.41	3.63	3.46	13.26	44.46	1.58	4.30	3.15
Tupaia	*tana*	*banguei*	FMNH	140935	1.29	3.22	2.28		39.85		3.68	2.75
Tupaia	*tana*	*banguei*	FMNH	140936	1.31	3.21	2.38		40.44		3.68	2.80
Tupaia	*tana*	*paitana*	FMNH	33031	1.61	3.57	3.16		47.09		3.56	3.13
Tupaia	*tana*	*kretami*	FMNH	68797							4.29	
Tupaia	*tana*	*paitana*	FMNH	76813	1.65	3.33	2.66		45.23		4.19	3.06
Tupaia	*tana*		MHN	746.11	1.68	3.75	3.25	15.66	48.31	1.46	4.95	2.99
Tupaia	*tana*		MNHN	1977-361	1.62	3.61	3.52		45.76	1.57	4.41	2.98
Tupaia	*tana*	*tana*	USNM	174611								
Tupaia	*tana*	*paitana*	USNM	396660	1.76	3.33	2.77	14.39	46.96	2.38	4.26	3.00
Tupaia	*tana*		USNM	449965	1.63	3.21	2.36	14.30	44.49	2.26	4.34	3.00
Tupaia	*tana*		USNM	449966	1.56	3.32	2.77	14.00	43.28	2.33	3.97	2.60
Tupaia	*tana*		USNM	449968	1.63	3.24	2.86	14.28	42.91	2.26	4.15	3.09

Genus	Species	Subspecies	Museum	Number	TMMW	TDASW	TDASL	TCL	FIL	FILML	FIHL	FILMW
Tupaia	*tana*		USNM	449969	1.64	3.23	3.00	15.48	46.41	2.40	4.44	3.14
Tupaia	*tana*	*utara*	USNM	83938	1.64	3.67	3.05	14.37	47.86	2.73	4.52	2.73
Tupaia	*tana*	*tana*	USNM	154341								
Tupaia	*tana*		ZS	1910/1462								
Tupaia	***tana***	**Mean**			**1.57**	**3.39**	**2.93**	**14.36**	**44.59**	**2.11**	**4.21**	**2.93**
		SD			**0.13**	**0.23**	**0.41**	**0.89**	**2.97**	**0.48**	**0.36**	**0.24**
		n			**15**	**15**	**15**	**10**	**15**	**11**	**15**	**15**
Urogale	*everetti*		FMNH	57312	1.86	3.52	2.77	14.36	46.34	1.76	4.60	3.29
Urogale	*everetti*		FMNH	57148	1.70	3.45	2.63		44.75		4.38	3.05
Urogale	*everetti*		FMNH	57307	1.79	3.49	2.69		46.21		4.55	2.98
Urogale	*everetti*		FMNH	57308	1.89	3.43	2.80		47.25		4.76	3.09
Urogale	*everetti*		FMNH	61418	1.60	3.52	2.58		46.29		4.82	3.09
Urogale	*everetti*		FMNH	61419	1.58	3.48	2.50		45.84		4.30	2.88
Urogale	*everetti*		FMNH	61420	1.61	3.41	2.64		46.55		4.73	2.86
Urogale	*everetti*		FMNH	57329	1.64	3.52	2.88		45.50		4.57	3.03
Urogale	*everetti*		FMNH	57464	1.96	3.43	2.85		45.54		4.70	2.70
Urogale	*everetti*		FMNH	57465	1.88	3.32	2.69		45.73		4.46	2.88
Urogale	*everetti*		FMNH	57311	1.39	3.05	2.84	12.69	45.26	1.60	4.60	2.81
Urogale	***everetti***	**Mean**			**1.72**	**3.42**	**2.72**	**13.53**	**45.93**	**1.68**	**4.59**	**2.97**
		SD			**0.17**	**0.14**	**0.12**	**1.18**	**0.69**	**0.11**	**0.16**	**0.16**
		n			**11**	**11**	**11**	**2**	**11**	**2**	**11**	**11**

CHAPTER 7: CHARACTER ANALYSIS AND SYSTEMATICS

TUPAIID SYSTEMATICS AND BIOGEOGRAPHY

Detailed analyses of the species-level phylogeny and biogeography of tupaiids have been, and will continue to be, based on cranial, dental, external, and molecular attributes (*e.g.*, see Han *et al.*, 2000). Postcranial morphology, while it is indicative of substrate preference and informative insofar as supraordinal relationships are concerned (see below), has contributed little to an understanding of the species- or genus-level phylogeny of tupaiids. However, the cluster analyses of the forelimb and hindlimb variables combined (Figs. 6.44-6.46) do show various degrees of similarity in the postcranium of several tupaiid species. They show that *Ptilocercus* is extremely different from all tupaiines (and that *Dendrogale* is not an intermediate), thereby supporting the distinct phylogenetic history of these two clades and the separation of these taxa into different subfamilies (Lyon, 1913; Le Gros Clark, 1926; Napier and Napier, 1967; Martin, 1968b, 1984, 1990; Steele, 1973; Butler, 1980; Luckett, 1980b; Zeller, 1986a,b; Corbet and Hill, 1992; Wilson, 1993; Nowak, 1999; contra Davis, 1938). In fact, as shown above, several postcranial characters distinguish the two subfamilies from one another (Table 7.1), which is important because Lyon (1913), as well as all subsequent studies, only recognized cranial, dental, and external morphological differences between the two subfamilies.

T. tana, which is sometimes separated from *Tupaia* (Lyon, 1913) into *Lyonogale* (Martin, 1968b, 1984, 1990; Butler, 1980; Luckett, 1980b), is nested among *Tupaia* species (Figs. 6.44-6.46), and the inclusion of this species in *Tupaia* certainly seems warranted (Napier and Napier, 1967; Steele, 1973; Dene *et al.*, 1978, 1980; Corbet and

Table 7.1. Postcranial characters that differentiate the two tupaiid subfamilies. Traits listed for *Ptilocercus* are also likely to be those of the ancestral tupaiid and possibly of the ancestral archontan (see text). Features under Tupaiinae represent the apomorphies of the prototupaiine.

Ptilocercus	**Subfamily Tupaiinae[a]**
Ecology and Behavior	**Ecology and Behavior**
nocturnal	diurnal
arboreal	terrestrial (scansorial)
more flexed limbs	more extended limbs
slower quadrupedalism	faster quadrupedalism
more abducted hallux	less abducted hallux[b]
capable of grasping	not capable of grasping[b]
Axial Skeleton	**Axial Skeleton**
wide[c] ribs	narrow ribs
wide[c] atlas	narrow atlas
axis spinous process projects cranially	axis spinous process projects caudally
cervical spinous processes short	cervical spinous processes longer
thoracic spinous processes short and wide[c]	thoracic spinous processes long and narrow
lumbar spinous processes very short	lumbar spinous processes long
lumbar transverse processes short and face laterally	lumbar transverse processes long and face ventrally
Forelimb	**Forelimb**
scapula short and wide	scapula long and narrow
coracoid process long and extends caudally	coracoid process shorter and extends medially
lesser tuberosity robust with strong medial protrusion	lesser tuberosity gracile with weak medial protrusion
rounded capitulum separated from trochlea	flatter capitulum continuous with trochlea
short olecranon process	longer olecranon process
circular radial central fossa	ovoid radial central fossa
ungual phalanges short and deep	ungual phalanges longer and shallower
Hindlimb	**Hindlimb**
ilio-pubic angle large (*e.g.*, above 145°)	ilio-pubic angle smaller (*e.g.*, below 130°)
short pubic symphysis	long pubic symphysis
small anterior inferior iliac spine	large anterior inferior iliac spine
narrow ilium	wide ilium
more elliptical acetabulum	more circular acetabulum
acetabular articular surface cranially expanded	acetabular articular surface evenly distributed

Table 7.1 (con.)

Ptilocercus	**Subfamily Tupaiinae**[a]
Hindlimb (con.)	**Hindlimb (con.)**
small greater trochanter	large greater trochanter
small third trochanter	large third trochanter
shallow femoral condyles	deep femoral condyles
patellar groove short and wide	patellar groove long and narrow
tibial distal articular surface longer than wide[d]	tibial distal articular surface wider than long
more concave and circular cuboid facet on the calcaneus (deeper calcaneocuboid pivot)	flatter and more ovoid cuboid facet on the calcaneus
distal facet of entocuneiform wide (expanded mediolaterally)	distal facet of entocuneiform narrow (restricted mediolaterally)
large plantar process of entocuneiform	smaller plantar process of entocuneiform

[a] This column summarizes the most common character states found among the species included in this subfamily.

[b] The arboreal *T. minor* has an abducted hallux and is capable of grasping (see chapter 3), but these conditions are not homologous to those seen in *Ptilocercus*, either behaviorally or structurally (see chapter 6).

[c] Width here refers to cranio-caudal width.

[d] The tibial distal articular surface of the ancestral archontan was likely as long as it was wide.

Hill, 1992; Wilson, 1993; Nowak, 1999; Han *et al.*, 2000). *Dendrogale* and *Urogale* are nested among species of *Tupaia* when fewer variables and more taxa are included in the analysis (Fig. 6.44), but they are separated from *Tupaia* species when more variables and fewer taxa are analyzed (Fig. 6.46). Hence, little can be said about the degree of similarity in limb morphology between these genera and *Tupaia*. This is unfortunate because Han *et al.* (2000) recently suggested, based on DNA hybridization and morphometric analysis of external characters, that *Urogale everetti*, which was originally described as *Tupaia everetti* Thomas, 1892 (Wilson, 1993), should be included in *Tupaia*.

Lyon (1913) suggested that *Urogale* and *T. tana* (which he did not include in *Tupaia*; see above) are closely related, and Steele (1973) found that these two taxa were very similar in their dentition. However, most molecular and morphological studies of tupaiids have shown that *T. tana* is most closely related to other species of *Tupaia* (Dene *et al.*, 1978, 1980; Butler, 1980; Luckett, 1980b; Han *et al.*, 2000). The postcranial morphology of *Urogale* and *T. tana* is not uniquely similar, and that of *T. tana* is more similar to that of other species of *Tupaia* than it is to *Urogale* (Figs. 6.44-6.46).

The absence of the entepicondylar foramen in *Urogale* (Fig. 5.14) may have some phylogenetic and biogeographic significance. *Urogale* and *T. palawanensis* are the only tupaiids found in the Philippines. However, these species are not closely related (Dene *et al.*, 1978, 1980), nor are they particularly similar morphologically (Fig. 6.44; Han *et al.*, 2000). This is not surprising because they are not found on the same islands (*Urogale* is mainly on Mindanao and *T. palawanensis* is mainly on Palawan), and numerous opportunities were available for repeated invasion of various southeast Asian islands, such as Palawan, due to sea level changes during the Pleistocene (Han *et al.*, 2000). In fact, Morley and Flenley (1987) have illustrated that there were likely independent land bridges to Palawan and Mindanao from Borneo during many Pleistocene glacial maxima. The distribution of the presence or absence of the entepicondylar foramen in tupaiids is interesting in light of this information. *T. palawanensis* retains an entepicondylar foramen and is closely related to *T. minor*, *T. tana*, and *T. montana* (Dene *et al.*, 1978, 1980; Han *et al.*, 2000), all of which are present on Borneo and also retain an entepicondylar foramen. While the entepicondylar foramen is present in some subspecies of *T. glis*, it has been lost in *T. glis longipes* and *T. glis belangeri* (see chapter

5). These taxa are sometimes recognized as species, *T. longipes* and *T. belangeri*, distinct from *T. glis* (Martin, 1984; Wilson, 1993), but the loss of the entepicondylar foramen represents the only postcranial feature examined here that would support the separation of these taxa from *T. glis*. However, the fact that *T. longipes*, like *Urogale*, lacks an entepicondylar foramen and is only present on Borneo (*Urogale's* ancestor was likely from Borneo; see above), might suggest a close relationship between these two taxa. However, as stated above, this character is extremely plastic and the entepicondylar foramen could certainly have been lost in these taxa independently.

Unfortunately, some hindlimb measurements (*e.g.*, tibia and fibula length) could not be taken on the single specimen of *T. nicobarica* due to breakage (see Table 6.28). Hence, this taxon is not included in the cluster analyses of the combined forelimb and hindlimb variables (Figs. 6.44-6.46). However, an examination of the cluster analyses of the forelimb variables (Figs. 5.39-5.40) reveals that this species is quite distinct from other species of *Tupaia*. Lyon (1913) also recognized *T. nicobarica* as one of the most distinct species of *Tupaia*, and Steele (1973) supported the distinctiveness of *T. nicobarica* in his study of the tupaiid dentition. This is interesting particularly because this species is endemic to the Nicobar Islands and there is disagreement concerning its substrate preference (see Table 1.2). It is unfortunate that only one specimen of this species could be examined in this study. *T. nicobarica* is obviously in need of further study, and more postcranial specimens, as well as more ecological data, should provide a great deal of information about this interesting and distinct species. The same could be said about *Anathana ellioti* (no postcranial specimens), *Dendrogale melanura* (1 specimen), and *D. murina* (1 specimen).

A better understanding of tupaiid systematics is confounded by several factors. First, the tupaiid fossil record is extremely poor (see chapter 1; Sargis, 1999). Second, the Tupaiidae has not been formally revised since Lyon's (1913) examination of tupaiid skins, skulls, and teeth. Third, the molecular phylogenies of tupaiids have consisted of an immunological divergence tree (Dene *et al.*, 1978, 1980) and a DNA hybridization tree (Han *et al.*, 2000), both phenetic measures (like the cluster analyses discussed above), so a molecular phylogeny based on sequence data is needed. A molecular phylogeny that includes all (or more) tupaiid species would also be helpful because earlier studies have not been able to incorporate more than ten species. Until such studies are undertaken, the intrafamilial relationships of tupaiids will likely remain relatively poorly understood.

