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TAXONOMY AND ECOLOGICAL MORPHOLOGY OF THE FLYING LEMURS (DERMOPTERA, CYNOCEPHALIDAE)

by

Brian J. Stafford

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

1999

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

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Abstract

TAXONOMY AND ECOLOGICAL MORPHOLOGY OF THE FLYING LEMURS (DERMOPTERA, CYNOCEPHALIDAE)

by

Brian J. Stafford

Adviser: Professor Frederick S. Szalay

The craniodental functional morphology of the extant dermopterans (Cynocephalus volans and Galeopterus variegatus) was studied to clarify the taxonomy and systematics of the group. Two taxa of generic rank were confirmed and functional hypotheses about the differences between the taxa are presented.

The postcranial morphology of the dermopterans was also evaluated in relation to other gliding mammals and their nongliding relatives, bats, and highly suspensory taxa. Characters common to dermopterans and other gliding mammals are evaluated in relation to aerodynamic theory. Other characters, common to dermopterans and suspensory taxa, are interpreted in relation to under-branch suspension.

The overall picture of dermopteran ecological and functional morphology is complex. Often dermopterans are similar to other gliding mammals. At the same time they are also often similar to bats, or to largely suspensory taxa like the sloths. Many dermopteran characters that have been interpreted as gliding

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adaptations, or as synapomorphies with bats, are also present in suspensory taxa. Many of the unique features that dermopterans and bats possess are currently coopted into the gliding or flight systems. However it seems likely that both bats and dermopterans have built their aerodynamic abilities upon a largely suspensory framework.

In general, dermopteran aerodynamics indicate an animal that can glide slower than comparable gliding mammals, and at shallower glide angles. It is also a picture of an animal that is more agile and maneuverable than comparable gliding mammals. This fits well with what has been proposed as a reasonable preflapping chiropteran.

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CHAPTER 1: INTRODUCTION

Colugos are an enigmatic order of mammals that have been little studied. For this reason alone they warrant study, but they may also be of particular relevance to interpretations of early primate evolution. Beard (1989, 1993) has proposed that the Dermoptera is the sister taxon to the Primates, in exclusion of the Tupaiidae and Chiroptera. For this grouping he coined the supraordinal taxon Primatomorpha. This interpretation is based on the study of plesiadapiform fossils in which Beard saw homologously shared and derived characteristics with the living dermopterans. The characters that Beard was using were from several areas of the postcranium, but the strongest evidence came from the hand. The implications of Beard's proposal (contested by Szalay and Lucas 1993, 1996) are far reaching and, if true, have a profound impact on the way that we must view not only primate evolution, but the evolution of the Archonta as a whole.

The first implication of this proposal is that gliding in mammals can now be dated to at least the Paleocene, making this the earliest evidence of mammalian gliders. The second implication is that at least one lineage of the plesiadapiforms must now be viewed and interpreted as a glider. Thirdly, Beard's interpretation eliminates the colugos as the closest relative of the bats. This makes the interpretation of the colugos as the sister group to, and an analog of a gliding bat ancestor, untenable. This requires that bats have evolved flight independently of the colugos and therefore gliding must have evolved twice

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within the Archonta. Following from this last point, the removal of the colugos from a monophyletic association with bats weakens the evidence for the placement of the bats within the Archonta. Although the colugos show all of the tarsal characters noted by Szalay and Decker (1974) for archontans, the bats show none of these characters, their tarsi being too highly specialized. The inclusion of the bats in the Archonta by these authors was based on the hypothesis of bat-colugo holophyly.

The dermopterans are only one group of mammals that have evolved the ability to glide. Among extant mammals the Pteromyinae (flying squirrels), Anomaluridae (scaly-tailed "flying squirrels"), Petauroides volans (the greater marsupial glider), Petaurus (the lesser marsupial gliders), and Acrobates pygmaeus (the feather-tailed marsupial glider) have all independently evolved the ability to glide (Fig. 1.1). Mammalian gliders are even prevalent in the fossil record with Eomys quercyi and Glirulus lissiensis both now identified as gliders (Mein and Romaggi, 1991; Storch et al., 1996). Whether or not the bats represent a ninth independent acquisition of gliding is a question open to debate. The colugos, however, possess the most extensive gliding membrane of any known vertebrate. It completely encloses the animal, with the exception of the rostrum. For this reason, the colugos have often been called the most accomplished of all mammalian gliders, but comparative data that can be used to evaluate relative gliding performance among mammals is nonexistent.

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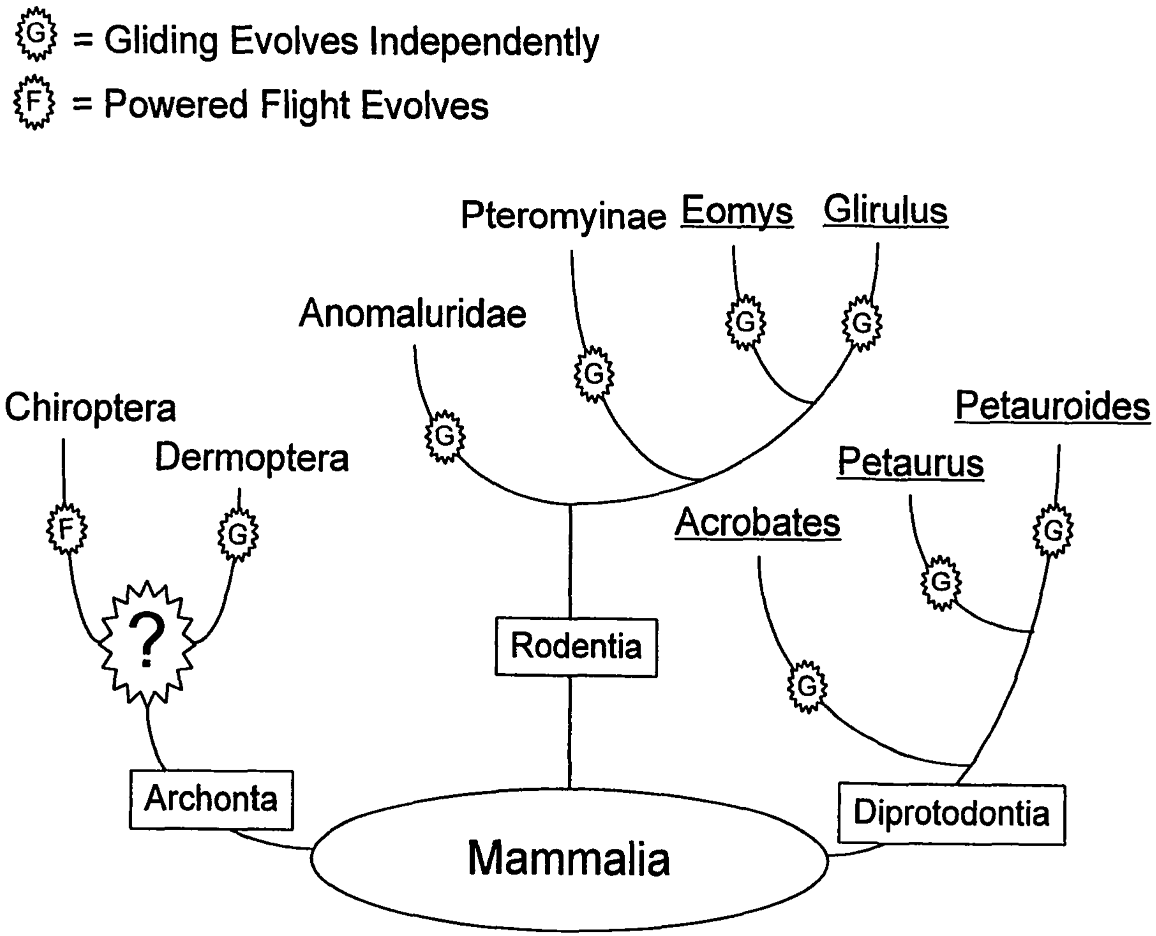

Figure 1.1: Phylogenetic relationships among gliding mammals.

The colugos have been known to science since before they were described as Lemur volans by Linneaus in 1758 (hence the misnomer flying lemur), but have only recently (Wischusen, 1990) been systematically studied in the wild. Up until this study all information on colugo behavior (Wallace, 1869; Chapman, 1902; Beebe, 1913; Pocock, 1926; Harrison, 1949, 1951 Wharton, 1950; Lim 1967) was anecdotal at best, and most of the work done on colugos has dealt with the question of their phylogenetic relationships. Linneaus (1758) placed them as a genus within the order Primates, but he also included Vespertilio (a genus of microbats) in the order. In 1811 Illiger placed the bats and colugos together in his Order Volitantia (Table 1.1). His reasons for this grouping were largely based on the presence of a manual interdigital patagium in colugos and bats, although he also cites general similarities of the dentitions, genitalia, and mammae. Through the early half of the 19th century many colugo genera and species were named but the next major work to discuss colugo morphology was that of Gervais (1854). However, he still considered colugos to have affinities with primates, based on the degree of dexterity of colugo hands, a belief based on the long slender digits of colugos.