ARCHONTAN SYSTEMATICS AND CHARACTER EVOLUTION

As noted above, the inclusion of Scandentia, Primates, Dermoptera, and Chiroptera in Archonta has been supported by numerous morphological studies (McKenna, 1975; Szalay, 1977; Smith and Madkour, 1980; Szalay and Drawhorn, 1980; Novacek and Wyss, 1986; Wible and Covert, 1987; Novacek *et al.*, 1988; Wible and Novacek, 1988; Novacek, 1989, 1990, 1992, 1993, 1994; Johnson and Kirsch, 1993; Szalay and Lucas, 1993, 1996; McKenna and Bell, 1997; Shoshani and McKenna, 1998). In contrast to these morphological studies, molecular analyses have consistently supported a grouping that includes Dermoptera, Scandentia, and Primates, but excludes Chiroptera (Cronin and Sarich, 1980; Adkins and Honeycutt, 1991, 1993; Honeycutt and Adkins, 1993; Allard *et al.*, 1996; Porter *et al.*, 1996; Liu and Miyamoto, 1999; Waddell *et al.*, 1999). This supraordinal grouping has been called Euarchonta by Waddell *et al.*

(1999). This exclusion of chiropterans from Archonta based on molecular data is not only a revision of the morphological concept of Archonta, but it is also a rejection of the Volitantia hypothesis (see chapter 1). The latter is more robustly corroborated than the Archonta and has been overwhelmingly supported in numerous morphological studies using extremely varied databases and phylogenetic methods (Szalay, 1977; Novacek, 1982, 1986, 1989, 1990, 1992, 1993, 1994; Novacek and Wyss, 1986; Wible and Covert, 1987; Novacek *et al.*, 1988; Wible and Novacek, 1988; Thewissen and Babcock, 1991, 1992, 1993; Johnson and Kirsch, 1993; Szalay and Lucas, 1993, 1996; Wible, 1993; Simmons and Quinn, 1994; Simmons, 1995; Shoshani and McKenna, 1998). Hence, the morphological concepts of Archonta and Volitantia are in contrast to the molecular concept of Euarchonta. It seems, therefore, that there is no congruence between morphological and molecular data concerning these alternative phylogenetic hypotheses. Beard (1989, 1993a,b), however, has proposed a hypothesis based on morphological evidence, the concept of Primatomorpha, that is concordant with the molecular concept of Euarchonta. This supraordinal grouping, which includes Dermoptera and Primates, is in stark contrast to the Volitantia. It is the competing hypotheses of Volitantia and Primatomorpha that will be considered below in a reexamination of some of the postcranial evidence.

As discussed above, Beard's (1989, 1993a,b) Primatomorpha hypothesis has been challenged on many grounds, as has his gliding and "mitten" or finger-gliding interpretation of paromomyids. These interpretations of paromomyids were rejected by Szalay and Lucas (1993, 1996), Runestad and Ruff (1995), and Hamrick *et al.* (1999), the latter of which interpreted similarities between the phalanges of dermopterans and paromomyids not as gliding adaptations, but as adaptations for vertical clinging and climbing on large arboreal supports. Also, the characters that Beard (1989, 1993a,b) used to support Primatomorpha were questioned and reevaluated by Szalay and Lucas (1993, 1996), Simmons (1994), Shoshani and McKenna (1998), and Stafford and Thorington (1998). My analysis differs from these in that I will reevaluate Beard's (1993b) characters specifically in light of the fact that Beard (1989, 1993b) did not use *Ptilocercus* to represent Scandentia in his analysis. Most previous studies, as well as my study, considered *Ptilocercus* to be primitive for Tupaiidae in both its ecology and most of its morphological attributes (see above; Le Gros Clark, 1926; Szalay, 1969; Campbell, 1974; Gould, 1978; Butler, 1980; Szalay and Drawhorn, 1980; Martin, 1990; Szalay and Lucas, 1993, 1996; but see Stafford and Thorington, 1998, on the carpus). It follows, therefore, that this taxon should represent Scandentia in any supraordinal phylogenetic analysis that includes tupaiids.

As Martin (1990) stated, "[*Ptilocercus*] generally seems to be more primitive than species in the subfamily Tupaiinae... For this reason, *Ptilocercus* could shed special light on the evolutionary radiation of tree-shrews. It is important to recognize the point that assessment of the likely phylogenetic relationships of tree-shrews must involve inference of the hypothetical ancestral condition from which all living tree-shrew species diverged. It is obvious that the common ancestral stock of modern tree-shrews must have been at least as primitive as the most primitive surviving species and was probably more primitive than any of them. Thus, assessment of the phylogenetic relationships of tree-shrews on the basis of a single surviving species (particularly if it happens to be one of the more advanced among them) is likely to confuse rather than clarify the question of actual ancestral relationships" (pp. 192-193). In other words, a better understanding of tupaiid supraordinal relationships is likely confounded by the common use of *Tupaia*, a relatively derived tupaiid, to represent Scandentia (*e.g.*, Beard, 1989, 1993b; Rose, 1999; Rose and Lucas, 2000), and these relationships would likely be better understood if *Ptilocercus* was used to represent the order. Hence, the distribution of characters (among archontans) used by Beard (1993b) will be reconsidered in light of the postcranial morphology of *Ptilocercus*. Characters used to support Volitantia will also be analyzed from this perspective. Functional analyses of all these characters were discussed above, and it should be pointed out that many of the characters interpreted as archontan features below could represent adaptive convergences related to arboreality and/or climbing.

Volitantian Characters

Using *Ptilocercus* to represent Scandentia affects very few of the characters used to support Volitantia. Wible and Novacek (1988), Szalay and Lucas (1993, 1996), Simmons and Quinn (1994), Simmons (1995), and Shoshani and McKenna (1998) all listed flattened ribs as a synapomorphy uniting Dermoptera and Chiroptera. The craniocaudal expansion of the ribs in *Ptilocercus* (Fig. 4.1), however, may imply that this is an archontan feature that was lost in primates (Tables 7.1-7.2). Wible and Novacek (1988), Simmons and Quinn (1994), and Simmons (1995) also listed "weak" or absent spinous processes on C3-C7 as a synapomorphy of Volitantia. However, compared to those of tupaiines, the cervical spinous processes of *Ptilocercus* (see Fig. 4.2d for C3-C5) are also short (Le Gros Clark, 1926). Hence, this feature may also represent an archontan feature rather than a volitantian feature (Table 7.1).

Table 7.2. Distribution of archontan postcranial features discussed in the text.

Taxon	Tupaiinae[a]	*Ptilocercus*	*Cynocephalus*	*Pteropus*	*Microcebus*	Plesiadapiformes
Ribs[b]	narrow	wide	wide	wide	intermediate	?
Lesser tuberosity	gracile, weak medial protrusion	robust, strong medial protrusion	robust, strong medial protrusion	robust, strong medial protrusion[c]	robust, strong medial protrusion[d]	robust, strong medial protrusion
Capitulum shape	flatter (continuous with trochlea)	rounded, (separated from trochlea)	rounded	flatter	rounded	rounded
Radial central fossa shape	ovoid	circular	circular	ovoid	circular	circular
Acetabulum shape	circular	elliptical	elliptical	elliptical	elliptical	elliptical
Patellar Groove shape	long, narrow	short, wide	short, wide	short, narrow	deep, narrow	short, wide

[a] This column summarizes the most common character states found among the species included in this subfamily.

[b] Width here refers to cranio-caudal width.

[c] This character state is not from *Pteropus* specifically, but from chiropterans in general (from Schlosser-Sturm and Schliemann, 1995). Simmons (1994) corrected Beard's (1993b) misinterpretation of an autapomorphic condition found in chiropterans for this feature.

[d] This character state is not from *Microcebus* specifically, but from euprimates in general (after Beard, 1993b).

There has been disagreement over which archontan taxa possess deep, mediolaterally compressed ungual phalanges. This feature has been considered to be a synapomorphy of Volitantia by Szalay and Lucas (1993, 1996) and Simmons (1995). Beard (1993b), however, claimed that the condition found in chiropterans is different from that found in dermopterans, and considered this feature to be a synapomorphy of a dermopteran-plesiadapiform clade (*i.e.*, Beard's dermopteran suborder Plesiadapiformes, which does not include Micromomyidae). Lemelin (2000), on the other hand, agreed with Szalay and Lucas (1993, 1996) and Simmons (1995) that the dermopteran and chiropteran conditions are similar. Regardless of these disagreements, the condition found in *Ptilocercus* is similar to that found in dermopterans, chiropterans, and plesiadapiforms (Fig. 7.1; see Szalay and Lucas, 1993, 1996). Hence, this condition is probably an archontan feature (Table 7.1) that was replaced in euprimates by nails.

These are the only three features that have been used to support Volitantia that are affected by a consideration of the character states present in the postcranium of *Ptilocercus*. These three characters represent only two of Szalay and Lucas' (1993, 1996) seven diagnostic character complexes of the protovolitantian, and only three of the seventeen volitantian synapomorphies listed by Simmons (1995). The inclusion of *Ptilocercus* in the analysis, therefore, does not greatly affect the supportive evidence for Volitantia.

As discussed above, the fusion of the scaphoid and lunate into the scapholunate in tupaiids could represent the antecedent condition to the fusion of the scaphoid, centrale, and lunate into the scaphocentralunate in volitantians. This is, however, unlikely considering the frequency of independent carpal fusion in therians, as well as the

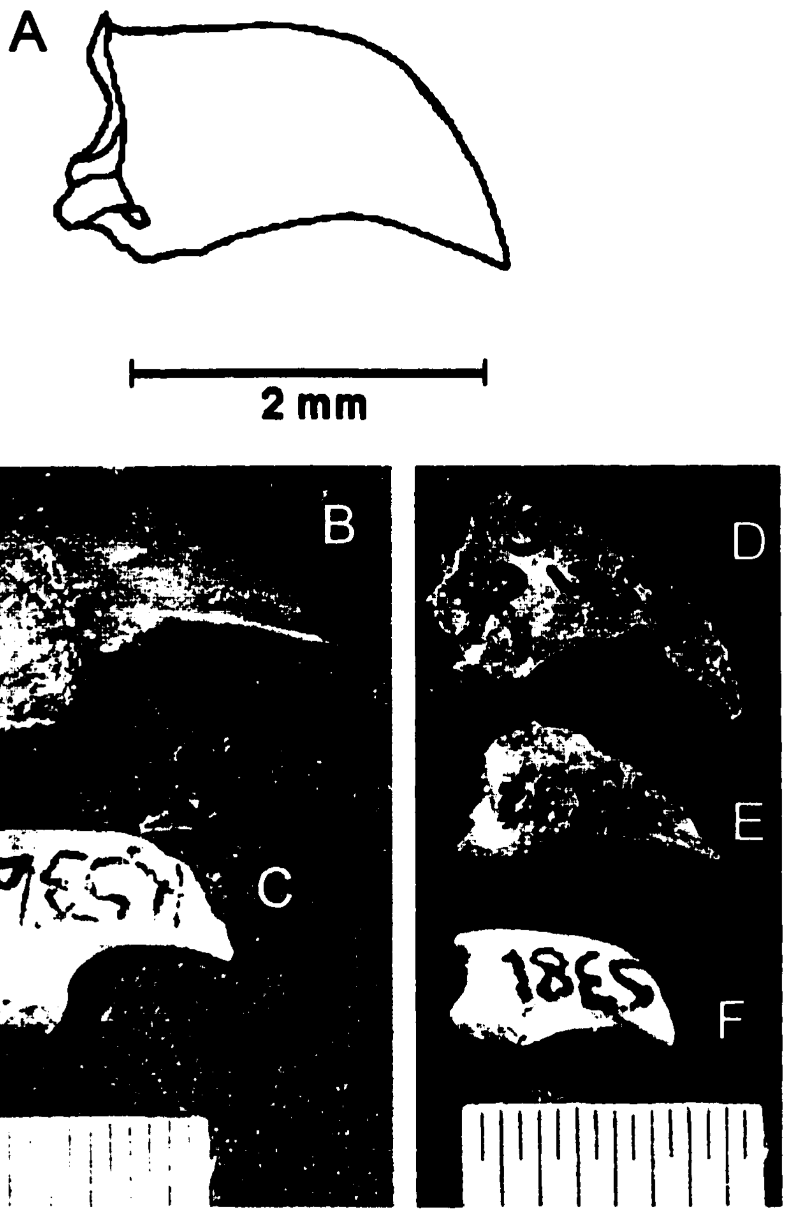


Figure 7.1. A) Ungual phalanx of 3rd manual digit of *Ptilocercus* (redrawn after Szalay, unpublished). Ungual phalanges of *Plesiadapis tricuspidens*: MNHN R 613 (B), R 5361 (C), R 5357 (D), R 5337 (E), and R 5381 (F). Subdivisions on scale are 0.5 mm. Note the similarity in ungual phalanx depth between *Ptilocercus* and *Plesiadapis*.

possibility that the ancestral tupaiid had an unfused scaphoid and lunate (especially considering the incomplete fusion found in both *Ptilocercus* and *Dendrogale*; see chapter 5).

Primatomorphan Characters

As stated above, Shoshani and McKenna (1998) did not include some of Beard's (1993b) characters in their 260 character data set because "[b]y his own admission, Beard (1993) remarked on some of his characters that were questionable" (p. 574). It is interesting that a Dermoptera-Primates clade (*i.e.*, Primatomorpha, *sensu stricto*) was supported neither when a larger database was analyzed (Shoshani and McKenna, 1998), nor when characters with little phylogenetic value were eliminated (Szalay and Lucas, 1993, 1996). In both of these cases, however, Volitantia was supported. In the analysis of Beard's (1993b) characters discussed below, only the 22 postcranial characters are considered (see Beard, 1993b, for a list of these characters). The seven cranio-dental characters are not considered at all, and only those postcranial characters that are affected by the inclusion of *Ptilocercus*, as well as those that have been challenged by others, will be discussed.

Deltopectoral Crest. Beard claimed that the lateral position of the deltopectoral crest is a synapomorphy of Primatomorpha (character #8). The inclusion of *Ptilocercus* does not affect this claim because *Ptilocercus*, like tupaiines, has a deltopectoral crest that is positioned anteriorly on the humerus (see chapter 5). However, while euprimates and plesiadapiforms have a laterally placed deltopectoral crest, dermopterans, like tupaiids and chiropterans, have an anteriorly placed deltopectoral crest. Beard (1993b), therefore, considered the lateral placement of the deltopectoral crest to be a synapomorphy of

Primatomorpha that was lost in dermopterans. However, this condition may more likely be a synapomorphy of Primates (*sensu lato*) because it is only found in euprimates and plesiadapiforms.