It was not until 1886 that Leche undertook a detailed and exhaustive study of the anatomy of the Dermoptera. His work was based entirely on the Sundaic colugo, and he did find numerous similarities between colugos and bats. So many in fact that he regarded colugos as incipient bats. It is interesting to note that Leche also found numerous similarities between colugos and prosimians, and between bats and prosimians, to the exclusion of "insectivores". Winge

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(1941) strongly criticized Leche's work, but these criticisms are difficult to evaluate. Winge's main objection seems to be that Leche did not fully appreciate the morphological diversity among bats. Many of Winge's refutations of Leche's interpretations simply point out that in some species of bats the condition that Leche described is different. Winge also felt, correctly, that dermopterans were too specialized to be the ancestor of bats. Extant dermopterans are highly derived from any ancestral stage that may be postulated for dermopterans..

Gregory (1910) was the first to recognize the supraordinal taxon Archonta which grouped the colugos with the bats, and the Volitantia with the Primates, Scandentia, and Macroscelidea (the elephant shrews have since been removed from this group). Undoubtedly, Gregory's support for the Volitantia would have been stronger had he been aware of the work of Shufeldt (1911). In this, the second major work on colugo morphology, Shufeldt provided a detailed description of the osteology of the Philippine kagwang. He does not consider the phylogenetic relationships of the dermopterans, but throughout his discussion he compared dermopterans only to insectivores and seemed to consider the dermopterans best placed in this group. Pocock (1926) described the external characteristics of dermopterans and, with some equivocating, eventually recognized close ties between dermopterans and bats.

The next major work to touch on dermopteran relationships was that of Simpson (1945), but between the turn of the century and the publication of this work there exists an extensive literature on colugo taxonomy (Table 1.1). Most of this work was conducted in the first decade of the twentieth century, and was

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Table 1.1: Taxonomy of the dermopterans[1]

Date	Author	Nomen	Notes
1758	Linnaeus, C.	Lemur volans	"Habitat in Asia", based on Cammeli's Faunula Insularum Philippinsium, no type mentioned.
1768	Boddaert, P.	Cynocephalus volans	Based on Lemur volans Linnaeus, 1758 or a specimen from "Ternate".
1783	Pallas, P.S.	Galeopithecus volans	Based on Lemur volans Linnaeus, 1758; discusses specimens from Halmahera and Ternate. Specimens figured are the Sundaic colugo however.
1796	Geoffroy, E. & Cuvier, G.	? variegatus ? rufus ? ternatensis	Not seen
1799	Lacépède, B.G.E.	Galeopithecus rufus	Not seen, reference in Sherborn.
1799	Audebert, J.B.	Galeopithecus variegatus	From Sig. River Java?
1811	Illiger, C.	Volitantia	An Order Including Chiroptera and Dermoptera as Families
1815	Rafinesque, C.S.	Galeopus	Not seen.
1817	Desmarest, A.G.	varius	Not seen.
1820	Desmarest, A.G.	Galeopithecus rufus	Not seen. Type from Pelew Id., Philippines.
		Galeopithecus ternatensis	Type from Ternate, Philippines?

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1821	Gray, J.E.	Galeopithecidae	Lists only "*Galeopithecus* Geoff. *Lemur volans* Lin.". Description "...canine obtusely tubercular, short, like the grinders." seems to describe Sundaic colugo.
1829	Burnett, G.T.	*Pleuropterus*	Suggested as genus name with species *rufus*, *variegatus*, and *ternatensis*. No mention of specimens except *L. volans*.
		Dermopterus	Suggested as genus name with species *rufus*, *variegatus*, and *ternatensis*. No mention of specimens except *L. volans*.
		Galeopithecus	Suggested as genus name with species *rufus*, *variegatus*, and *ternatensis*. No mention of specimens except *L. volans*.
1829	Geoffroy, E.	*Galeopithecus variegatus*	Not Seen. Type *Galeopithecus variegatus* Audebert, 1799.
1838	Waterhouse,	*Galeopithecus temminckii*	BMNH 7.1.1.220 according to Thomas (1908). Correctly describes Sundaic form.
		Galeopithecus phillippinensis	Correctly describes Philippine form.
1840	Wagner, J.A.	*Galeopithecus undatus*	Not seen. Java?
1870	Gray	*Colugo*	Type *Galeopithecus phillippinensis* Waterhouse.
1900	Miller	*Galeopithecus volans*	"Two specimens, both from Pulo Adang." These are Sundaic.

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1903	Miller	Galeopithecus pumilus	USNM 104448, Pulo Adang, Butang Ids., dwarf.
		Galeopithecus aoris	USNM 112428, Pulo Aor, Johore.
		Galeopithecus gracilis	USNM 104601, Sirhassen Id., South Natuna Ids.
		Galeopithecus natunae	USNM 104602, Bunguran, Id., North Natuna Ids.
		Galeopithecus stauratus	USNM 121750, Tana Bala Id., Batu Ids., Sumatra.
		Galeopithecus tuancus	USNM 114375, Pulo Tuangku, Banjak Ids., Sumatra.
1906	Miller	Colugidae	Based on Galeopithecidae Gray, 1821.
		Colugo	Type Colugo Gray, 1870.
		Cynocephalus	Type Cynocephalus Boddaert, 1768 and Galeopithecus Pallas 1783.
1908	Lyon	Cynocephalus tellonis	BMNH 7.6.18.2, Pulo Tello, Batu Ids., Sumatra.
1908	Thomas	Cynocephalus volans	Type Lemur volans Linnaeus, 1758.
		Galeopterus temminckii	Type Galeopithecus temminckii Waterhouse, 1838
		Galeopteridae	
1908	Thomas	Galeopterus taylori	BMNH 8.1.25.3, Pulo Tioman.
1908	Thomas	Galeopterus peninsulae	BMNH 8.7.20.10, Semanghk Pass, Selangor-Pahang, Malay Peninsula.
1909	Lyon	Galeopterus chombolis	USNM 144375, Pulo Jombol, Rhio-Linga Arch.
1911	Lyon	Galeopterus borneanus	USNM 151888, Tjantung, SE Borneo.

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		Galeopterus lautensis	USNM 151886, Pulo Luat, SE Borneo.
		Galeopterus abbotti	USNM 145577, Pulo Panebangan, W Borneo.
1919	Gyldenstolpe	*Galeopterus lechei*	ZMC 24, Toembang Maroewe, Central Borneo.
1924	Cabrera	*Galeopterus hantu*	MNCN 20.11.19.9, Baram District, Sarawak.
1925	Cabrera		Recognizes *Cynocephalus volans* from the Philippines, and 17 species of *Galeopterus* from everywhere else.
1945	Simpson	Cynocephalidae	Recognizes one genus, *Cynocephalus*, with two subgenera.

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[1] MNCN = Museo Nacional de Ciencias Naturales; USNM = National Museum of Natural History, Smithsonian Institution; ZMC = Zoological Museum at Christiania

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characterized by the naming of a new dermopteran species on each island on which they were found (Lyon, 1908, 1911; Miller, 1900, 1903, 1906; Thomas, 1908). Some later authors (i.e. Cabrera, 1925) recognized as many as 25 distinct species. However, the work of Thomas (1908) for the first time correctly recognized Cynocephalus and Galeopterus as separate genera. Still, because Simpson recognized only one genus with two species, this view continues to be reflected in all standard mammalogical texts and classifications.

Interest in the relationships of the dermopterans was rekindled with the entrance of cladistic methodology into the English speaking community. Szalay (1969), working primarily on cranial morphology considered the relevance of dermopterans to mixodectids and microsyopids, and later (Szalay and Decker, 1974; Szalay, 1977; Szalay and Drawhorn, 1980) dealt also with broader interordinal issues. During this time period Rose (Rose, 1973; Rose and Simons, 1977; Rose and Walker, 1981) also considered the dental evidence of a link between dermopterans and plagiomenids. Other studies followed (Novacek et al., 1988; Novacek and Wyss, 1986; Wible and Covert, 1987) but generally tended to confirm the link between the bats and dermopterans. Even so, by the early 1980s molecular methods began to be used in phylogenetic studies (Sarich and Cronin, 1976; Cronin and Sarich, 1980), and in the mid to late 1980s the results produced by these studies (Adkins and Honeycutt, 1991; Ammerman and Hillis, 1992; Goodman et al., 1982, 1985) and the works of Beard (1989, 1990a, 1990b, 1991, 1993) and Kay and colleagues (Kay et al., 1990; Kay et al., 1992) rekindled interest in the dermopterans (Allard et al., 1996; MacPhee, 1993 and

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included contributions; Simmons, 1994, 1995; Stafford and Szalay, in press; Stafford and Thorington, 1998; Szalay and Lucas, 1993, 1996; Szalay et al., 1993 and included contributions; Wible 1993). The controversy over the non-monophyly of bats (Ammerman and Hillis, 1992; Baker at al., 1991a, 199b; Greenwald, 1990; Hutcheon et al., 1998; Luckett, 1993; Pettigrew, 1991a, 1991b; Pettigrew et al., 1989; Simmons et al., 1991; Thewissen and Babcock, 1991, 1992; Wible and Novacek, 1988) also fueled interest in dermopterans. However, there is still no consensus among workers as to the sister taxon of the dermopterans. Dermotherium major [Ducrocq], 1992 from the Upper Eocene of Thailand remains the best candidate for a fossil dermopteran, but appears to be quite similar to G. variegatus and therefore sheds no light on the question of dermopteran interordinal relationships.

In this study the Archonta (Chiroptera + Dermoptera + Primates + Scandentia) is assumed to be monophyletic, but no assumptions are made as to the monophyly of the Volitantia (Chiroptera + Dermoptera). This study is primarily an assessment of the functional morphology of various aspects of the patagium and postcranial skeleton of dermopterans. Chapter two describes materials and methods used in this study. Chapter three reviews all that we currently know about dermopteran behavior and ecology, and is consequently a very short chapter. Most of what is known about dermopteran behavior and ecology is anecdotal at best. This makes the interpretation of character complexes somewhat tenuous, and all such hypotheses must be treated as preliminary pending field studies designed to illuminate form-function relationships.

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Chapter four contains a consideration of the cranio-dental functional morphology of the dermopterans designed to evaluate the level of taxonomic distinctness between the two forms. Many studies (Beard, 1989, 1990a, 1990b, 1991, 1993; Kay et al., 1990, 1992; Simmons, 1993,1994; Simmons et al., 1991; Simmons and Quinn, 1994; Wible, 1993; Wible and Martin, 1993; Wible and Novacek, 1988) have used one of the taxa as representative of the Order without recognizing the very real morphological disparity between the two taxa, as pointed out be Szalay and Lucas (1993, 1996). What follows this is a consideration of aspects of dermopteran postcranial functional morphology with specific reference to other mammalian gliders, bats, and other mammalian taxa that are highly suspensory. In the past (Beard, 1989, 1990a, 1990b, 1991, 1993; Simmons, 1993,1994; Simmons et al., 1991), dermopteran morphological characters have too readily been described as gliding adaptations without any consideration of alternative explanations, although there have been some notable exceptions (Simmons and Quinn, 1994; Szalay and Lucas, 1993, 1996) including the works of Beard (1989, 1990a, 1990b, 1991, 1993).

Chapters five through nine examine major areas of the dermopteran postcranial skeleton. In each of these chapters the dermopterans are compared to other gliding mammals and their non-gliding relatives, as well as the sloths and Cyclopes, lorises, tree shrews, and bats. This selection of taxa (Table 1.2) was chosen to uncover adaptations related not only to gliding, but to suspensory or slow climbing behaviors in dermopterans. Chapter ten contains a review of aerodynamic theory. Chapter 11 is an application of aerodynamic theory to

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gliding mammals in light of the information gained in the previous chapters. Chapter twelve includes a summary of the conclusions from the previous chapters.

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Table 1.2: List of specimens examined in this study.[1]

Taxon	Museum #	Sex	Age	Site	
Chiroptera					
Megachiroptera					
Cynopterus brachyotis	USNM 573383	M	A	Philippines	Luzon
Cynopterus brachyotis	USNM 573387	M	A	Philippines	Luzon
Cynopterus brachyotis	USNM 573400	M	A	Philippines	Luzon
Cynopterus brachyotis	USNM 573403	F	A	Philippines	Luzon
Cynopterus brachyotis	USNM 573409	F	A	Philippines	Luzon
Cynopterus brachyotis	USNM 573410	F	A	Philippines	Luzon
Hypsignathus monstrosus	USNM 396650	F	A	NZP	
Hypsignathus monstrosus	USNM 396640	F	A	NZP	
Hypsignathus monstrosus	USNM 396675	M	A	NZP	
Hypsignathus monstrosus	USNM 463935	F	A	NZP	
Hypsignathus monstrosus	USNM 464511	M	A	NZP	
Hypsignathus monstrosus	USNM 464514	M	A	NZP	
Hypsignathus monstrosus	USNM 464996	F	A	NZP	
Hypsignathus monstrosus	USNM 464998	F	A	NZP	
Microchiroptera					
Artibeus jamaicensis	USNM 362098	F	A	Dominica	Clarke Hall
Desmodus rotundus	USNM 523439	M	A	Mexico	Las Piedras
Furipterus horrens	USNM 549507	M	A	Brazil	Para
Macroderma gigas	USNM 396827	F	A	Australia	NT

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Mystacina tuberculata	USNM 120576	F	S	New Zealand	
Myzopoda aurita	USNM 577065	M	A	Madagascar	Toliara
Tadarida condylura	USNM 365686	F	A	Mozambique	Tete
Thyroptera discifera	USNM 102922	?	A	Venezuela	San Julian
Dermoptera					
Cynocephalus volans	FMNH 61032	M	A	Philippines	Mindanao
Cynocephalus volans	FMNH 56442	F	A	Philippines	Mindanao
Cynocephalus volans	FMNH 62067	M	A	Philippines	Mindanao
Cynocephalus volans	FMNH 61030	F	A	Philippines	Mindanao
Cynocephalus volans	FMNH 56441	F	A	Philippines	Mindanao
Cynocephalus volans	USNM 144662	M	S	Philippines	Basilan
Cynocephalus volans	USNM 239191	F	A	Philippines	Basilan
Cynocephalus volans	USNM 578084	M	A	Philippines	Biliran
Cynocephalus volans	Uncatalogued	?	A	Philippines	?
Galeopterus variegatus	USNM 155363	?	A	Indonesia	East Java
Galeopterus variegatus	USNM 154600	F	S	Indonesia	Mt. Salk
Galeopterus variegatus	USNM 49640	F	A	Indonesia	Pulo Bintang
Galeopterus variegatus	USNM 49693	F	A	Sumatra	Pulo Kundur
Galeopterus variegatus	USNM 198704	M	A	Borneo	Laham
Galeopterus variegatus	USNM 197202	F	A	Borneo	Labuan Klambu
Galeopterus variegatus	USNM 197203	F	J	Borneo	Labuan Klambu
Galeopterus variegatus	USNM 196905	M	A	Borneo	Mt. Talisaian
Galeopterus variegatus	USNM 151887	M	A	Borneo	Pulo Sebuku
Galeopterus variegatus	USNM 317118	?	A	Borneo	Jesselton

Galeopterus variegatus	USNM 49470	?	A	Malaysia	Peninsula
Diprotodontia					
Petauridae					
Petaurus australis	USNM 221150	F	A	NSW	Wandandian
Petaurus breviceps	USNM 237728	M	A	NSW	Ebor
Petaurus breviceps	USNM 221215	M	A	NSW	Wandandian
Petaurus breviceps	USNM 319791	?	A	NZP	
Petaurus breviceps	USNM 221218	M	A	NSW	Wandandian
Petaurus breviceps	USNM 297823	?	A	NZP	
Petaurus breviceps	USNM 270812	M	A	NZP	
Petaurus breviceps	USNM 49937	M	A	NSW	
Petaurus breviceps	USNM 396817	F	A	NT	162 mi SE Darwin
Petaurus breviceps	USNM 543146	M	A	N. Moluccas	Halmahera Id
Petaurus breviceps	USNM 534229	M	A	New Guinea	Mt. Hageb
Petaurus norfolcensis	USNM 293168	M	A	Australia	
Petaurus norfolcensis	USNM 362186	?	A	?	
Pseudocheiridae					
Hemibelideus lemuroides	USNM 238366	M	A	Queensland	Atherton
Petauroides volans	USNM 221137	F	S	NSW	Wandandian
Petauroides volans	USNM 238417	M	S	Queensland	Atherton
Pseudocheirus herbertensis	USNM 238391	F	A	Queensland	Atherton
Pseudocheirus herbertensis	USNM 238396	M	A	Queensland	Atherton
Pseudocheirus occidentalis	USNM 237653	M	A	W. Australia	Busselton
Pseudocheirus occidentalis	USNM 237694	F	S	W. Australia	Busselton

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Pseudocheirus perigrinus	USNM 221155	F	A	NSW	Wandandian
Pseudocheirus perigrinus	USNM 238377	M	A	Queensland	Atherton
Pseudocheirus perigrinus	USNM 277372	?	A	NSW	Blue Mts
Acrobatidae					
Acrobates pygmaeus	USNM 582004	M	A	?	San Diego Zoo
Primates					
Arctocebus calabarensis	USNM 511930	?	A	Cameroon	Kumba
Loris tardigradus	USNM 256737	F	A	Sri Lanka	Northwest
Nycticebus coucang	USNM 300000	M	A	Malaysia	Kuala Lumpur
Perodicticus potto	USNM 481774	F	A	Liberia	Tars Town
Rodentia					
Anomaluridae					
Anomalurops beecrofti	USNM 84546	F	A	W. Africa	Benito River
Anomalurops beecrofti	USNM 84547	?	A	W. Africa	
Anomalurops beecrofti	USNM 466118	F	J	Ivory Coast	Sienso
Anomalurus derbianus	USNM 466119	F	A	Ivory Coast	Sassandra River
Anomalurus derbianus	USNM 466120	M	A	Ivory Coast	Niebe
Anomalurus derbianus	USNM 466121	F	S	Ghana	Adamso
Anomalurus peli	USNM 429832	F	A	Ghana	Oda
Anomalurus peli	USNM 466126	M	S	Ivory Coast	Yabrasso
Anomalurus peli	USNM 399470	?	A	?	?
Sciuridae					
Pteromyinae					
Aeromys tephromelas	USNM 196743	F	A	Borneo	Telok, Sombong