Lesser Tuberosity. Beard described a robust lesser tuberosity that exhibits strong medial protrusion as a synapomorphy of Primatomorpha (character #9) because this condition is present in dermopterans, euprimates, and plesiadapiforms. While this is not present in tupaiines, it is present in *Ptilocercus* (Figs. 5.10, 7.2). Beard (1993b) described a condition in chiropterans where the lesser tuberosity projects proximally above the humeral head, and he considered this condition to be autapomorphous. However, Simmons (1994) corrected this erroneous observation by explaining that this condition is only present in some microchiropterans. This, in combination with the fact that chiropterans have a robust, strongly medially protruding lesser tuberosity (see Schlosser-Sturm and Schliemann, 1995) makes it quite likely that this character state represents an archontan, rather than primatomorphan, feature (Tables 7.1-7.2).

Capitulum and Radial Central Fossa. The shape of the capitulum and the shape and excavation of the radial central fossa (which articulates with the capitulum) are directly related to one another, but Beard (1993b) treated them as separate characters. Beard considered a spheroidal capitulum to be another synapomorphy of Primatomorpha (character #10) because it is present in euprimates, plesiadapiforms, and dermopterans. However, while this condition is not present in tupaiines, it is present in *Ptilocercus* (Fig. 5.13). This character state, therefore, may represent another archontan feature (Tables 7.1-7.2; Szalay and Lucas, 1993, 1996). Euprimates, plesiadapiforms, and dermopterans also have a circular and deep radial central fossa (character #11), so Beard interpreted

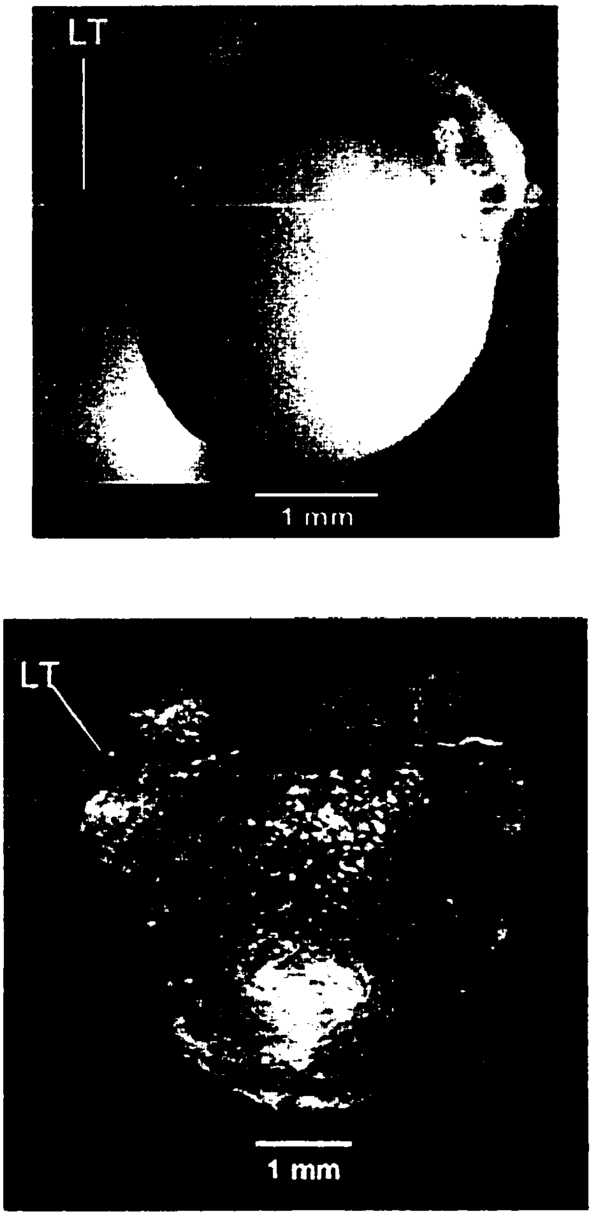


Figure 7.2. Proximal humeri (proximal view) of *Ptilocercus* (top) and *Phenacolemur simonsi* (bottom: USNM 442266). LT: lesser tuberosity. Note the similarity in size and medial protrusion of the lesser tuberosity between *Ptilocercus* and *Phenacolemur*.

this feature as a primatomorphan synapomorphy. Once again, however, this character state is also found in *Ptilocercus* (but not tupaiines; Fig. 5.35), and probably represents another archontan feature (Tables 7.1-7.2; Szalay and Lucas, 1993, 1996).

Ulnocarpal Articulation. The form of the ulnocarpal articulation described by Beard (character #13) as present in dermopterans and paromomyids is not affected by the inclusion of *Ptilocercus*. However, Beard (1993b) described an autapomorphous condition for Megachiroptera where the articulation between the ulna and cuneiform is absent. Stafford and Thorington (1998), on the other hand, stated that the ulnar styloid process articulates with the cuneiform in megachiropterans just as it does in dermopterans. This character, which Beard (1993b) interpreted as a synapomorphy of a Dermoptera-Paromomyidae clade (*i.e.*, Beard's dermopteran infraorder Eudermoptera), may, therefore, represent a synapomorphy of the emended volitantian concept of Thewissen and Babcock (1992), Simmons and Quinn (1994), and Simmons (1995). This concept of Volitantia is a grouping of Dermoptera with Chiroptera, but the paromomyids are included in the order Dermoptera (see chapter 1).

Position of Lunate. There are many problems with Beard's character (#15) that deals with the position of the lunate in relation to the scaphoid, and these have been discussed in detail by Stafford and Thorington (1998). Beard (1993b) claimed that the lunate is distal (rather than ulnar) to the scaphoid in dermopterans, plesiadapids, and paromomyids (see below), so the lunate would not articulate with the radius in these taxa. Beard considered this character state to be a synapomorphy of a dermopteran-plesiadapiform clade. Perhaps more importantly, the lunate of dermopterans is fused to the scaphoid and centrale just as it is in chiropterans (but not plesiadapiforms). It is remarkable that the position of the lunate (which was incorrectly interpreted; see below) was included in the analysis, while the fusion of the scaphoid, lunate, and centrale was not (despite the fact that this condition in dermopterans was mentioned). Of course, the latter character supports Volitantia, and its inclusion in the analysis would likely have reduced the support for Primatomorpha. Hence, this choice of characters compellingly weights the data set in favor of one hypothesis over another. Regardless of this problem, Stafford and Thorington (1998) have shown that there is no evidence for Beard's (1993b) claim regarding the position of the lunate in dermopterans. The distal cartilage of the scaphocentralunate in dermopterans is the centrale (not the lunate), and the lunate cartilage coalesces to the scaphoid cartilage on its ulnar (not distal) side (Stafford and Thorington, 1998). The possibility of having a lunate positioned distal to the scaphoid in plesiadapiforms will be discussed below.

Articulations of Cuneiform. Beard claimed that the cuneiform articulates with both the scaphoid and lunate radially in dermopterans, plesiadapids, and paromomyids (character #16), and this condition was considered to be a synapomorphy of a dermopteran-plesiadapiform clade. It is remarkable that this character was considered separately from the character above, especially because the character state for the position of the lunate relative to the scaphoid was determined from the condition of the cuneiform in paromomyids (as the scaphoid, lunate, and centrale are not known for this taxon)! Again, splitting up these two interrelated characters further weights the data set in favor of specific hypotheses. As with the character above, Stafford and Thorington (1998) have shown that the cuneiform articulates radially with the lunate (more proximally) and centrale (more distally) portions of the scaphocentralunate in dermopterans. Beard

(1993b) extended his interpretation of the cuneiform articulations of dermopterans to the plesiadapiforms, which do have two articular facets on the radial side of their cuneiform, by proposing that the more proximal facet is for articulation with the scaphoid and the more distal facet is for articulation with the lunate. However, Stafford and Thorington's (1998) rejection of this (derived) pattern in dermopterans likely applies to plesiadapiforms too, and other less derived alternatives do exist. The more proximal facet probably articulates with the lunate (not the scaphoid) and the more distal facet may articulate with the centrale (as in *Ptilocercus*), magnum (as in *Dendrogale*), or unciform (as in chiropterans; Stafford and Thorington, 1998). This is important because there is no reason to assume that the more proximal facet articulates with the scaphoid and the more distal facet articulates with the lunate. This also shows that Beard's (1993b) claim that the cuneiform of scandentians and chiropterans only articulates radially with the lunate is incorrect (Stafford and Thorington, 1998).

Pisiform. Beard claimed that the pisiform is absent in chiropterans (character #17), and interpreted this as an autapomorphous condition. Simmons (1994) and Stafford and Thorington (1998), however, have shown that this was an erroneous observation and that chiropterans retain a large pisiform.

Phalanges. The intermediate phalanges of dermopterans and paromomyids are longer than the proximal phalanges in these taxa (character #18), and Beard has considered this to be a synapomorphy of a Dermoptera-Paromomyidae clade. This condition, however, also exists in chiropteran manual phalanges (Thewissen and Babcock, 1992) and pedal phalanges (Hamrick *et al.*, 1999), and may thus represent a synapomorphy of the emended volitantian concept of Thewissen and Babcock (1992), Simmons and Quinn

(1994), and Simmons (1995). Beard's analysis of the shape of the ungual phalanges (character #19) in archontans was discussed above in the section on volitantian characters.

Acetabulum. Beard described the shape of the acetabulum as elliptical in euprimates, plesiadapiforms, dermopterans, and chiropterans (character #20), and interpreted this feature as a synapomorphy of a Primatomorpha-Chiroptera clade. However, the acetabulum of *Ptilocercus* appears to be at least as elliptical as that of plesiadapiforms (Fig. 7.3), so this feature is likely primitive for Archonta (Tables 7.1-7.2). Beard also described bony buttressing on the cranial side of the acetabulum in euprimates, plesiadapiforms, dermopterans, and chiropterans (character #21), and again interpreted this feature as a synapomorphy of a Primatomorpha-Chiroptera clade. Here again, *Ptilocercus* also exhibits this character state (Fig. 7.3), making it likely that this represents an archontan feature (Table 7.1). It should be noted that while Beard (1993b) stated that the phylogenetic value of these characters was weak due to plasticity, they were not weighted accordingly because none of the characters in the analysis were weighted. These were the only innominate features used in Beard's (1993b) analysis, but it should be pointed out that the innominate of *Ptilocercus* (but not tupaiines) is very similar to that of other archontans (Fig. 7.4). This applies particularly to the narrow ilium, large ilio-pubic angle, small anterior inferior iliac spine, and short pubic symphysis (Fig. 7.4; Tables 6.6, 7.1).

Quadratus Femoris. Beard listed an enlarged, flattened, triangular area of attachment for a well-developed quadratus femoris muscle on the posterior part of the proximal femur between the greater and lesser trochanters as a synapomorphy of Primatomorpha

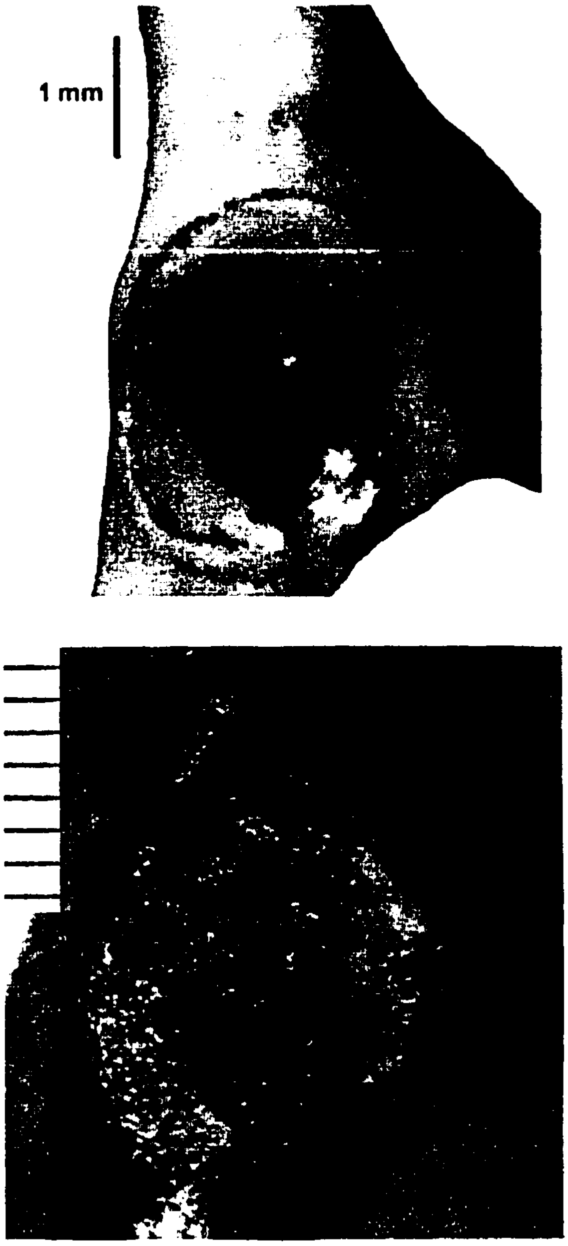


Figure 7.3. Acetabulum of *Ptilocercus* (above) and *Ignacius graybullianus* (bottom: USNM 442285). Subdivisions on scale are 0.5 mm. Note the similarity in acetabular shape and expansion of the cranial portion of the articular surface between *Ptilocercus* and *Ignacius*.

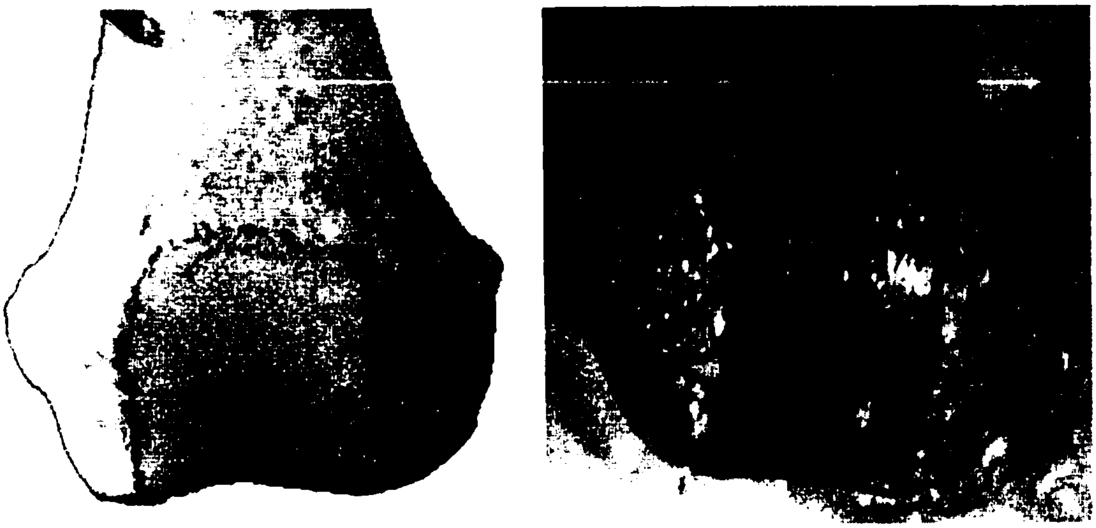
Figure 7.4. Innominates of *Ptilocercus* (top left), *Tinimomys graybulliensis* (top right: USNM 442277), and *Cynocephalus* (bottom: redrawn after Beard, 1989; fig. 75). Not to scale. Note the similarity between all three taxa in ilium width, ilio-pubic angle, and anterior inferior iliac spine size. Also note the similarity in pubic symphysis length between *Ptilocercus* and *Cynocephalus*.