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Glaucomys sabrinus	USNM 397068	M	A	Michigan	Alger Co.
Glaucomys sabrinus	USNM 551841	M	A	Michigan	Schoolcraft Co.
Glaucomys sabrinus	USNM 398288	F	A	California	Sierra Co.
Glaucomys sabrinus	USNM 235940	M	A	Alberta	Peace Point
Glaucomys sabrinus	USNM 332333	M	A	Tennessee	Carter Co.
Glaucomys sabrinus	USNM 267440	M	A	Tennessee	Roan Mt.
Glaucomys sabrinus	USNM 524544	F	S	Michigan	Schoolcraft Co.
Glaucomys sabrinus	USNM 524543	F	S	Michigan	Schoolcraft Co.
Glaucomys sabrinus	USNM 397065	F	A	Michigan	Chippewa Co.
Glaucomys sabrinus	USNM 397040	F	A	Michigan	Cheyboygan Co.
Glaucomys sabrinus	USNM 397021	F	A	Wisconsin	
Glaucomys sabrinus	USNM 397022	F	A	Michigan	Chippewa Co.
Glaucomys sabrinus	USNM 398287	F	A	Washington	Chelan Co.
Glaucomys sabrinus	USNM 397017	F	A	Michigan	Chippewa Co.
Hylopetes fimbriatus	USNM 173363	F	A	Kashmir	Pelawar
Hylopetes fimbriatus	USNM 173365	F	A	Kashmir	Kamri
Hylopetes fimbriatus	USNM 353243	F	S	Pakistan	Hazara, Snogran
Hylopetes fimbriatus	USNM 173361	F	S	Kashmir	Pelawar
Hylopetes phayrei	USNM 267267	?	S	Thailand	Chiengmai
Iomys horsfieldi	USNM 292654	F	S	Borneo	Mt. Kinabalu
Petaurista alborufus	USNM 332937	?	S	Taiwan	Nan Tou Hsien
Petaurista elegans	USNM 292647	M	A	Borneo	Mt. Kinabalu
Petaurista leucogenys	USNM 20941	F	A	Japan	Tokyo Market
Petaurista petaurista	USNM 256914	?	A	China	Cochin, Prang

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Petaurista petaurista	USNM 174080	?	A	Kashmir	Dachin, Khistwar
Petaurista petaurista	USNM 174079	M	A	Kashmir	Dachin, Khistwar
Petaurista petaurista	USNM 197320	F	A	Borneo	Landas
Petaurista petaurista	USNM 173374	F	A	Kashmir	Kamri Nullah
Petaurista petaurista	USNM 49660	F	A	Batu Islands	Tana Bala
Petaurista philippensis	USNM 258016	F	A	China	Cochin, Bienhoa
Petaurista philippensis	USNM 258017	M	A	China	Cochin, Bienhoa
Petaurista philippensis	USNM 257844	F	A	China	Cochin, Bien Hoa
Petaurista philippensis	USNM 307073	M	S	NZP	NZP
Petaurista sp	USNM 267209	F	A	Siam	Doi Chiengtao
Petaurista sp	USNM 254807	?	S	China	Szechwan, Mupin
Trogopterus xanthipes	USNM 258520	F	S	China	Szechwan, Wei Chow
Trogopterus xanthipes	USNM 268872	?	A	China	Szechwan
Sciurinae					
Sciurus carolinensis	USNM 528045	M	A	North Carolina	Wake Co., Raleigh
Sciurus carolinensis	USNM 500992	M	A	Massachusetts	Middlesex Co.
Sciurus carolinensis	USNM 503982	M	A	Virginia	Arlington Co.
Sciurus carolinensis	USNM 528175	M	A	W. Virginia	Monogalia Co.
Sciurus carolinensis	USNM 396202	?	A	Virginia	Fairfax Co.
Sciurus carolinensis	USNM 398003	F	A	Maryland	Montgomery Co.
Sciurus deppei	USNM 244953	M	A	Guatemala	Peten, Remote
Sciurus deppei	USNM 244934	M	A	Guatemala	Peten, Chuntuqui
Sciurus deppei	USNM 244938	M	A	Guatemala	Peten, Chuntuqui
Sciurus deppei	USNM 244954	M	A	Guatemala	Peten, Remote

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Sciurus deppei	USNM 244956	F	A	Guatemala	Peten, Libertad
Sciurus deppei	USNM 244958	F	A	Guatemala	Peten, Libertad
Sciurus niger	USNM 397160	F	A	Michigan	Wayne Co.
Sciurus niger	USNM 270303	?	A	S. Carolina	Georgetown
Sciurus niger	USNM 564075	F	A	Minnesota	St. Peter
Sciurus niger	USNM 261765	M	A	Maryland	Aireys
Sciurus niger	USNM 257984	M	A	Florida	Tallahassee
Scandentia					
Tupaia glis	USNM 397984	?	A	?	?
Tupaia glis	USNM 574901	M	A	?	?
Xenarthra					
Bradypodidae					
Bradypus variegatus	USNM 252306	M	A	Costa Rica	NZP
Bradypus variegatus	USNM 252299	F	A	Costa Rica	NZP
Bradypus tridactylus	USNM 256676	F	A	Guyana	NZP
Megalonychidae					
Choloepus didactylus	USNM 548401	M	A	?	NZP
Choloepus hoffmanni	USNM 260868	F	A	?	NZP
Choloepus didactylus	USNM 257009	?	A	British Guiana	NZP
Myrmecophagidae					
Cyclopes didactylus	USNM 200353	?	A	Brazil	Para
Cyclopes didactylus	USNM 283876	F	A	Panama	NZP
Cyclopes didactylus	USNM 583067	F	A	Belize	Toledo

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[1] USNM = National Museum of Natural History, Smithsonian Institution; FMNH = Field Museum of Natural history; M = Male; F = Female; A = Adult, replacement dentition fully erupted, all suture and epiphyses fully fused; S = Sub-adult, replacement dentition fully erupted but some sutures and epiphyses not fully fused; J = Juvenile, replacement dentition not fully erupted, sutures and epiphyses not fully fused, these specimens may be plotted on graphs but **were not** included in statistical analyses; NZP = national Zoological Park, Smithsonian Institution; NT = Northern territory, Australia; NSW = New South Wales, Australia. Site information is as listed on specimen labels and has not been updated for subsequent political changes.

CHAPTER 2: MATERIAL AND METHODS

This chapter describes the various materials, methods, and techniques used in this study. The general conceptual methodology consists of a comparison of dermopterans with bats, flying squirrels, anomalurids, and gliding marsupials. The nongliding sister taxa to these gliding forms were also studied, when available, as were largely suspensory or climbing taxa. Tables 1.2 and 2.1 lists the specimens studied here. This selection of taxa was chosen in the hopes of uncovering common features related to the functional requirements of gliding among unrelated gliding taxa. Such features would be considered convergences, and if these were present in both dermopterans and bats then they could not be easily justified as unique homologies for volitantians. Similarly, arboreal xenarthrans and lorises were studied in order to illuminate features related to slow climbing and suspensory positional behaviors. This approach toward the analysis of convergence provides a means of discovering which dermopteran features may be related to gliding and/or suspension.

Throughout this study, measurements were made using dial calipers or a binocular dissecting microscope equipped with a reticle. Measurements were recorded to the nearest 0.01 mm. Analysis of Variance with a post hoc Bonferroni's test was used to test for pairwise differences among taxa or groupings of taxa. Bonferroni's method is used because it is difficult to evaluate the degree of independence in the data set. This method uses a

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Table 2.1: Specimens examined for carpal morphology in this study.

TAXON	AGES[1] AND NUMBER OF SPECIMENS EXAMINED	PREPARATIONS[2]
Chiroptera		
MEGACHIROPTERA		
Pteropodidae		
Acerodon jubatus	3A	SK
Cynopterus brachyotis	3A	SK
Dobsonia crenulata	3A	SK
Ediolon helvum	3A	SK
Eonycteris spelaea	3A	SK
Epomops franquenti	3A	SK
Haplonycteris fisheri	3A	SK
Hypsignathus monstrosus	1J, 8A	SK
Macroglossus minimus	3A	SK
Melonycteris melanops	3A	SK
Micropterus pusillus	3A	SK
Nyctimene albiventer	3A	SK
Otopterus cartilagonodus	3A	SK
Ptenochirus jagori	3A	SK
Pteropus alecto	3A	SK
Pteropus conspicillatus	3J	SK
Pteropus dasymallus	1J, 3A	AL, SK
Pteropus personatus	1J	SK
Pteropus vampyrus	2A	SK
Rousettus amplexicaudatus	6A	SK

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Rousettus madagascarensis	3A	SK
Syconycteris australis	3A	SK
MICROCHIROPTERA		
Rhinopomatidae		
Rhinopoma muscatellum	6A	SK
Emballonuridae		
Emballonura semicaudata	6A	SK
Saccopteryx bilineata	5A	SK
Taphozus georgianus	1A	SK
Nycteridae		
Nycteris arge	1A	SK
Megadermatidae		
Lavia frons	1A	SK
Macroderma gigas	2A	SK
Megaderma spasma	5A	SK
Rhinolophidae		
Hipposideros armiger	4A	SK
Rhinolophus inops	6A	SK
Triaenops rufus	2A	SK
Noctilionidae		
Noctilio leporinus	6A	SK
Mormoopidae		
Mormoops megalophylla	6A	SK
Pteronatus davyi	4A	SK
Phyllostomidae		
Artibeus jamacensis	1J, 6A	CS, SK
Desmodus rotundus	6A	SK

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Erophylla sezekorni	2J, 6A	CS, SK
Phyllonycteris poeyi	4J, 3A	CS, SK
Phyllostomus hastatus	6A	SK
Uroderma bilobatum	1J, 6A	CS, SK
Natalidae		
Natalus stramineus	6A	SK
Furipteridae		
Furipterus horrens	4A	SK
Thyropteridae		
Thyroptera tricolor	2A	SK
Myzopodidae		
Myzopoda aurita	1A	SK
Vespertilionidae		
Antrozous dubiaquercus	5A	SK
Miniopterus minor	6A	SK
Scotophilus kuhlii	6A	SK
Molossidae		
Molossus molossus	7A	SK
Molossus obscurus	1A	SK
Otomops martiensseni	3A	SK
Promops sp.	1J	CS
Tadarida condylura	6A	SK
Dermoptera		
Cynocephalidae[3]		
Cynocephalus volans	4A	SK
Galeopterus variegatus	1F, 2J, 4A	CS, AL, & SK
Primates		

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Cheirogaleidae		
Cheirogaleus major	1A	SK
Daubentoniidae		
Daubentonia madagascarensis	1A	SK
Galagidae		
Otolemur crassicaudatus	6A	SK
Lemuridae		
Eulemur fulvus	1A	SK
Eulemur macacao	1A	SK
Eulemur mongoz	2A	SK
Hapalemur griseus	3A	SK
Lemur catta	1A	SK
Loridae		
Nycticebus coucang	4A	SK
Perodicticus potto	1A	SK
Megaladapidae		
Lepilemur mustelinus	1A	SK
Tarsiidae		
Tarsius bancanus	3A	SK
Rodentia		
Muridae		
Peromyscus leucopus	9J, 6A	CS, SK
Sciuridae		
Callosciurus finlaysonii	1J, 2A	AL, SK
Sciurus carolinensis	1J, 6A	AL, SK
Scandentia		
Ptilocercinae[3]		

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Ptilocercus lowii	1J, 4A	SK, X-ray
Tupaiinae[3]		
Anathana ellioti	1A	X-ray
Dendrogale melanura	2A	X-ray
Dendrogale murina	1J	X-ray
Tupaia chinensis	4J	CS
Tupaia glis	6A	SK
Tupaia gracilis	1A	SK
Tupaia minor	1J, 6A	CS
Tupaia montana	1A	SK
Tupaia tana	2J, 6A	CS
Urogale everetti	2A	X-ray

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[1] A = adult, all epiphyses fused and adult dentition fully erupted. J = juvenile, postnatal but epiphyses unfused and/or adult dentition not fully erupted. F = fetus, prenatal.

[2] AL = alcohol preserved specimens used for identifying cartilages via gross dissection. CS = cleared and stained specimens. SK = skeletal material. X-ray = x-rays of museum skins.

[3] Because this interpretation of the morphology of these taxa differs from that in the literature, I list ages and specimen numbers. Cynocephalidae: *Cynocephalus volans*, FMNH 56442 (A), FMNH 61032 (A), USNM 144662 (A), USNM 578084 (A); *Galeopterus variegatus*, USNM 144374 (F), USNM 143326 (J), USNM 197203 (J), USNM 49470 (A), USNM 49640 (A), USNM 49693 (A), USNM 317118 (A). Ptilocercinae; *Ptilocercus lowii*, USNM 121885 (A). Tupaiinae: *Anathana ellioti*, FMNH 91265 (A); *Dendrogale melanura*, USNM 292544 (A), USNM 300913 (A); *Dendrogale murina*, USNM 256752 (A); *Tupaia chinensis*, USNM 399596 (5 days), USNM 399594 (11 days), USNM (#116)[4] (15 days), USNM 399591 (20 days); *Tupaia glis*, USNM 320721 (A), USNM 396665 (A), USNM 396666 (A), USNM 396673 (A), USNM 397663 (A), USNM 535137 (A); *Tupaia gracilis*, USNM 578656 (A); *Tupaia minor*, NZP 110705 (32 days), USNM 396668 (A), USNM 396669 (A), USNM 396670 (A), USNM 548410 (A), USNM 574130 (A); *Tupaia montana*, USNM 449964 (A); *Tupaia tana*, NZP 109835 (4 days), NZP 109834 (11 days), USNM 396661 (A), USNM 396663 (A), USNM 449968 (A), USNM 449969 (A), USNM 574901 (A), USNM 579556 (A); *Urogale everetti*, USNM 292292 (A), USNM 292293 (A).

[4] Uncatalogued USNM specimen.

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conservative experimentwise error rate that reduces the probability of making a type I error (Sokal and Rohlf, 1981, 1987). A type I error is "[t]he rejection of a true null hypothesis..." (Sokal and Rohlf, 1981, p. 159). Since the null hypothesis in this study must be that there are no significant differences among taxa, the rejection of a true null hypothesis would result in recognizing differences among taxa where none exist. Differences were considered significant when $p \leq 0.001$.

When examining cranio-dental morphology, tests for pairwise differences among the three recognized types of dermopterans were conducted. These three dermopteran morphs were the kagwang or Philippine flying lemur, the colugo or Sundaic flying lemur, and dwarfed forms of the colugo that occur on many of the smaller Sundaic islands and in central Laos.

In the study of postcranial morphology, data were analyzed at five different levels.

1. A test was conducted for differences among all taxa in the sample. If there was no statistical difference among any of the taxa, data were still analyzed as described in 2-4 below. In some cases specific taxa were removed from the analysis if they were drastically different from all other taxa. The taxa removed were usually either the bats or xenarthrans. Once these taxa were removed, all remaining taxa were again analyzed.
2. A test was conducted for differences among taxa grouped by locomotor categories. In some cases, locomotor categories correspond

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to taxonomic categories. For example, only bats fly. It was hoped that such a comparison could reveal locomotor specific features.

3. A test was conducted for differences among gliding mammals. In this case taxa were grouped by genus. The main objective of this comparison was to determine whether or not dermopterans differed from other gliding mammals for the features being considered.
4. A test was conducted for differences among either the rodents or the diprotodontian marsupials. In examining relative limb bone lengths the test among rodents was used as a means of evaluating differences between gliding taxa and their nongliding sister taxa. However, when examining relative phalangeal lengths this test was replaced by a test among diprotodontian marsupials. This group is represented by fewer samples than the rodents, but was considered because of specific hypotheses concerning digital elongation in Petaurus. Namely that the attachment of the patagium to the ulnar side of the fifth digit in Petaurus, should cause this digit to be elongate compared to nongliding diprotodontians.
5. Finally, a pairwise t-test was performed on just the two dermopteran taxa.

The first step in this project dealt with the craniodental morphology of the extant dermopterans. This was required in order to determine the number of valid dermopteran taxa. Skins and skulls of dermopterans were examined at the United States National Museum of Natural History and from the Field

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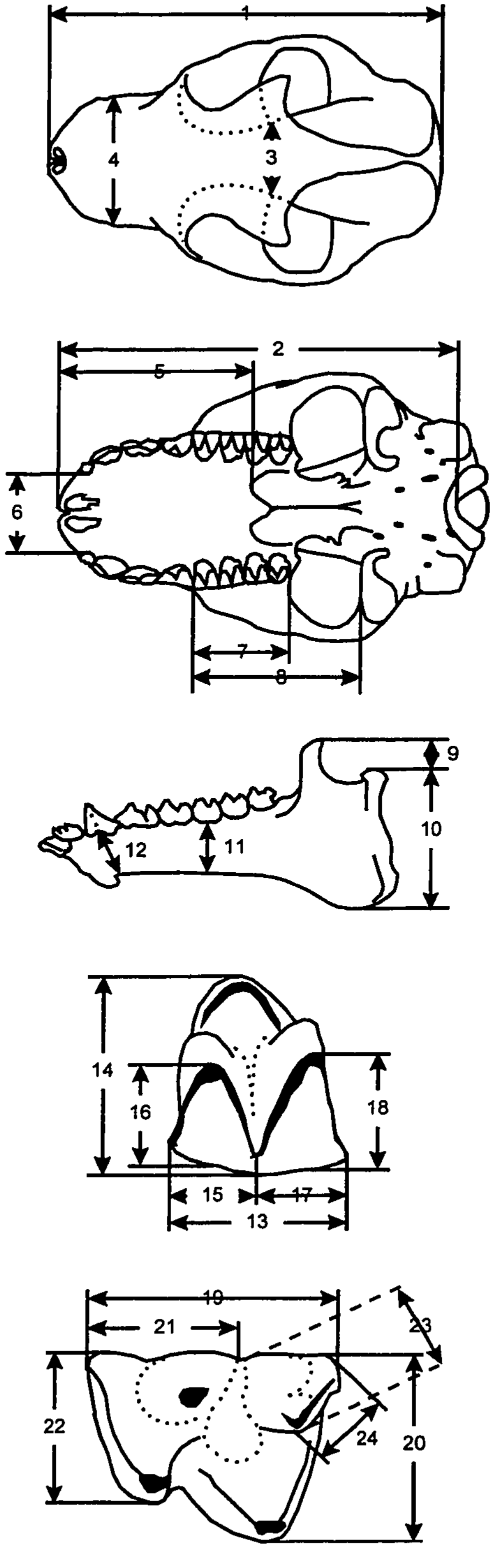