(character #23) because it is present in dermopterans, euprimates, paromomyids, and micromomyids (but not plesiadapids). *Ptilocercus* also appears to exhibit this condition (Fig. 7.5), and Le Gros Clark (1926) described the quadratus femoris muscle of *Ptilocercus* as well-developed. It is also significant that the most proximal part of the attachment of this muscle on the femur is the tip of the greater trochanter in *Ptilocercus* (Le Gros Clark, 1926) and the base of the greater trochanter in *Tupaia* (Le Gros Clark, 1924a). The quadratus femoris is a lateral rotator of the thigh that may be important for climbing vertical supports (Beard, 1989), an activity that *Ptilocercus* commonly engages in (Stafford and Thorington, 1998). The presence of this character state in *Ptilocercus* implies that this is an archontan, rather than primatomorphan, character, although detailed dissections of the hip of *Ptilocercus* are needed to further confirm the condition found in this taxon.

Patellar Groove. Beard considered a short, wide, shallow patellar groove (character #24) to be a synapomorphy of a dermopteran-plesiadapiform clade (*i.e.*, Beard's order Dermoptera, which includes Micromomyidae), as this feature is present in dermopterans and plesiadapiforms. It is, however, also present in *Ptilocercus* (Fig. 7.6) and may, therefore, represent another archontan feature (Tables 7.1-7.2; Szalay and Lucas, 1993, 1996). As stated above, the patellar groove of the ancestral euprimate likely became elongated and deepened in response to graspleaping locomotion, a conclusion attested to by the entire skeleton of early euprimates (see Szalay and Dagosto, 1980, 1988; Dagosto, 1988; Szalay and Lucas, 1996).

Distal Tibiofibular Joint. The presence of a synovial distal tibiofibular joint (rather than a syndesmosis) in dermopterans, plesiadapiforms, and euprimates (character #25) was

Figure 7.5. Proximal femora (posterior view) of *Ptilocercus* (left) and *Phenacolemur simonsi* (right: USNM 442243). Subdivisions on scale are 0.5 mm. Note the similarity in the attachment area for the quadratus femoris muscle between *Ptilocercus* and *Phenacolemur*.



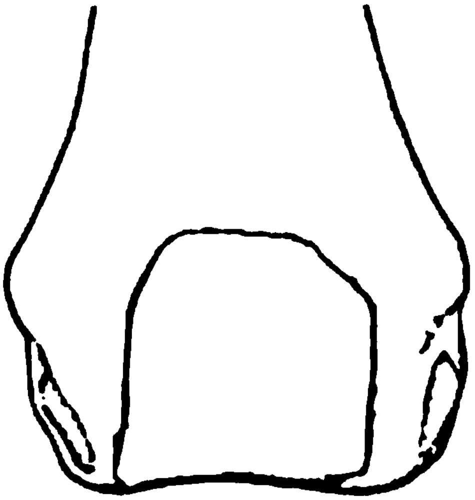


Figure 7.6. Distal femora of *Ptilocercus* (top left), *Tinimomys graybulliensis* (top right: USNM 442280; photographically reversed), and *Cynocephalus* (bottom: redrawn after Beard, 1989; fig. 79). Not to scale. Note the similarity between all three taxa in patellar groove shape.

interpreted by Beard as a synapomorphy of Primatomorpha. Carleton (1941), however, noted the presence of a synovial distal tibiofibular joint in *Ptilocercus*, as well (see also Dagosto, 1985). Here again, this character state may represent an archontan feature, as opposed to a primatomorphan one.

Sustentaculum. Beard noted the articular facet for the tibial medial malleolus on the posterior side of the sustentaculum (character #27) in tupaiids (see Beard, 1989, figs. 80-81). However, despite this uniquely derived condition within Archonta, this character was still scored as primitive in tupaiids (*i.e.*, it was still scored as a zero). This represents an autapomorphy of Tupaiidae (Szalay and Lucas, 1996), and hence should be scored as such.

Calcaneocuboid Joint. Beard interpreted a concave cuboid facet on the calcaneus (calcaneocuboid pivot) as a synapomorphy of Primatomorpha (character #28) because it is present in euprimates, plesiadapiforms, and dermopterans. It is, however, also present in *Ptilocercus*, which has a more circular and concave cuboid facet on the calcaneus than do tupaiines (Szalay and Drawhorn, 1980, fig. 9). Hence, this character state likely represents an archontan feature, rather than a primatomorphan feature (Table 7.1; Szalay and Drawhorn, 1980; Szalay and Lucas, 1993, 1996).

Entocuneiform. Beard considered a wide distal facet of the entocuneiform, combined with a reduced or absent plantodistal process, to be a synapomorphy of Primatomorpha (character #29). This condition is present in dermopterans and euprimates, and a wide distal entocuneiform facet is also present in plesiadapiforms (Fig. 7.7; Szalay and Dagosto, 1988). To describe the entocuneiform plantar process of plesiadapiforms as reduced, however, is a remarkable statement because, if anything, this feature is

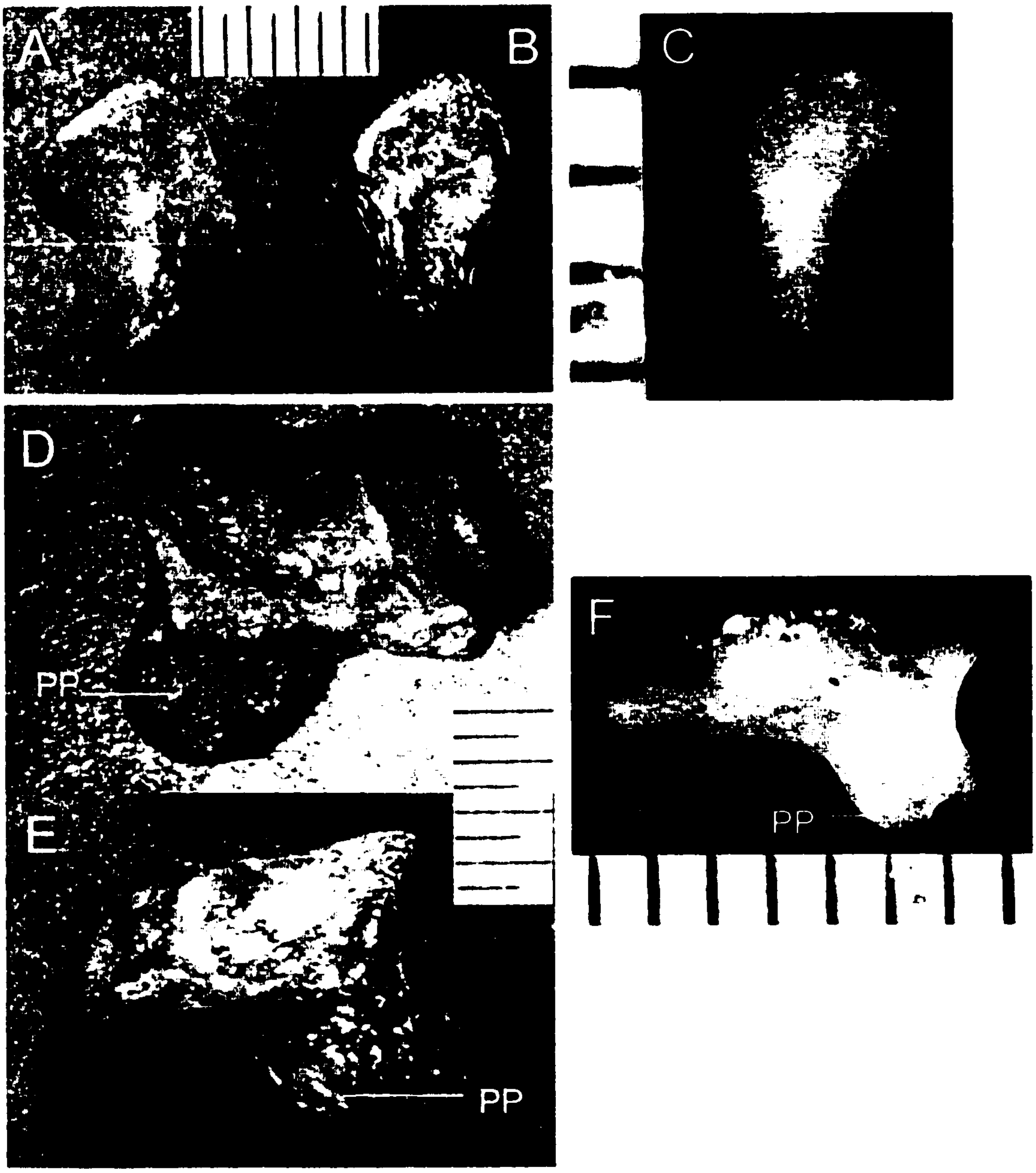


Figure 7.7. A-C) Distal view of left entocuneiform of *Plesiadapis tricuspidens* (A: MNHN R 416) and right entocuneiforms of *P. tricuspidens* (B: MNHN R 5359) and *Ptilocercus* (C). D-F) Lateral view of left entocuneiform of *P. tricuspidens* (D: MNHN R 416) and right entocuneiforms of *P. tricuspidens* (E: MNHN R 5359) and *Ptilocercus* (F). PP: plantar process. Subdivisions on scale are 0.5 mm. Note the similarity in distal entocuneiform facet width and plantar process size between *Ptilocercus* and *Plesiadapis*.

hypertrophied in this group (Fig. 7.7; Szalay and Dagosto, 1988). *Ptilocercus* also has a wide distal entocuneiform facet (with a large plantar process; Fig. 7.7), so this character state may again represent an archontan, rather than primatomorphan, feature (Table 7.1; Szalay and Lucas, 1996). In fact, *Ptilocercus* is similar to plesiadapiforms in these features, although the distal entocuneiform facet of plesiadapiforms is wider than that of *Ptilocercus* and the plantar process of *Ptilocercus* is located more proximally than that of plesiadapiforms (Fig. 7.7). In relation to the similarity in the distal entocuneiform facet, the proximal facet of the first metatarsal is also similar in these two taxa (Fig. 7.8).

In summary, this character analysis has shown that 12 of Beard's (1993b) 22 postcranial characters should be interpreted differently when *Ptilocercus*, rather than *Tupaia*, is used to represent Scandentia. This greatly reduces the evidence for Primatomorpha, and when this is considered together with the results of the character analyses conducted by Szalay and Lucas (1993, 1996), Stafford and Thorington (1998), and Hamrick *et al.* (1999), the Primatomorpha hypothesis must be rejected. The evidence for Volitantia, on the other hand, is not greatly affected by the inclusion of *Ptilocercus* in this character analysis (see above), and this hypothesis has been further corroborated by the character analyses of Thewissen and Babcock (1992), Szalay and Lucas (1993, 1996), Stafford and Thorington (1998), and Hamrick *et al.* (1999). Hence, at present, it seems that one must conclude that the sister taxon of Dermoptera is Chiroptera, not Primates (Szalay, 1977; Novacek, 1982, 1986, 1989, 1990, 1992, 1993, 1994; Novacek and Wyss, 1986; Wible and Covert, 1987; Novacek *et al.*, 1988; Wible and Novacek, 1988; Thewissen and Babcock, 1991, 1992, 1993; Johnson and Kirsch, 1993; Szalay and Lucas, 1993, 1996; Wible, 1993; Simmons and Quinn, 1994; Simmons,

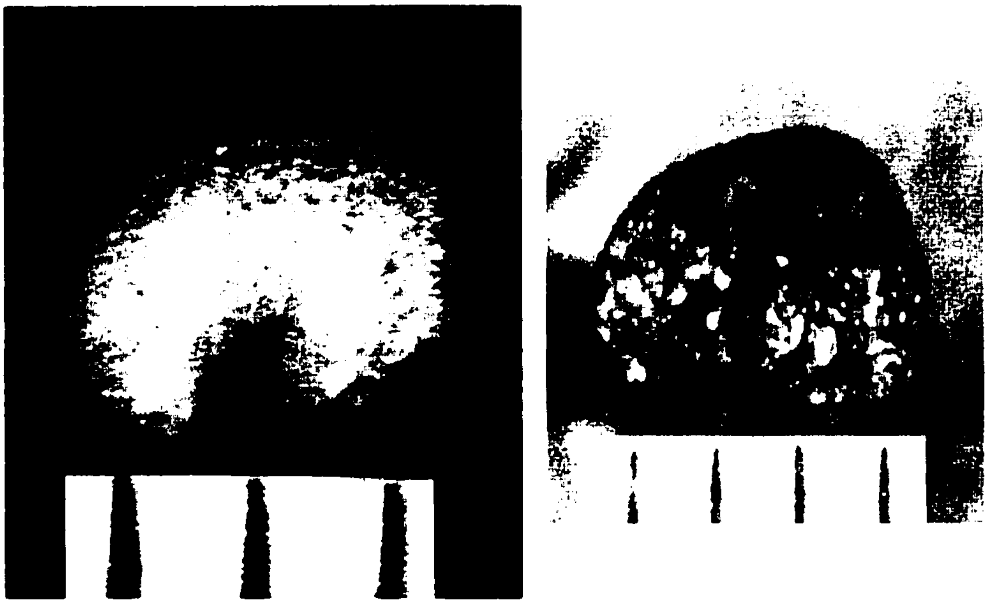


Figure 7.8. 1st metatarsals (proximal view) of *Ptilocercus* (left) and *Phenacolemur simonsi* (right: USNM 442257; photographically reversed). Subdivisions on scale are 0.5 mm. Note the similarity in the proximal facet of the first metatarsal between *Ptilocercus* and *Phenacolemur*.

1995; Shoshani and McKenna, 1998; contra Beard, 1989, 1993a,b; McKenna and Bell, 1997). In other words, while Volitantia represents a well-tested phylogenetic hypothesis, Primatomorpha likely represents an unnatural grouping based more on archontan plesiomorphies than meaningful synapomorphies of its own.

It seems likely that the ancestral archontan was, like *Ptilocercus*, an arboreal quadruped and climber, and that the evolution of the protoarchontan was related to a transition from terrestrial to arboreal locomotion (Szalay and Drawhorn, 1980; Szalay and Lucas, 1993, 1996). In fact, just as *Ptilocercus* is more likely to exhibit primitive features for Scandentia than is any tupaiine, it is also more likely to exhibit primitive characters for Archonta than is any living dermopteran (specialized for gliding), chiropteran (specialized for flying), or euprimate (primitively specialized for graspleaping; see Szalay and Dagosto, 1980, 1988; Dagosto, 1988; Szalay and Lucas, 1996). Hence, the list of features in the left column of Table 7.1 represents several character complexes that were probably present in the ancestral archontan, which likely evolved in response to a shift to arboreal locomotion (Szalay and Drawhorn, 1980; Szalay and Lucas, 1993, 1996). This hypothesis concerning the ancestral morphotype of Archonta can be further tested against future fossil discoveries of early archontans.

The relationships of Scandentia and Primates within Archonta remain unclear. *Ptilocercus* and plesiadapiforms exhibit several similarities in their postcranial morphology, but these are likely archontan plesiomorphies. A Scandentia-Euprimates clade has been supported by cranial evidence (Wible and Covert, 1987; Wible and Novacek, 1988; Kay *et al.*, 1992), but I found no postcranial evidence to support such a clade. Shoshani and McKenna (1998) found evidence for a Volitantia-Euprimates clade (that they called "Primatomorpha"), but I found no evidence for this clade either. Hence, based on the postcranial evidence examined here, no definitive conclusions about the relationships of Scandentia or Primates within Archonta can be made at present.

CHAPTER 8: SUMMARY

The primary aim of this study was to document variation in postcranial morphology in relation to differential substrate use within the order Scandentia, but tupaiid postcranial morphology was also considered from a phylogenetic perspective. The inclusion of *Ptilocercus* in this study was pivotal because *Ptilocercus* has been proposed in the past to be the living tupaiid taxon that retains the most conservative skeletal features for Scandentia. However, in most of the past phylogenetic studies it was *Tupaia*, rather than *Ptilocercus*, that was often used as an outgroup when the relationships among various groups of primates were examined, and it was also *Tupaia* that represented Scandentia in studies of mammalian supraordinal relationships (chapter 1). The inclusion of *Ptilocercus* in this study allows a more robust character analysis to be performed on scandentian, "primatomorphan," volitantian, and archontan features. The major conclusions drawn from this study are summarized below.

1) **Grasping:** The terrestrial *T. tana* was never observed grasping, whereas the arboreal *T. minor* was frequently (in 84% of dowel crossings) observed grasping small branches and dowels in its cages, particularly with its feet but occasionally with its hands as well. The hallux of *T. minor*, but not of *T. tana*, was habitually divergent from the other digits. Even on larger branches that could not be grasped due to their large size, the four non-hallucial digits were typically held on the side of the branch and the hallux was placed on top of it. The pollex of *T. minor* was often quite divergent, particularly in certain positions, and the manual digits were often spread apart from one another. In contrast, those of *T. tana* were always less splayed. It is thus evident that in addition to

Ptilocercus, the arboreal *T. minor* is capable of grasping, while the terrestrial *T. tana* is not (chapter 3).

Differences in entocuneiform-1st metatarsal morphology between *Ptilocercus* and *T. minor* likely reflect differences in the way these taxa abduct their hallux and grasp. Hallucial abduction occurs at the tarsometatarsal joint in *Ptilocercus*, while it occurs at the metatarsophalangeal joint in *T. minor*. Thus, grasping in *T. minor* and *Ptilocercus* is not homologous. The condition seen in *Ptilocercus* is likely primitive for Scandentia, and perhaps for Archonta as well. The capability for grasping was probably lost in the terrestrial ancestral tupaiine, and grasping in *T. minor* probably evolved secondarily (chapter 6).

2) Models for Early Primates: Lemelin (1999) proposed didelphid marsupials as models for some aspects of early euprimates because, like primates, didelphids have evolved grasping extremities. The results reported here, however, suggest that arboreal tupaiids such as *T. minor* and especially *Ptilocercus* may represent better models for early primates than didelphids. Arboreal tupaiids are not only far more closely related to primates than are didelphids, but they are also, as this study shows, capable of grasping. This is not to say that grasping in tupaiids is mechanically identical to that seen in primates. In fact, tupaiid grasping may be considered to be only “incipient” grasping in comparison to the more fully developed grasping of euprimates, and it is possible that the two conditions are not homologous. However, the type of grasping seen in tupaiids may represent the antecedent condition to that seen in primates, and grasping may be primitive for archontan mammals. The first archontan may have evolved (“incipient”) grasping capabilities similar to those of *Ptilocercus*, and the powerful grasping of primates may not have evolved until the origin of the first euprimates. *Ptilocercus* can, at the very least, be used as a living model for the extinct plesiadapiforms because both taxa are clawed mammals, and they share similarities in their entocuneiform-1st metatarsal morphology (chapters 3 and 6).

3) Axial Skeleton: Several differences that relate to differential substrate use were found in the ribs and vertebrae. These differences included cranio-caudal width of the ribs; number of thoracic, lumbar, and caudal vertebrae; cranio-caudal width of the atlas; orientation of the spinous process of the axis; length and cranio-caudal width of the spinous processes of the thoracic vertebrae; length of the spinous processes of the lumbar vertebrae; length and orientation of the transverse processes of the lumbar vertebrae; and the number of sacral vertebrae that articulate with the ilia. The ribs and vertebrae of the arboreal *Ptilocercus* exhibit adaptations for a stable thorax that may facilitate bridging locomotion. The vertebral columns of tupaiines, on the other hand, are more mobile and allow more flexion and extension of the spine; this increased flexion and extension increases stride length, which in turn increases speed in bounding or galloping mammals such as terrestrial tupaiines. It is proposed here that the attributes of *Ptilocercus*' thorax are primitive for the Tupaiidae, that the ancestral tupaiid was arboreal, that the tupaiine condition is derived, and that the ancestral tupaiine was terrestrial. It is also proposed that *Ptilocercus* may be primitive for the Archonta in its axial skeletal features; that a stable thorax was first evolved in an arboreal ancestral archontan; that the adaptations for stability of the thorax were retained in the Volitantia (dermopterans and chiropterans) for certain locomotor modes, including gliding or flying; and that a mobile thorax evolved in conjunction with the shift to graspleaping in the ancestral euprimate (chapter 4).

4) **Limb Morphology:** The forelimb and hindlimb of *Ptilocercus* are better adapted for arboreal locomotion, while those of tupaiines are better adapted for terrestrial (or scansorial) locomotion. Even the most arboreal tupaiines remain similar to their terrestrial relatives in their limb morphology, providing strong evidence for the terrestrial ancestry of Tupaiinae (but not Tupaiidae). It seems clear that the limb morphology of tupaiines has been constrained by their terrestrial heritage. While the limbs of *Ptilocercus* appear to be habitually flexed and exhibit more joint mobility, a necessity for movement on uneven, discontinuous arboreal supports, tupaiines are characterized by more extended limbs and more stability in their joints. These stable joints restrict movements more to the parasagittal plane, which increases the efficiency of locomotion on a more even and continuous surface like the ground. Tupaiine limbs are more adapted for powerful flexion and extension and, consequently, for rapid terrestrial locomotion. The forelimb of *Urogale* stands out among tupaiines in that it exhibits adaptations for scratch-digging. The tarsus of *Ptilocercus* facilitates inversion of the foot, and its grasping hallux is capable of a great range of abduction. Finally, the character states of the limbs of *Ptilocercus* are more similar to those of other archontans than are those of tupaiines (chapters 5 and 6).

5) **Supraordinal Relationships:** A character analysis showed that 12 of Beard's (1993b) 22 postcranial characters should be interpreted differently when *Ptilocercus*, rather than *Tupaia*, is used to represent Scandentia. This greatly reduces the evidence for Primatomorpha (Primates + Dermoptera, including plesiadapiforms), and when this is considered together with the results of other character analyses, the Primatomorpha hypothesis must be rejected. The evidence for Volitantia (Chiroptera + Dermoptera), on

the other hand, is not greatly affected by the inclusion of *Ptilocercus* in this character analysis, and this hypothesis has been further corroborated by several other character analyses. Hence, at present, it seems that one must conclude that the sister taxon of Dermoptera is Chiroptera, not Primates. Volitantia represents a well-tested phylogenetic hypothesis, while Primatomorpha likely represents an unnatural grouping based more on archontan plesiomorphies than meaningful synapomorphies of its own. While the relationships of Dermoptera and Chiroptera are relatively well understood, the relationships of Scandentia and Primates within Archonta remain unclear at present (chapter 7).

6) **Ancestral Archontan:** While the ancestral tupaiine was probably terrestrial and the ancestral tupaiid was probably arboreal, it seems likely that the ancestral archontan was, like *Ptilocercus*, an arboreal quadruped and climber and that the evolution of the protoarchontan was related to a transition from terrestrial to arboreal locomotion. In fact, just as *Ptilocercus* is more likely to exhibit primitive features for Scandentia than is any tupaiine, it is also more likely to exhibit primitive characters for Archonta than is any living dermopteran (specialized for gliding), chiropteran (specialized for flying), or euprimate (primitively specialized for graspleaping). Hence, the list of features in the left column of Table 7.1 represents several character complexes that were probably present in the ancestral archontan, which likely evolved in response to a shift to arboreal locomotion (chapter 7).

7) **Primate Outgroup:** The postcranium of *Ptilocercus* is proposed to exhibit many features that are primitive for the Tupaiidae. Hence, in studies of primate supraordinal relationships that include comparisons of postcranial characters to those in tupaiids,

Ptilocercus should be chosen to represent Scandentia. Similarly, if tupaiids are chosen as an outgroup in primate phylogenetic analyses that include postcranial evidence, then *Ptilocercus* should be used as the outgroup because its attributes are more conservative for the order.

BIBLIOGRAPHY

Adkins, R. M. and Honeycutt, R. L. (1991) Molecular phylogeny of the superorder Archonta. *Proceedings of the National Academy of Sciences* 88: 10317-10321.

Adkins, R. M. and Honeycutt, R. L. (1993) A molecular examination of archontan and chiropteran monophyly. In MacPhee, R. D. E. (ed.): *Primates and their Relatives in Phylogenetic Perspective.* New York: Plenum Press, pp. 227-249.

Allard, M. W., McNiff, B. E., and Miyamoto, M. M. (1996) Support for interordinal eutherian relationships with an emphasis on primates and their archontan relatives. *Molecular Phylogenetics and Evolution* 5: 78-88.

Anemone, R. L. (1993) The functional anatomy of the hip and thigh in primates. In Gebo, D. L. (ed.): *Postcranial Adaptation in Nonhuman Primates.* Dekalb: Northern Illinois University Press, pp. 150-174.

Ankel, F. (1972) Vertebral morphology of fossil and extant primates. In Tuttle, R. H. (ed.): *The Functional and Evolutionary Biology of Primates.* Chicago: Aldine, pp. 223-240.

Argot, C. (in press) Functional anatomy of the forelimb of *Mayulestes ferox* and *Pucadelphys andinus* (Marsupialia, Mammalia) from the early Palaeocene of Bolivia, using myological data from living didelphids. *Journal of Morphology.*

Baba, H. (1985) Comparative hindlimb osteometry of mammals and the locomotor evolution of the primates. In Kondo, S. (ed.): *Primate Morphophysiology, Locomotor Analyses, and Human Bipedalism.* Tokyo: University of Tokyo Press, pp. 181-199.

Bailey, W. J., Slightom, J. L., and Goodman, M. (1992) Rejection of the "flying primate" hypothesis by phylogenetic evidence from the ε-globin gene. *Science* 256: 86-89.

Banks, E. (1931) A popular account of the mammals of Borneo. *Journal of the Malayan Branch of the Royal Asiatic Society* 9: 1-139.

Bauchot, R. and Stephan, H. (1966) Données nouvelles sur l'encéphalisation des insectivores et des prosimiens. *Mammalia* 30: 160-196.

Beard, K. C. (1989) *Postcranial Anatomy, Locomotor Adaptations, and Paleoecology of Early Cenozoic Plesiadapidae, Paromomyidae, and Micromomyidae (Eutheria, Dermoptera).* Ph.D. Dissertation, Johns Hopkins University.

Beard, K. C. (1990) Gliding behavior and paleoecology of the alleged primate family Paromomyidae (Mammalia, Dermoptera). *Nature* 345: 340-341.

Beard, K. C. (1991) Vertical postures and climbing in the morphotype of Primatomorpha: implications for locomotor evolution in primate history. In Coppens, Y. and Senut, B. (eds.): *Origine(s) de la Bipédie chez les Hominidés.* Paris: CNRS, pp. 79-87.

Beard, K. C. (1993a) Origin and evolution of gliding in Early Cenozoic Dermoptera (Mammalia, Primatomorpha). In MacPhee, R. D. E. (ed.): *Primates and their Relatives in Phylogenetic Perspective.* New York: Plenum Press, pp. 63-90.

Beard, K. C. (1993b) Phylogenetic systematics of the Primatomorpha, with special reference to Dermoptera. In Szalay, F. S., Novacek, M. J., and McKenna, M. C. (eds.): *Mammal Phylogeny: Placentals.* New York: Springer-Verlag, pp. 129-150.

Beard, K. C. and Godinot, M. (1988) Carpal anatomy of *Smilodectes gracilis* (Adapiformes, Notharctinae) and its significance for lemuriform phylogeny. *Journal of Human Evolution* 17: 71-92.

Benton, R. S. (1967) Morphological evidence for adaptations within the epaxial region of the primates. In Vagtborg, H. (ed.): *The Baboon in Medical Research.* Austin: University of Texas Press, pp. 201-216.

Bishop, A. (1962) Control of the hand in lower primates. *Annals of the New York Academy of Sciences* 102: 316-337.