Figure 2.1: Schematics showing measurements taken on dermopteran crania and dentition. 1. Skull length; 2. Basal length; 3. Postorbital constriction, taken at the point where the floor of the orbit intersects the cranium; 4. Rostral breadth; 5. Minimum palate length; 6. Upper incisor gap; 7. P4 to M3 length; 8. Approximate length of lever arm of masseter muscle; 9. Approximate length of lever arm of temporalis muscle; 10. Height of ascending ramus from base of mandibular angle; 11. Depth of mandible below M_1, measured below center of tooth; 12. Depth of mandible below canine, measured from middle of tooth parallel to long axis of tooth; 13. Upper molariform tooth length; 14. Upper molariform tooth width; 15. Mesial stylar shelf length (associated with paracone); 16. Mesial stylar shelf width; 17. Distal stylar shelf length; 18. Distal stylar shelf width; 19. Tooth length; 20. Lower molariform tooth (and talonid) width; 21. Lower molariform trigonid length; 22. Trigonid width; 23. Entoconid-hypoconulid width; 24. Hypoconulid-distocuspid length.

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Museum of Natural History. The measurements taken are illustrated in Figure 2.1 and listed in Table 4.1. Dental nomenclature is illustrated in Figure 4.4. Once it was reaffirmed and determined, based on previously unavailable data, that there were only two valid taxa (see Chapter 4), an investigation of postcranial morphology was conducted.

The study of postcranial morphology concentrated on the gross morphology of limb bones and the vertebral column. Other authors (Beard, 1989, 1990a,b, 1991, 1993a,b; Szalay and Decker, 1974; Szalay and Drawhorn, 1980; Szalay and Lucas, 1993, 1996) have explored in detail the morphology of the dermopteran joints, and their functional correlates, and little could be added here. Relative lengths of limb bones were studied because of Thorington and Heaney (1981), and a preliminary inspection, showed flying squirrels to be distinct from tree squirrels in such measures. Also, measures of limb bone strength (i.e., second moments of area and polar moments) were evaluated because they reflect forces acting on the bones (Alexander, 1968; Wainwright et al., 1976) It was hoped that this would provide a means of evaluating whether or not dermopteran and bat wings are subject to similar forces, distinct from other gliding mammals, during flight.

In order to estimate relative limb lengths and the relative strengths of bones, an estimator of body size was needed. Because of the dearth of associated body weights skeletal trunk length was used as a surrogate for body size in this study. The possibility that gliding mammals have relatively

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longer trunks for their body weight than their nongliding relatives could not be evaluated because there were too few body weights associated with the postcranial remains in museum collections. Head and body lengths taken from skins also could not be used for such an analysis because relative neck lengths are not constant among taxa (see chapter 5).

Skeletal trunk length was calculated as the sum of the cranio-caudal length of the thoracic, lumbar, and sacral vertebral bodies measured ventrally. Least squares regression was used to test for isometry of head and body lengths, and relative tail lengths in some taxa. ANOVA with post hoc Bonferroni's tests of pairwise differences were used to test for differences among taxa in relative vertebral segment lengths. Neural arch thickness was scored into two classes. Thin neural arches are those without interarch contact when the cervical segment of the vertebral column is neither flexed or extended. Thick arches are those that do show interarch contact. Vertebrae were also examined for qualitative differences in morphology. The results of these analyses are presented in chapter 5.

Limb bone lengths were measured from the proximal-most articular surface to the ventral-most articular surface, giving an estimate of the maximum functional length of the bone (Fig. 2.2). Medio-lateral and anterior-posterior diameters were measured at midshaft. When the deltopectoral crest intruded onto the midshaft, diameter measures were taken below the termination of the deltopectoral crest. The length of the scapular spine was measured from the middle of the glenoid fossa of the scapula to the

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intersection of the dorsal scapular spine with the vertebral border of the scapula. The length of the vertebral border of the scapula was measured from the most caudal portion of the vertebral border to the cranial most point on the vertebral border of the scapula. Lengths of the metacarpals, proximal phalanges, and intermediate phalanges were also measured using dial calipers, or under a binocular microscope equipped with a reticle. Digit length was estimated by adding the lengths of the proximal and intermediate phalanges. For the first digit proximal phalanx length alone was used as an estimator of digit length. Digit length and metacarpal length were then corrected for body size by dividing them by skeletal trunk length and multiplying the result by 100. The intermediate phalangeal index was calculated by dividing intermediate phalanx length by proximal phalanx length and multiplying by 100. The data collected are presented in the appendix. Limb bones and vertebral morphology are illustrated in figures 2.3, 2.4, and 2.5.

Total cross sectional area at midshaft (**TCSA**) for any limb bone was calculated as the area of an ellipse with its major and minor axes in the medio-lateral and anterior-posterior planes using the equation

$$\mathbf{TCSA = (\Pi * anterior\text{-}posterior\ diameter * medio\text{-}lateral\ diameter)/4.}$$

Polar moments (J), anterior-posterior, and medio-lateral second moments of area ($\mathbf{I_{AP}}$ and $\mathbf{I_{ML}}$) were also calculated (see Alexander, 1968; Wainwright et al., 1976; Runestad and Ruff, 1994). Medio-lateral second moments of area

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Figure 2.2: Measurements taken on limb bones. Bones illustrated are a, the humerus in anterior view; b, the humerus in medial view; c, the radius and ulna in anterior view; d, the radius and ulna in ulnar view; e, the femur in anterior view; f, the femur in medial view; g, the tibia in anterior view; h, the tibia in medial view; i, the fibula in anterior view; and j, the fibula in medial view. Limb bone lengths are illustrated by dimensions 1, 4, 9, 12, 14, and 18. Medio-lateral midshaft diameters are illustrated by dimensions 2, 5, 6, 10, 13, and 16. Anterior-posterior midshaft diameters are illustrated by dimensions 3, 7, 8, 11, 15, and 17.

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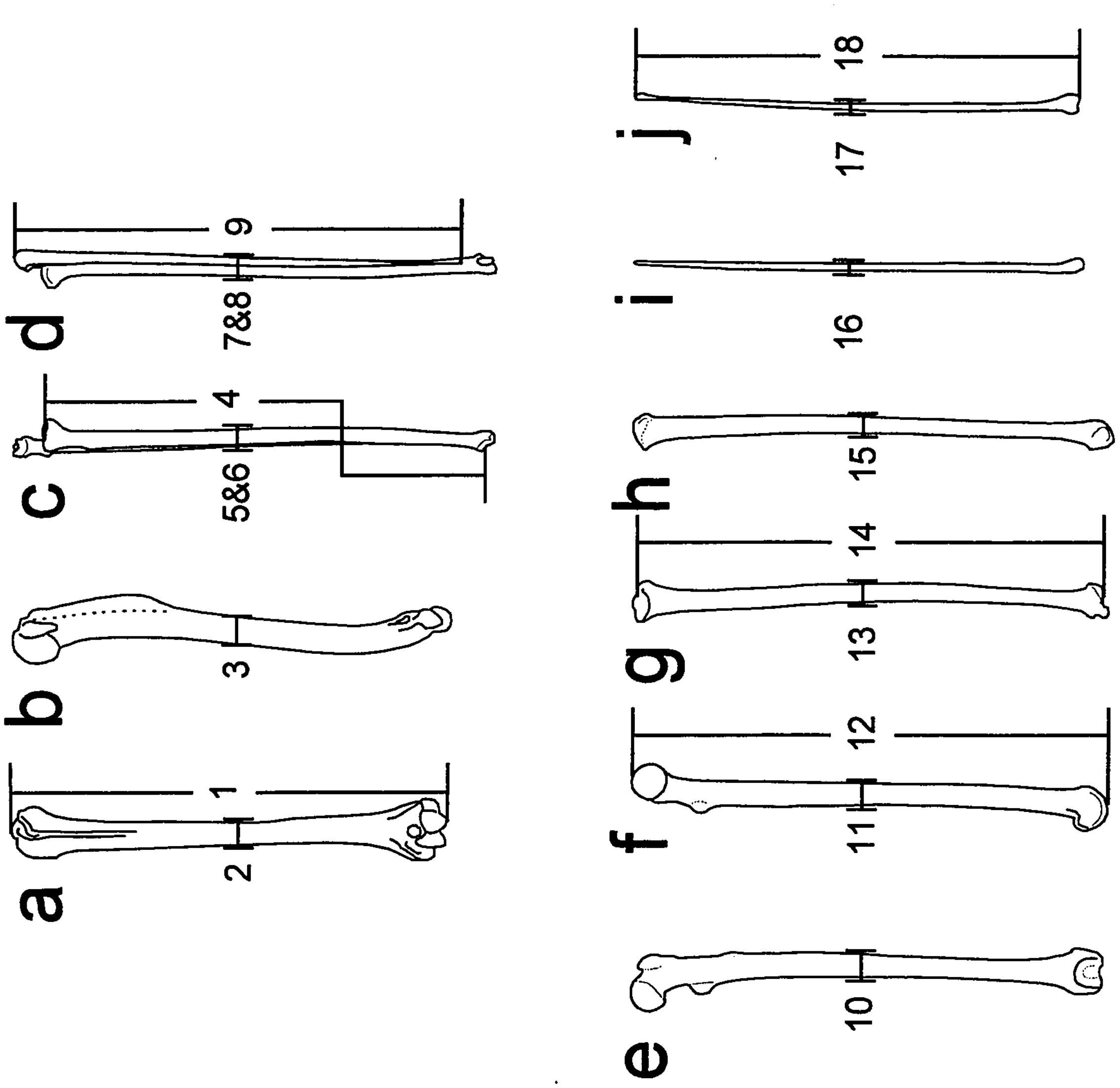

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Figure 2.3: Vertebral morphology of Cynocephalus volans USNM 578084: a) ventral view of cervical vertebrae; b) left lateral view of cervical vertebrae, c) ventral view of thoracic vertebrae, topmost vertebrae is T2; d) dorsal view of thoracic vertebrae, topmost vertebrae is T2; e) ventral view of lumbar vertebrae, topmost vertebrae is L1; f) dorsal view of lumbar vertebrae, topmost vertebrae is L1. Scale bars equal 1 cm.

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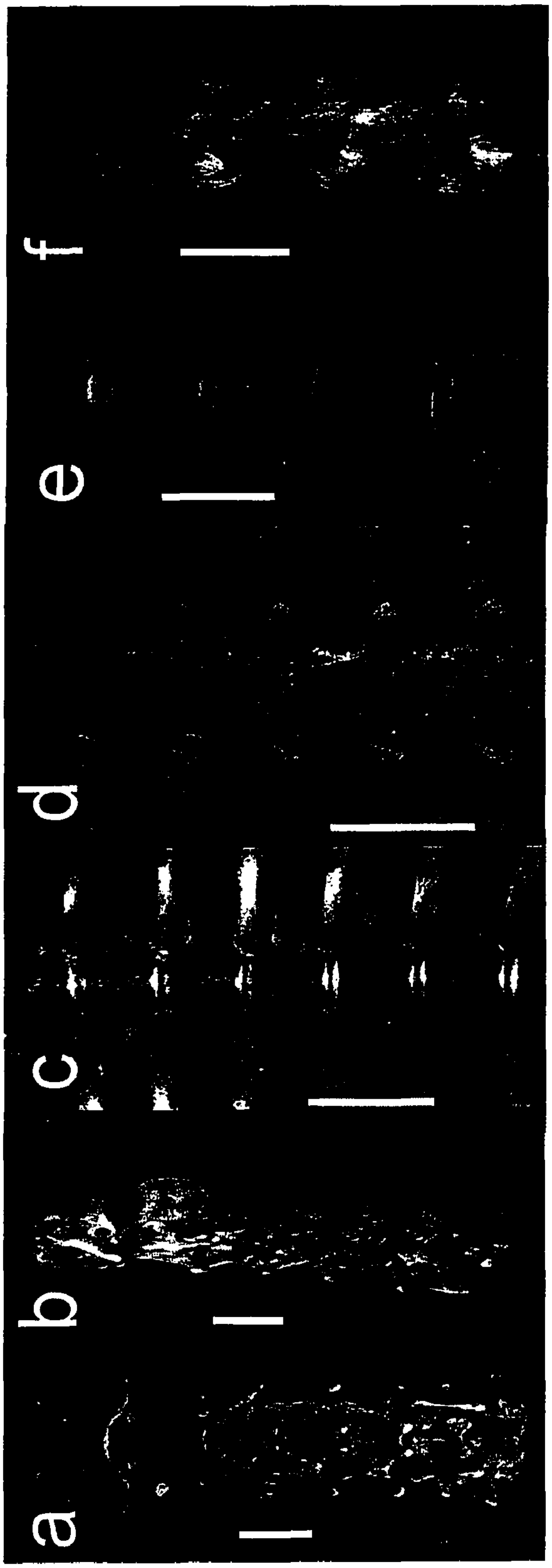

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Figure 2.4: Limb bones of *Cynocephalus volans* USNM 578084: a) anterior, and b) medial views of the left humerus; c) anterior, and d) medial views of the radius and ulna; e) anterior, and f) medial views of the femur; g) anterior, and h) medial views of the tibia; and l) anterior, and j) medial views of the fibula. Scale bars equal 1 cm.

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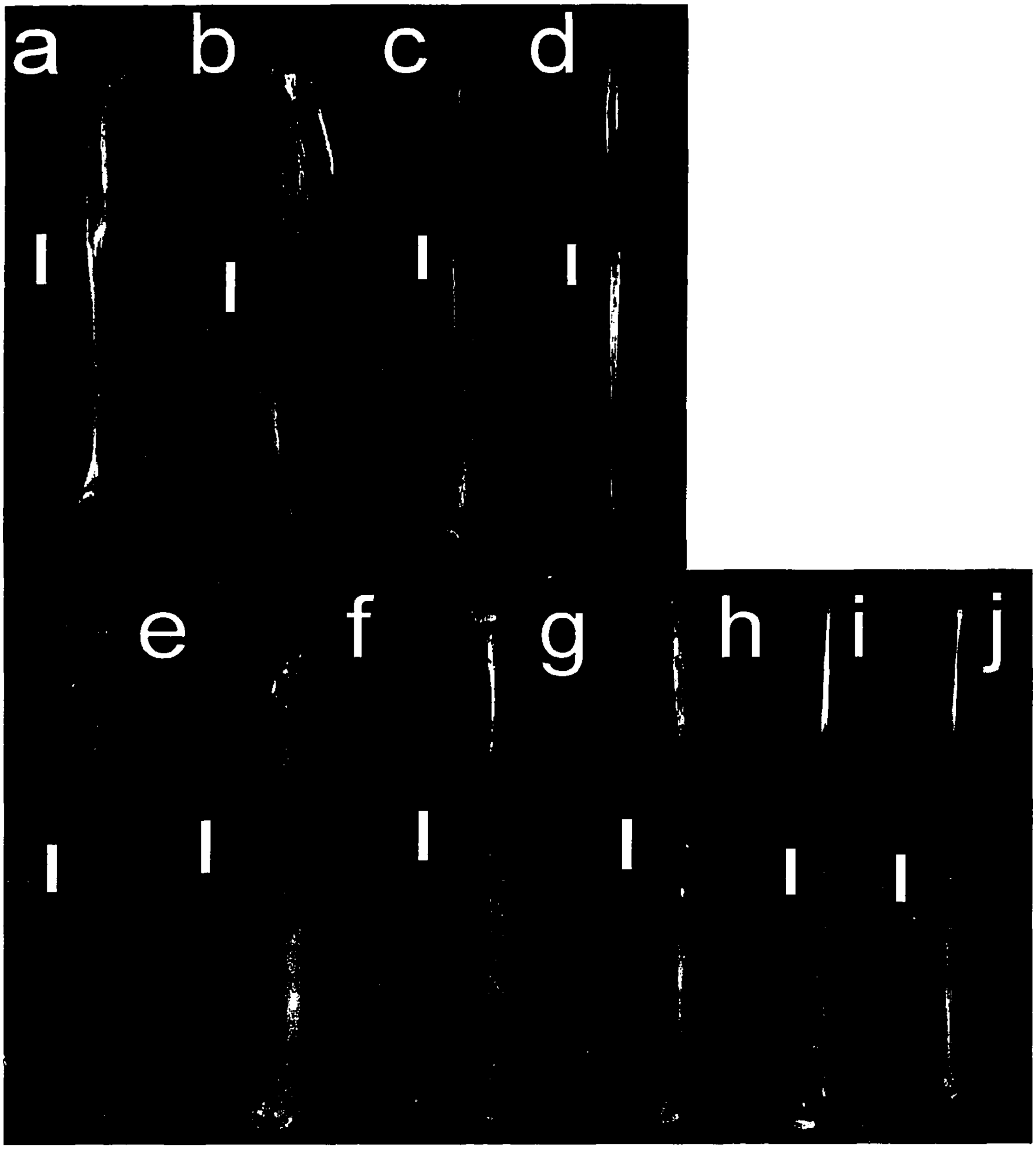