Bishop, A. (1964) Use of the hand in lower primates. In Buettner-Janusch, J. (ed.): *Evolutionary and Genetic Biology of Primates, Vol. 2.* New York: Academic, pp. 133-225.

Butler, P. M. (1972) The problem of insectivore classification. In Joysey, K. A. and Kemp, T. S. (eds.): *Studies in Vertebrate Evolution.* Edinburgh: Oliver and Boyd, pp. 253-265.

Butler, P. M. (1980) The tupaiid dentition. In Luckett, W. P. (ed.): *Comparative Biology and Evolutionary Relationships of Tree Shrews.* New York: Plenum, pp. 171-204.

Campbell, C. B. G. (1966a) Taxonomic status of tree shrews. *Science* 153: 436-436.

Campbell, C. B. G. (1966b) The relationships of the tree shrews: the evidence of the nervous system. *Evolution* 20: 276-281.

Campbell, C. B. G. (1974) On the phyletic relationships of the tree shrews. *Mammal Review* 4: 125-143.

Carleton, A. (1941) A comparative study of the inferior tibio-fibular joint. *Journal of Anatomy* 76: 45-55.

Carlsson, A. (1922) Über die Tupaiidae und ihre Beziehungen zu den Insectivora und den Prosimiae. *Acta Zoologica, Stockholm* 3: 227-270.

Cartmill, M. (1985) Climbing. In Hildebrand, M., Bramble, D. M., Liem, K. F., and Wake, D. B. (eds.): *Functional Vertebrate Morphology.* Cambridge, MA: Belknap, pp. 73-88.

Cartmill, M. and MacPhee, R. D. E. (1980) Tupaiid affinities: the evidence of the carotid arteries and cranial skeleton. In Luckett, W. P. (ed.): *Comparative Biology and Evolutionary Relationships of Tree Shrews.* New York: Plenum, pp. 95-132.

Cartmill, M. and Milton, K. (1977) The lorisiform wrist joint and the evolution of "brachiating" adaptations in the Hominoidea. *American Journal of Physical Anthropology* 47: 249-272.

Chopra, S. R. K. and Vasishat, R. N. (1979) Sivalik fossil tree shrew from Haritalyangar, India. *Nature* 281: 214-215.

Chopra, S. R. K., Kaul, S., and Vasishat, R. N. (1979) Miocene tree shrews from the Indian Sivaliks. *Nature* 281: 213-214.

Chorazyna, H. and Kurup, G. U. (1975) Observations on the ecology and behavior of *Anathana ellioti* in the wild. In Kondo, S., Kawai, M., and Ehara, A. (eds.): *Contemporary Primatology.* Basel: Karger, pp. 342-344.

Corbet, G. B. and Hill, J. E. (1992) *The Mammals of the Indomalayan Region: A Systematic Review.* Oxford: Oxford University Press.

Cronin, J. E. and Sarich, V. M. (1980) Tupaiid and Archonta phylogeny: the macromolecular evidence. In Luckett, W. P. (ed.): *Comparative Biology and Evolutionary Relationships of Tree Shrews.* New York: Plenum, pp. 293-312.

Curtis, D. J. (1995) Functional anatomy of the trunk musculature in the slow loris (*Nycticebus coucang*). *American Journal of Physical Anthropology* 97: 367-379.

D'Souza, F. (1974) A preliminary field report on the lesser tree shrew *Tupaia minor.* In Martin, R. D., Doyle, G. A., and Walker, A. C. (eds.): *Prosimian Biology.* London: Duckworth, pp. 167-182.

Dagosto, M. (1983) Postcranium of *Adapis parisiensis* and *Leptadapis magnus* (Adapiformes, Primates). *Folia Primatologica* 41: 49-101.

Dagosto, M. (1985) The distal tibia of primates with special reference to the Omomyidae. *International Journal of Primatology* 6: 45-75.

Dagosto, M. (1988) Implications of postcranial evidence for the origin of euprimates. *Journal of Human Evolution* 17: 35-56.

Davis, D. D. (1938) Notes on the anatomy of the tree shrew *Dendrogale. Zoological Series of the Field Museum of Natural History* 20: 383-404.

Davis, D. D. (1962) Mammals of the lowland rain forest of North Borneo. *Bulletin of the Singapore National Museum* 31: 1-129.

Dene, H., Goodman, M., and Prychodko, W. (1978) An immunological examination of the systematics of Tupaioidea. *Journal of Mammalogy* 59: 697-706.

Dene, H., Goodman, M., Prychodko, W., and Matsuda, G. (1980) Molecular evidence for the affinities of Tupaiidae. In Luckett, W. P. (ed.): *Comparative Biology and Evolutionary Relationships of Tree Shrews.* New York: Plenum, pp. 269-291.

Dutta, A. K. (1975) Micromammals from Siwaliks. *Indian Minerals* 29: 76-77.

Elliot, O. and Wong, M. (1969) Blood sugar of Malayan tree shrews. *Journal of Mammalogy* 50: 361-362.

Elliot Smith, G. (1924) *The Evolution of Man: Essays.* London: Oxford University Press.

Emmons, L. H. (in press) *Tupai: A Field Study of Bornean Tree Shrews.* Berkeley: University of California Press.

Endo, H., Rerkamuaychoke, W., Kimura, J., Sasaki, M., Kurohmaru, M., and Yamada, J. (1999) Functional morphology of the locomotor system in the northern smooth-tailed tree shrew (*Dendrogale murina*). *Annals of Anatomy* 181: 397-402.

English, A. W. (1980) The functions of the lumbar spine during stepping in the cat. *Journal of Morphology* 165: 55-66.

Erikson, G. E. (1963) Brachiation in New World monkeys and in anthropoid apes. *Symposia of the Zoological Society of London* 10: 135-164.

Evans, F. G. (1939) The morphology and functional evolution of the atlas-axis complex from fish to mammals. *Annals of the New York Academy of Sciences* 39: 29-104.

Fenton, M. B. and Crerar, L. M. (1984) Cervical vertebrae in relation to roosting posture in bats. *Journal of Mammalogy* 65: 395-403.

Fischer, M. S. (1994) Crouched posture and high fulcrum, a principle in the locomotion of small mammals: the example of the rock hyrax (*Procavia capensis*) (Mammalia: Hyracoidea). *Journal of Human Evolution* 26: 501-524.

Fleagle, J. G. and Simons, E. L. (1982) The humerus of *Aegyptopithecus zeuxis*: a primitive anthropoid. *American Journal of Physical Anthropology* 59: 175-193.

Flower, W. H. (1885) *An Introduction to the Osteology of the Mammalia.* London: Macmillan.

Gadow, H. F. (1933) *The Evolution of the Vertebral Column.* Cambridge: Cambridge University Press.

Gambaryan, P. P. (1974) *How Mammals Run.* New York: John Wiley & Sons.

Gebo, D. L. (1989) Postcranial adaptation and evolution in Lorisidae. *Primates* 30: 347-367.

Gebo, D. L. (1992) Locomotor and postural behavior in *Alouatta palliata* and *Cebus capucinus. American Journal of Primatology* 26: 277-290.

Gebo, D. L. (1993) Functional morphology of the foot in primates. In Gebo, D. L. (ed.): *Postcranial Adaptation in Nonhuman Primates.* Dekalb: Northern Illinois University Press, pp. 175-196.

Gebo, D. L. and Sargis, E. J. (1994) Terrestrial adaptations in the postcranial skeletons of guenons. *American Journal of Physical Anthropology* 93: 341-371.

Gebo, D. L., Beard, K. C., Teaford, M. F., Walker, A. C., Larson, S. G., Jungers, W. L., and Fleagle, J. G. (1988) A hominoid proximal humerus from the early Miocene of Rusinga Island, Kenya. *Journal of Human Evolution* 17: 393-401.

George, R. M. (1973) *The Musculature of the Limbs of Urogale everetti with reference to the Comparative Anatomy of the Tupaiidae.* Ph.D. Dissertation, University of Washington.

George, R. M. (1977) The limb musculature of the Tupaiidae. *Primates* 18: 1-34.

Goodman, M., Bailey, W. J., Hayasaka, K., Stanhope, M. J., Slightom, J., and Czelusniak, J. (1994) Molecular evidence on primate phylogeny from DNA sequences. *American Journal of Physical Anthropology* 94: 3-24.

Gould, E. (1978) The behavior of the moonrat, *Echinosorex gymnurus* (Erinaceidae) and the pentail tree shrew, *Ptilocercus lowii* (Tupaiidae) with comments on the behavior of other Insectivora. *Zeitschrift für Tierpsychologie* 48: 1-27.

Grand, T. I. (1967) The functional anatomy of the ankle and foot of the slow loris (*Nycticebus coucang*). *American Journal of Physical Anthropology* 26: 207-218.

Grand, T. I. (1968) Functional anatomy of the upper limb. In Malinow, M. R. (ed.): *Biology of the Howler Monkey (Alouatta caraya).* Basel: Karger, pp. 104-125.

Grand, T. I. (1983) Body weight: its relationship to tissue composition, segmental distribution of mass, and motor function III. The Didelphidae of French Guyana. *Australian Journal of Zoology* 31: 299-312.

Graur, D., Duret, L., and Gouy, M. (1996) Phylogenetic position of the order Lagomorpha (rabbits, hares and allies). *Nature* 379: 333-335.

Gregory, W. K. (1910) The orders of mammals. *Bulletin of the American Museum of Natural History* 27: 1-524.

Gregory, W. K. (1913) Relationship of the Tupaiidae and of Eocene lemurs, especially *Notharctus. Bulletin of the Geological Society of America* 24: 247-252.

Haeckel, E. (1866) *Generelle Morphologie der Organismen.* Berlin: Georg Reimer.

Haines, R. W. (1955) The anatomy of the hand of certain insectivores. *Proceedings of the Zoological Society of London* 125: 761-777.

Haines, R. W. (1958) Arboreal or terrestrial ancestry of placental mammals. *Quarterly Review of Biology* 33: 1-23.

Hamrick, M. W., Rosenman, B. A., and Brush, J. A. (1999) Phalangeal morphology of the Paromomyidae (?Primates, Plesiadapiformes): the evidence for gliding behavior reconsidered. *American Journal of Physical Anthropology* 109: 397-413.

Han, K.-H., Sheldon, F. H., and Stuebing, R. B. (2000) Interspecific relationships and biogeography of some Bornean tree shrews (Tupaiidae: Tupaia), based on DNA hybridization and morphometric comparisons. *Biological Journal of the Linnean Society* 70: 1-14.

Harrison, J. L. (1964) *An Introduction to the Mammals of Sabah.* Jesselton: The Sabah Society.

Harrison, J. L. (1974) *An Introduction to Mammals of Singapore and Malaya.* Singapore: Malayan Nature Society.

Harrison, T. (1989) New postcranial remains of *Victoriapithecus* from the middle Miocene of Kenya. *Journal of Human Evolution* 18: 3-54.

Hatt, R. T. (1932) The vertebral columns of ricochetal rodents. *Bulletin of the American Museum of Natural History* 63: 599-738.

Hildebrand, M. (1959) Motions of the running cheetah and horse. *Journal of Mammalogy* 40: 481-495.

Hildebrand, M. (1985) Digging of quadrupeds. In Hildebrand, M., Bramble, D. M., Liem, K. F., and Wake, D. B. (eds.): *Functional Vertebrate Morphology.* Cambridge, MA: Belknap, pp. 89-109.

Honeycutt, R. L. and Adkins, R. M. (1993) Higher level systematics of eutherian mammals: an assessment of molecular characters and phylogenetic hypotheses. *Annual Review of Ecology and Systematics* 24: 279-305.

Howell, A. B. (1944) *Speed in Animals.* Chicago: University of Chicago Press.

Hurov, J. R. (1987) Terrestrial locomotion and back anatomy in vervets (*Cercopithecus aethiops*) and patas monkeys (*Erythrocebus patas*). *American Journal of Primatology* 13: 297-311.

Iwaniuk, A. N., Nelson, J. E., Ivanco, T. L., Pellis, S. M., and Whishaw, I. Q. (1998) Reaching, grasping and manipulation of food objects by two tree kangaroo species, *Dendrolagus lumholtzi* and *Dendrolagus matschiei. Australian Journal of Zoology* 46: 235-248.

Jacobs, L. L. (1980) Siwalik fossil tree shrews. In Luckett, W. P. (ed.): *Comparative Biology and Evolutionary Relationships of Tree Shrews.* New York: Plenum, pp. 205-216.

Jane, J. A., Campbell, C. B. G., and Yashon, D. (1965) Pyramidal tract: a comparison of two prosimian primates. *Science* 147: 153-155.

Jenkins, F. A., Jr. (1970) Anatomy and function of expanded ribs in certain edentates and primates. *Journal of Mammalogy* 51: 288-301.

Jenkins, F. A., Jr. (1971) Limb posture and locomotion in the Virginia opossum (*Didelphis marsupialis*) and in other non-cursorial mammals. *Journal of Zoology* 165: 303-315.

Jenkins, F. A., Jr. (1973) The functional anatomy and evolution of the mammalian humero-ulnar articulation. *American Journal of Anatomy* 137: 281-298.

Jenkins, F. A., Jr. (1974) Tree shrew locomotion and the origins of primate arborealism. In Jenkins, F. A., Jr. (ed.): *Primate Locomotion.* New York: Academic, pp. 85-116.

Jenkins, F. A., Jr. and McClearn, D. (1984) Mechanisms of hind foot reversal in climbing mammals. *Journal of Morphology* 182: 197-219.

Johnson, J. I. and Kirsch, J. A. W. (1993) Phylogeny through brain traits: interordinal relationships among mammals including Primates and Chiroptera. In MacPhee, R. D. E. (ed.): *Primates and their Relatives in Phylogenetic Perspective.* New York: Plenum Press, pp. 293-331.

Johnson, S. E. and Shapiro, L. J. (1998) Positional behavior and vertebral morphology in atelines and cebines. *American Journal of Physical Anthropology* 105: 333-354.

Jolly, C. J. (1967) The evolution of the baboons. In Vagtborg, H. (ed.): *The Baboon in Medical Research, Vol.2.* Austin: University of Texas Press, pp. 23-50.

Jouffroy, F. K. (1975) Osteology and myology of the lemuriform postcranial skeleton. In Tattersall, I. and Sussman, R. W. (eds.): *Lemur Biology.* New York: Plenum, pp. 149-192.

Kappelman, J. (1988) Morphology and locomotor adaptations of the bovid femur in relation to habitat. *Journal of Morphology* 198: 119-130.

Kaufmann, J. H. (1965) Studies on the behavior of captive tree shrews (*Tupaia glis*). *Folia Primatologica* 3: 50-74.

Kawamichi, T. and Kawamichi, M. (1979) Spatial organization and territory of tree shrews (*Tupaia glis*). *Animal Behavior* 27: 381-393.

Kay, R. F., Thorington, R. W., and Houde, P. (1990) Eocene plesiadapiform shows affinities with flying lemurs not primates. *Nature* 345: 342-344.

Kay, R. F., Thewissen, J. G. M., and Yoder, A. D. (1992) Cranial anatomy of *Ignacius graybullianus* and the affinities of the Plesiadapiformes. *American Journal of Physical Anthropology* 89: 477-498.

Kloss, C. B. (1903) *In the Andamans and Nicobars.* London: John Murray.

Krause, D. W. (1991) Were paromomyids gliders? Maybe, maybe not. *Journal of Human Evolution* 21: 177-188.

Langham, N. P. E. (1982) The ecology of the common tree shrew *Tupaia glis* in peninsular Malaysia. *Journal of Zoology* 197: 323-344.

Larson, S. G. (1988) Subscapularis function in gibbons and chimpanzees: implications for interpretation of humeral head torsion in hominoids. *American Journal of Physical Anthropology* 76: 449-462.

Larson, S. G. (1993) Functional morphology of the shoulder in primates. In Gebo, D. L. (ed.): *Postcranial Adaptation in Nonhuman Primates.* Dekalb: Northern Illinois University Press, pp. 45-69.

Le Gros Clark, W. E. (1924a) The myology of the tree shrew (*Tupaia minor*). *Proceedings of the Zoological Society of London* 1924: 461-497.

Le Gros Clark, W. E. (1924b) On the brain of the tree shrew (*Tupaia minor*). *Proceedings of the Zoological Society of London* 1924: 1053-1074.

Le Gros Clark, W. E. (1925) On the skull of *Tupaia*. *Proceedings of the Zoological Society of London* 1925: 559-567.

Le Gros Clark, W. E. (1926) On the anatomy of the pen-tailed tree shrew (*Ptilocercus lowii*). *Proceedings of the Zoological Society of London* 1926: 1179-1309.

Le Gros Clark, W. E. (1927) Exhibition of photographs of the tree shrew (*Tupaia minor*). Remarks on the tree shrew, *Tupaia minor*, with photographs. *Proceedings of the Zoological Society of London* 1927: 254-256.

Le Gros Clark, W. E. (1962) *The Antecedents of Man*, 2nd ed. Edinburgh: Edinburgh University Press.

Lekagul, B. and McNeely, J. A. (1977) *Mammals of Thailand.* Bangkok: Association for the Conservation of Wildlife.

Lemelin, P. (1999) Morphological correlates of substrate use in didelphid marsupials: implications for primate origins. *Journal of Zoology* 247: 165-175.

Lemelin, P. (2000) Micro-anatomy of the volar skin and interordinal relationships of primates. *Journal of Human Evolution* 38: 257-267.

Lemelin, P. and Grafton, B. W. (1998) Grasping performance in *Saguinus midas* and the evolution of hand prehensility in primates. In Strasser, E., Fleagle, J. G., Rosenberger, A. L., and McHenry, H. M. (eds.): *Primate Locomotion: Recent Advances.* New York: Plenum, pp. 131-144.

Lim, B. L. (1967) Note on the food habits of *Ptilocercus lowii* Gray (Pentail tree shrew) and *Echinosorex gymnurus* (Raffles) (Moonrat) in Malaya with remarks on "ecological labelling" by parasite patterns. *Journal of Zoology* 152: 375-379.

Lim, B. L. (1969) Distribution of the primates of West Malaysia. *Proceedings of the 2nd International Congress of Primatology* 2: 121-130.

Liu, F.-G. R. and Miyamoto, M. M. (1999) Phylogenetic assessment of molecular and morphological data for eutherian mammals. *Systematic Biology* 48: 54-64.

Luckett, W. P. ed. (1980a) *Comparative Biology and Evolutionary Relationships of Tree Shrews.* New York: Plenum Press.

Luckett, W. P. (1980b) The suggested evolutionary relationships and classification of tree shrews. In Luckett, W. P. (ed.): *Comparative Biology and Evolutionary Relationships of Tree Shrews.* New York: Plenum, pp. 3-31.

Luckett, W. P. (1993) Developmental evidence from the fetal membranes for assessing archontan relationships. In MacPhee, R. D. E. (ed.): *Primates and their Relatives in Phylogenetic Perspective.* New York: Plenum Press, pp. 149-186.

Lyon, M. W. (1913) Tree shrews: an account of the mammalian family Tupaiidae. *Proceedings of the United States National Museum* 45: 1-188.

MacLeod, N. and Rose, K. D. (1993) Inferring locomotor behavior in Paleogene mammals via eigenshape analysis. *American Journal of Science* 293-A: 300-355.

MacPhee, R. D. E. (1981) *Auditory Regions of Primates and Eutherian Insectivores: Morphology, Ontogeny, and Character Analysis.* Basel: Karger.

MacPhee, R. D. E. ed. (1993) *Primates and their Relatives in Phylogenetic Perspective.* New York: Plenum Press.

Martin, R. D. (1966) Tree shrews: unique reproductive mechanism of systematic importance. *Science* 152: 1402-1404.

Martin, R. D. (1968a) Towards a new definition of primates. *Man* 3: 377-401.

Martin, R. D. (1968b) Reproduction and ontogeny in tree shrews (*Tupaia belangeri*), with reference to their general behavior and taxonomic relationships. *Zeitschrift für Tierpsychologie* 25: 409-532.

Martin, R. D. (1982) Et tu, tree shrew? *Natural History* 8: 26-33.

Martin, R. D. (1984) Tree shrews. In Macdonald, D. (ed.): *The Encyclopedia of Mammals.* New York: Facts on File, pp. 440-445.

Martin, R. D. (1990) *Primate Origins and Evolution.* Princeton: Princeton University Press.

Matthew, W. D. (1904) The arboreal ancestry of the Mammalia. *American Naturalist* 38: 811-818.

McArdle, J. E. (1981) *Functional Morphology of the Hip and Thigh of the Lorisiformes.* Basel: Karger.

McKenna, M. C. (1966) Paleontology and the origin of the primates. *Folia Primatologica* 4: 1-25.

McKenna, M. C. (1975) Toward a phylogenetic classification of the Mammalia. In Luckett, W. P. and Szalay, F. S. (eds.): *Phylogeny of the Primates: A Multidisciplinary Approach.* New York: Plenum Press, pp. 21-46.

McKenna, M. C. and Bell, S. K. (1997) *Classification of Mammals Above the Species Level.* New York: Columbia University Press.

Mein, P. and Ginsburg, L. (1997) Les mammifères du gisement miocène inférieur de Li Mae Long, Thaïlande: systématique, biostratigraphie et paléoenvironnement. *Geodiversitas* 19: 783-844.

Miller, R. A. (1935) Functional adaptations in the forelimb of the sloths. *Journal of Mammalogy* 16: 38-51.

Miyamoto, M. M. (1996) A congruence study of molecular and morphological data for eutherian mammals. *Molecular Phylogenetics and Evolution* 6: 373-390.

Morley, R. J. and Flenley, J. R. (1987) Late Cainozoic vegetational and environmental changes in the Malay Archipelago. In Whitmore, T. C. (ed.): *Biogeographical Evolution of the Malay Archipelago.* Oxford: Clarendon Press, pp. 50-59.

Muizon, C. de (1998) *Mayulestes ferox*, a borhyaenoid (Metatheria, Mammalia) from the early Palaeocene of Bolivia. Phylogenetic and palaeobiologic implications. *Geodiversitas* 20: 19-142.

Muul, I. and Lim, B. L. (1971) New locality records for some mammals of West Malaysia. *Journal of Mammalogy* 52: 430-437.

Napier, J. R. (1961) Prehensility and opposability in the hands of primates. *Symposia of the Zoological Society of London* 5: 115-132.

Napier, J. R. (1967) Evolutionary aspects of primate locomotion. *American Journal of Physical Anthropology* 27: 333-342.

Napier, J. R. (1993) *Hands.* Princeton: Princeton University Press.

Napier, J. R. and Napier, P. H. (1967) *A Handbook of Living Primates.* London: Academic.

Neff, N. A. and Marcus, L. F. (1980) *A Survey of Multivariate Methods for Systematics.* New York: Privately Published and AMNH.

Novacek, M. J. (1980) Cranioskeletal features in tupaiids and selected Eutheria as phylogenetic evidence. In Luckett, W. P. (ed.): *Comparative Biology and Evolutionary Relationships of Tree Shrews.* New York: Plenum, pp. 35-93.

Novacek, M. J. (1982) Information for molecular studies from anatomical and fossil evidence on higher eutherian phylogeny. In Goodman, M. (ed.): *Macromolecular Sequences in Systematic and Evolutionary Biology.* New York: Plenum Press, pp. 3-41.

Novacek, M. J. (1986) The skull of leptictid insectivorans and the higher-level classification of eutherian mammals. *Bulletin of the American Museum of Natural History* 183: 1-112.

Novacek, M. J. (1989) Higher mammal phylogeny: the morphological-molecular synthesis. In Fernholm, B., Bremer, K., and Jornvall, H. (eds.): *The Hierarchy of Life.* Amsterdam: Elsevier, pp. 421-435.

Novacek, M. J. (1990) Morphology, paleontology, and the higher clades of mammals. In Genoways, H. H. (ed.): *Current Mammalogy.* New York: Plenum Press, pp. 507-543.

Novacek, M. J. (1992) Mammalian phylogeny: shaking the tree. *Nature* 356: 121-125.

Novacek, M. J. (1993) Reflections on higher mammalian phylogenetics. *Journal of Mammalian Evolution* 1: 3-30.

Novacek, M. J. (1994) Morphological and molecular inroads to phylogeny. In Grande, L. and Rieppel, O. (eds.): *Interpreting the Hierarchy of Nature.* New York: Academic Press, pp. 85-131.

Novacek, M. J. and Wyss, A. R. (1986) Higher-level relationships of the recent eutherian orders: morphological evidence. *Cladistics* 2: 257-287.

Novacek, M. J., Wyss, A. R., and McKenna, M. C. (1988) The major groups of eutherian mammals. In Benton, M. J. (ed.): *The Phylogeny and Classification of the Tetrapods, Vol. 2: Mammals.* Oxford: Clarendon Press, pp. 31-71.

Nowak, R. M. (1999) *Walker's Mammals of the World.* Baltimore: Johns Hopkins University Press.

Porter, C. A., Goodman, M., and Stanhope, M. J. (1996) Evidence on mammalian phylogeny from sequences of exon 28 of the von Willebrand factor gene. *Molecular Phylogenetics and Evolution* 5: 89-101.

Prashanth, M. and Veenakumari, K. (1996) Perspectives on the zoogeography of the Andaman and Nicobar Islands, India. *Malayan Nature Journal* 50: 99-106.

Pridmore, P. A. (1992) Trunk movements during locomotion in the marsupial *Monodelphis domestica* (Didelphidae). *Journal of Morphology* 211: 137-146.

Qiu, Z. (1986) Fossil tupaiid from the hominoid locality of Lufeng, Yunnan. *Vertebrata PalAsiatica* 24: 308-319.

Rabinowitz, A. (1990) Notes on the behavior and movements of leopard cats, *Felis bengalensis*, in a dry tropical forest mosaic in Thailand. *Biotropica* 22: 397-403.

Rasmussen, D. T. (1990) Primate origins: lessons from a neotropical marsupial. *American Journal of Primatology* 22: 263-277.

Ridley, H. N. (1895) The mammals of the Malay Peninsula. *Natural Science* 6: 23-29.

Roberts, D. (1974) Structure and function of the primate scapula. In Jenkins, F. A., Jr. (ed.): *Primate Locomotion.* New York: Academic, pp. 171-200.

Roberts, D. and Davidson, I. (1975) The lemur scapula. In Tattersall, I. and Sussman, R. W. (eds.): *Lemur Biology.* New York: Plenum, pp. 125-147.

Rockwell, H., Evans, F. G., and Pheasant, H. C. (1938) The comparative morphology of the vertebrate spinal column. Its form as related to function. *Journal of Morphology* 63: 87-117.

Roonwal, M. L. and Mohnot, S. M. (1977) *Primates of South Asia.* Cambridge: Harvard University Press.

Rose, K. D. (1999) Postcranial skeleton of Eocene Leptictidae (Mammalia), and its implications for behavior and relationships. *Journal of Vertebrate Paleontology* 19: 355-372.

Rose, K. D. and Lucas, S. G. (2000) An early Paleocene palaeanodont (Mammalia, ?Pholidota) from New Mexico, and the origin of Palaeanodonta. *Journal of Vertebrate Paleontology* 20: 139-156.

Rose, M. D. (1975) Functional proportions of primate lumbar vertebral bodies. *Journal of Human Evolution* 4: 21-38.

Rose, M. D. (1988) Another look at the anthropoid elbow. *Journal of Human Evolution* 17: 193-224.

Rose, M. D. (1989) New postcranial specimens of catarrhines from the middle Miocene Chinji Formation, Pakistan: descriptions and a discussion of proximal humeral functional morphology in anthropoids. *Journal of Human Evolution* 18: 131-162.

Rose, M. D. (1993) Functional anatomy of the elbow and forearm in primates. In Gebo, D. L. (ed.): *Postcranial Adaptation in Nonhuman Primates.* Dekalb: Northern Illinois University Press, pp. 70-95.

Rudd, R. L. (1965) Weight and growth in Malaysian rain forest mammals. *Journal of Mammalogy* 46: 588-594.

Runestad, J. A. and Ruff, C. B. (1995) Structural adaptations for gliding in mammals with implications for locomotor behavior in Paromomyids. *American Journal of Physical Anthropology* 98: 101-119.

Sanders, W. J. and Bodenbender, B. E. (1994) Morphometric analysis of lumbar vertebra UMP 67-28: implications for spinal function and phylogeny of the Miocene Moroto hominoid. *Journal of Human Evolution* 26: 203-237.

Sargis, E. J. (1999) Tree shrews. In Singer, R. (ed.): *Encyclopedia of Paleontology.* Chicago: Fitzroy Dearborn, pp. 1286-1287.

Schilling, N. and Fischer, M. S. (1999) Kinematic analysis of treadmill locomotion of tree shrews, *Tupaia glis* (Scandentia: Tupaiidae). *Zeitschrift für Säugetierkunde* 64: 129-153.

Schlosser-Sturm, E. and Schliemann, H. (1995) Morphology and function of the shoulder joint of bats (Mammalia: Chiroptera). *Zeitschrift für zoologische Systematik und Evolutions-forschung* 33: 88-98.

Schultz, A. H. (1961) Vertebral column and thorax. *Primatologia* 4: 1-66.

Shapiro, L. J. (1993) Functional morphology of the vertebral column of primates. In Gebo, D. L. (ed.): *Postcranial Adaptation in Nonhuman Primates.* Dekalb: Northern Illinois University Press, pp. 121-149.

Shapiro, L. J. (1995) Functional morphology of indrid lumbar vertebrae. *American Journal of Physical Anthropology* 98: 323-342.

Shapiro, L. J. and Demes, B. (1996) Spinal kinematics in lorids and cheirogaleids. *American Journal of Physical Anthropology* Supp. 22: 213-213.

Shapiro, L. J., Jungers, W. L., Godfrey, L. R., and Simons, E. L. (1994) Vertebral morphology of extinct lemurs. *American Journal of Physical Anthropology* Supp. 18: 179-180.

Shoshani, J., Groves, C. P., Simons, E. L., and Gunnell, G. F. (1996) Primate phylogeny: morphological vs molecular results. *Molecular Phylogenetics and Evolution* 5: 102-154.

Shoshani, J. and McKenna, M. C. (1998) Higher taxonomic relationships among extant mammals based on morphology, with selected comparisons of results from molecular data. *Molecular Phylogenetics and Evolution* 9: 572-584.

Shukor, M. N. (1996) The mammalian fauna on the islands at the northern tip of Sabah, Borneo. *Fieldiana, Zoology* 83: 1-51.

Simmons, N. B. (1994) The case for chiropteran monophyly. *American Museum Novitates* 3103: 1-54.

Simmons, N. B. (1995) Bat relationships and the origin of flight. *Symposia of the Zoological Society of London* 67: 27-43.

Simmons, N. B. and Quinn, T. H. (1994) Evolution of the digital tendon locking mechanism in bats and dermopterans: a phylogenetic perspective. *Journal of Mammalian Evolution* 2: 231-254.

Simpson, G. G. (1945) The principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History* 85: 1-350.

Simpson, G. G. (1965) Long-abandoned views. *Science* 147: 1397

Slijper, E. J. (1946) Comparative biologic-anatomical investigations on the vertebral column and spinal musculature of mammals. *Verhandelingen der Koninklijke Nederlandsche Akademie van Wetenschappen Natuurkunde (Tweede Sectie)* 42: 1-128.

Smith, J. D. and Madkour, G. (1980) Penial morphology and the question of chiropteran phylogeny. In Wilson, D. E. and Gardner, A. L. (eds.): *Proceedings of the Fifth International Bat Research Conference.* Lubbock, Texas: Texas Tech Press, pp. 347-365.

Smith, J. M. and Savage, R. J. G. (1956) Some locomotory adaptations in mammals. *Zoological Journal of the Linnean Society* 42: 603-622.

Sorenson, M. W. (1970) Behavior of tree shrews. In Rosenblum, L. A. (ed.): *Primate Behavior: Developments in Field and Laboratory Research, Vol.1.* New York: Academic Press, pp. 141-193.

Sorenson, M. W. and Conaway, C. H. (1964) Observations of tree shrews in captivity. *Sabah Society Journal* 2: 77-91.

Stafford, B. J. and Thorington, R. W. (1998) Carpal development and morphology in archontan mammals. *Journal of Morphology* 235: 135-155.

Stanhope, M. J., Bailey, W. J., Czelusniak, J., Goodman, M., Si, J.-S., Nickerson, J., Sgouros, J. G., Singer, G. A. M., and Kleinschmidt, T. K. (1993) A molecular view of primate supraordinal relationships from the analysis of both nucleotide and amino acid sequences. In MacPhee, R. D. E. (ed.): *Primates and their Relatives in Phylogenetic Perspective.* New York: Plenum Press, pp. 251-292.

Stanhope, M. J., Smith, M. R., Waddell, V. G., Porter, C. A., Shivji, M. S., and Goodman, M. (1996) Mammalian evolution and the interphotoreceptor retinoid binding protein (IRBP) gene: convincing evidence for several superordinal clades. *Journal of Molecular Evolution* 43: 83-92.

Steele, D. G. (1973) Dental variability in the tree shrews (Tupaiidae). In Zingeser, M. R. (ed.): *Craniofacial Biology of Primates: Symposium of the IVth International Congress of Primatology, Vol. 3.* Basel: Karger, pp. 154-179.

Straus, W. L. and Wislocki, G. B. (1932) On certain similarities between sloths and slow lemurs. *Bulletin of the Museum of Comparative Zoology* 74: 43-56.

Szalay, F. S. (1968) The beginnings of primates. *Evolution* 22: 19-36.

Szalay, F. S. (1969) Mixodectidae, Microsyopidae, and the insectivore-primate transition. *Bulletin of the American Museum of Natural History* 140: 193-330.

Szalay, F. S. (1977) Phylogenetic relationships and a classification of the eutherian Mammalia. In Hecht, M. K., Goody, P. C., and Hecht, B. M. (eds.): *Major Patterns in Vertebrate Evolution.* New York: Plenum Press, pp. 315-374.

Szalay, F. S. (1981) Phylogeny and the problem of adaptive significance: the case of the earliest primates. *Folia Primatologica* 36: 157-182.

Szalay, F. S. (1984) Arboreality: is it homologous in metatherian and eutherian mammals? In Hecht, M. K., Wallace, B., and Prance, G. T. (eds.): *Evolutionary Biology, Vol. 18.* New York: Plenum Press, pp. 215-258.

Szalay, F. S. (1994) *Evolutionary History of the Marsupials and an Analysis of Osteological Characters.* New York: Cambridge University Press.

Szalay, F. S. (1999) Review of "Classification of Mammals above the Species Level" by M.C. McKenna and S.K. Bell. *Journal of Vertebrate Paleontology* 19: 191-195.

Szalay, F. S. and Dagosto, M. (1980) Locomotor adaptations as reflected on the humerus of Paleogene primates. *Folia Primatologica* 34: 1-45.

Szalay, F. S. and Dagosto, M. (1988) Evolution of hallucial grasping in the primates. *Journal of Human Evolution* 17: 1-33.

Szalay, F. S. and Delson, E. (1979) *Evolutionary History of the Primates.* New York: Academic Press.

Szalay, F. S. and Drawhorn, G. (1980) Evolution and diversification of the Archonta in an arboreal milieu. In Luckett, W. P. (ed.): *Comparative Biology and Evolutionary Relationships of Tree Shrews.* New York: Plenum, pp. 133-169.

Szalay, F. S. and Lucas, S. G. (1993) Cranioskeletal morphology of archontans, and diagnoses of Chiroptera, Volitantia, and Archonta. In MacPhee, R. D. E. (ed.): *Primates and their Relatives in Phylogenetic Perspective.* New York: Plenum Press, pp. 187-226.

Szalay, F. S. and Lucas, S. G. (1996) The postcranial morphology of Paleocene *Chriacus* and *Mixodectes* and the phylogenetic relationships of archontan mammals. *Bulletin of the New Mexico Museum of Natural History & Science* 7: 1-47.

Szalay, F. S. and Sargis, E. J. (submitted) Model-based analysis of postcranial osteology of marsupials from the Paleocene of Itaboraí, Brazil, and the phylogenetics and biogeography of Metatheria. *Geodiversitas.*

Szalay, F. S. and Trofimov, B. A. (1996) The Mongolian Late Cretaceous *Asiatherium*, and the early phylogeny and paleobiogeography of Metatheria. *Journal of Vertebrate Paleontology* 16: 474-509.

Szalay, F. S., Rosenberger, A. L., and Dagosto, M. (1987) Diagnosis and differentiation of the order Primates. *Yearbook of Physical Anthropology* 30: 75-105.

Szalay, F. S., Tattersall, I., and Decker, R. L. (1975) Phylogenetic relationships of *Plesiadapis* - postcranial evidence. In Szalay, F. S. (ed.): *Approaches to Primate Paleobiology.* Basel: Karger, pp. 136-166.

Tattersall, I. (1984) The tree-shrew, *Tupaia*: A "living model" of the ancestral primate? In Eldredge, N. and Stanley, S. M. (eds.): *Living Fossils.* New York: Springer-Verlag, pp. 32-37.

Taylor, M. E. (1974) The functional anatomy of the forelimb of some African Viverridae (Carnivora). *Journal of Morphology* 143: 307-336.

Taylor, M. E. (1976) The functional anatomy of the hindlimb of some African Viverridae (Carnivora). *Journal of Morphology* 148: 227-254.

Thewissen, J. G. M. and Babcock, S. K. (1991) Distinctive cranial and cervical innervation of wing muscles: new evidence for bat monophyly. *Science* 251: 934-936.

Thewissen, J. G. M. and Babcock, S. K. (1992) The origin of flight in bats. *Bioscience* 42: 340-345.

Thewissen, J. G. M. and Babcock, S. K. (1993) The implications of the propatagial muscles of flying and gliding mammals for archontan systematics. In MacPhee, R. D. E. (ed.): *Primates and their Relatives in Phylogenetic Perspective.* New York: Plenum Press, pp. 91-109.

Tong, Y. (1988) Fossil tree shrews from the Eocene Hetaoyuan Formation of Xichuan, Henan. *Vertebrata PalAsiatica* 26: 214-220.

Van Valen, L. M. (1965) Tree shrews, primates, and fossils. *Evolution* 19: 137-151.

Vandenbergh, J. G. (1963) Feeding, activity and social behavior of the tree shrew, *Tupaia glis*, in a large outdoor enclosure. *Folia Primatologica* 1: 199-207.

Vaughan, T. A. (1970) The skeletal system. In Wimsatt, W. A. (ed.): *Biology of Bats, Vol. 1.* New York: Academic Press, pp. 97-138.

Verma, K. (1965) Notes on the biology and anatomy of the Indian tree-shrew, *Anathana wroughtoni. Mammalia* 29: 289-330.

Waddell, P. J., Okada, N., and Hasegawa, M. (1999) Towards resolving the interordinal relationships of placental mammals. *Systematic Biology* 48: 1-5.

Wagner, J. A. (1855) *Die Säugethiere in Abbildungen nach der Natur.* Leipzip: Weiger. Supplementband, Abt. 5: 1-810.

Walker, A. C. (1974) Locomotor adaptations in past and present prosimian primates. In Jenkins, F. A., Jr. (ed.): *Primate Locomotion.* New York: Academic Press, pp. 349-381.

Walton, D. W. and Walton, G. M. (1970) Post-cranial osteology of bats. In Slaughter, B. H. and Walton, D. W. (eds.): *About Bats: A Chiropteran Biology Symposium.* Dallas: Southern Methodist University Press, pp. 93-126.

Ward, C. V. (1993) Torso morphology and locomotion in *Proconsul nyanzae. American Journal of Physical Anthropology* 92: 291-328.

Ward, C. V., Walker, A. C., Teaford, M. F., and Odhiambo, I. (1993) Partial skeleton of *Proconsul nyanzae* from Mfangano Island, Kenya. *American Journal of Physical Anthropology* 90: 77-111.

Wharton, C. H. (1950) Notes on the Philippine tree shrew, *Urogale everetti* Thomas. *Journal of Mammalogy* 31: 352-354.

Whishaw, I. Q., Sarna, J. R., and Pellis, S. M. (1998) Evidence for rodent-common and species-typical limb and digit use in eating, derived from a comparative analysis of ten rodent species. *Behavioural Brain Research* 96: 79-91.

Whittow, G. C. and Gould, E. (1976) Body temperature and oxygen consumption of the Pentail Tree Shrew (*Ptilocercus lowii*). *Journal of Mammalogy* 57: 754-756.

Wible, J. R. (1993) Cranial circulation and relationships of the colugo *Cynocephalus* (Dermoptera, Mammalia). *American Museum Novitates* 3072: 1-27.

Wible, J. R. and Covert, H. H. (1987) Primates: cladistic diagnosis and relationships. *Journal of Human Evolution* 16: 1-22.

Wible, J. R. and Martin, J. R. (1993) Ontogeny of the tympanic floor and roof in archontans. In MacPhee, R. D. E. (ed.): *Primates and their Relatives in Phylogenetic Perspective.* New York: Plenum Press, pp. 111-148.

Wible, J. R. and Novacek, M. J. (1988) Cranial evidence for the monophyletic origin of bats. *American Museum Novitates* 2911: 1-19.

Wible, J. R. and Zeller, U. A. (1994) Cranial circulation of the pen-tailed tree shrew *Ptilocercus lowii* and relationships of Scandentia. *Journal of Mammalian Evolution* 2: 209-230.

Wilson, D. E. (1993) Order Scandentia. In Wilson, D. E. and Reeder, D. M. (eds.): *Mammal Species of the World: A Taxonomic and Geographic Reference.* Washington: Smithsonian Institution Press, pp. 131-133.

Wöhrmann-Repenning, A. (1979) Primate characters in the skull of *Tupaia glis* and *Urogale everetti* (Mammalia, Tupaiiformes). *Senckenbergiana Biologica* 60: 1-6.

Zeller, U. A. (1986a) Ontogeny and cranial morphology of the tympanic region of the Tupaiidae, with special reference to *Ptilocercus*. *Folia Primatologica* 47: 61-80.

Zeller, U. A. (1986b) The systematic relations of tree shrews: evidence from skull morphogenesis. In Else, J. G. and Lee, P. C. (eds.): *Primate Evolution*. Cambridge: Cambridge University Press, pp. 273-280.

Zeller, U. A. (1987) Morphogenesis of the mammalian skull with special reference to *Tupaia*. In Kuhn, H. J. and Zeller, U. A. (eds.): *Morphogenesis of the Mammalian Skull*. Hamburg: Verlag Paul Parey, pp. 17-50.

Ziemer, L. K. (1978) *Functional Morphology of Forelimb Joints in the Woolly Monkey Lagothrix lagothricha*. Basel: Karger.