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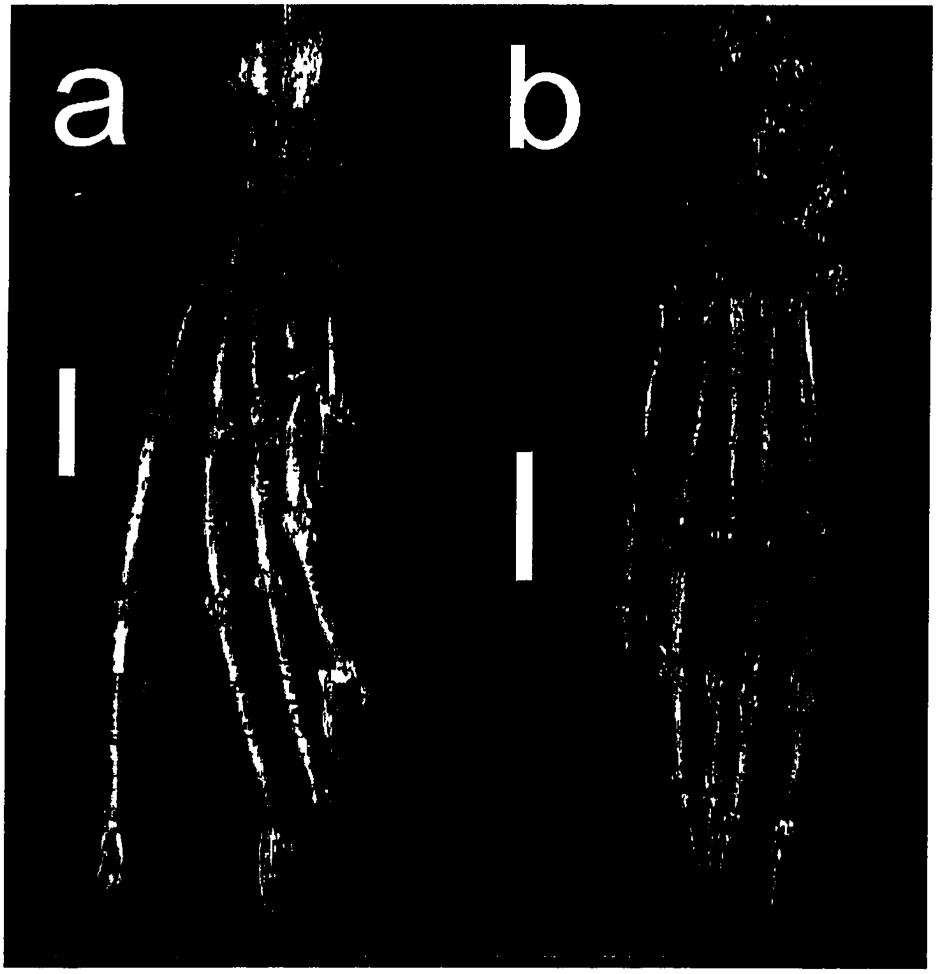

Figure 2.5: Dorsal views of a) the right manus, and b) the left pes of Galeopterus variegatus USNM 49640. Scale bars equal 1 cm.

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were calculated as

$$I_{ML} = (\Pi * \tfrac{1}{2}\text{anterior-posterior diameter} * (\tfrac{1}{2}\text{medio-lateral diameter})^3)/4,$$

anterior-posterior second moments of area were calculated as

$$I_{AP} = (\Pi * (\tfrac{1}{2}\text{anterior-posterior diameter})^3 * \tfrac{1}{2}\text{medio-lateral diameter})/4,$$

and polar moments were calculated as

$$J = I_{ML} + I_{AP}.$$

The utility of these measures is discussed in detail by Wainwright, et al. (1976), Ruff, (1992), Ruff et al. (1993) and Lazenby (1995, 1998). To summarize, I_{ML} and I_{AP} reflect resistance to bending forces in the medio-lateral and anterior-posterior planes, while J reflects resistance to torsion of the element. Each of these measures scales to length to the fourth power. The total cross sectional area (**TCSA**) of the limb bone scales to length squared, and gives a measure of the robusticity of the limb bone. Relative **TCSA** can serve as a general surrogate for limb bone strength, but because it ignores elements of cross sectional geometry that second moments of area and polar moment capture, relative **TCSA** is only used a measure of limb robusticity in this study.

It is important to realize that the above methods model limb bones as solid beams. Different equations are used for calculating I_{ML}, I_{AP}, and **J** for hollow cylinders (Alexander, 1968; Wainwright et al., 1976) and will yield different values. It is also important to realize that uneven distribution of cortical thickness will also effect these parameters. Consequently, studies of

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second moments and polar moments based on external diameters of limb bones should be interpreted with caution.

It was initially thought that bats would have higher values of these parameters due to the demands of powered flight. If dermopterans differed from all other mammals, especially other gliding mammals, in the same way as the bats differ from all other mammals, then perhaps such differences are due to similar forces acting on the limbs of bats and dermopterans. Specifically, it was hypothesized that the use of the dactylopatagia to control the glide might place similar stresses on the forelimbs of bats and dermopterans and that these parameters would then differ in similar ways in these taxa. If the forces acting on the forelimbs of bats and dermopterans were simply the result of the extensive patagium in these taxa, one might expect that other gliding taxa with wing tip extensions (i.e., flying squirrels and lesser gliding marsupials) might also show similar forces acting on their limb bones. The comparison is not perfect because not all of these tax have wing tip extensions composed of dactylopatagia as do the volitantians. However, it allows a means of eliminating the mere presence of some wing tip extension as causing any similarities seen between dermopterans and bats.

Limb bone lengths were divided by skeletal trunk length and multiplied by 100 to correct for differences in body size. Cross sectional areas of limb bones were divided by skeletal trunk length squared and multiplied by 100; **((TCSA/STL^2)*100)**. Second moments of area (I) and polar moments (J)

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were divided by skeletal trunk length raised to the fourth power and multiplied by 100 [i.e. $((I/STL^4)*100)$, $((J/STL^4)*100)$; see Wainwright et al., 1976]. This allows an evaluation of limb element strength in relation to body size. Particular measures are indicated by subscripts. For example, $J_{Humerus}$ is the polar moment of the humerus. Polar moment of the humerus corrected by skeletal trunk length is $J_{Humerus(STL)}$.

These data were also analyzed after being corrected for limb component length in order to evaluate hypotheses of functional equivalence. For example, $TCSA_{Humerus}$ was divided by humerus length squared and then multiplied by 100 $((TCSA_{Humerus}/\text{Humerus Length}^2)*100)$. Similarly, $J_{Humerus}$, $I_{AP,Humerus}$, and $I_{ML,Humerus}$ were divided by humerus length raised to the fourth power and multiplied by 100. The notation for these indices would be $J_{Humerus(Hum)}$, $I_{AP,Humerus(Hum)}$, and $I_{ML,Humerus(Hum)}$ respectively. These indices reflect the overall strength of the limb element because the length of the limb element is used as an estimator of the lever arm of the forces acting on the limb element (see Wainwright, et al., 1976).

Since dermopterans are gliding mammals, the results of the postcranial investigations were evaluated with respect to aerodynamics. The data on limb bone lengths were used to create models of gliding mammals. Published photographs of animals gliding were used to determine the angles of limbs from the midline of the body. In order to create the least confounding model, limb angles among taxa were set to one of two values. Petauroides appears to glide with the forelimbs and hindlimbs perpendicular

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to the vertebral column so all pseudocheirid marsupials were modeled with the limbs held at 90^0 to the trunk. All other taxa were modeled with the forelimbs angled at 62.5^0 to the vertebral column, and the hindlimb held at 45^0 to the vertebral column. Because gliding is such a dynamic behavior, measures taken from single photos are not likely to well represent common or optimal gliding positions. Aerodynamic parameters were also calculated for limb positions that would produce maximum aspect ratios. From these wing area, the areas of the various wing components, wing loading, and the lengths of the leading and trailing edges of the wing were calculated.

Gliding is here considered to have four distinct phases. The first is the launch phase where the animal leaps or drops from a support and deploys the gliding membrane. The second phase is the glide phase after the launch phase and prior to the third phase, the terminal flaring phase of the glide. The terminal phase of the glide is where the animal changes from using the patagium as a flight membrane that produces lift to using it as a braking parachute prior to landing. The fourth phase of the glide is the landing phase where the animal is using the patagium as a braking parachute to reduce velocity before contacting the substrate. Only during the second and third phases are the principles of aerodynamics applicable. During the launch and landing phases the animal is subject to ballistic forces. The wing modes were evaluated with respect to performance and control issues. Both the general shape of the wing and more subtle aspects of wing morphology were considered.

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One not fully evaluated area of skeletal morphology that has potential relevance to the phylogenetic history of dermopterans, and other taxa, is the development and morphology of the carpal elements. A detailed investigation of carpal morphology was therefore included here as a test of hypotheses about archontan evolution (see Stafford and Thorington, 1998). There was no statistical analysis in this portion of the study. Specimens were obtained from the National Museum of Natural History, Smithsonian Institution (USNM), the Field Museum of Natural History (FMNH), and the Department of Zoological Research, National Zoological Park, Smithsonian Institution (DZR-NZP) (Table 2.1). Four types of preparations were used here; osteological material available at USNM and from FMNH, dissections of fluid preserved and frozen specimens at USNM and DZR-NZP, cleared and stained specimens provided by USNM and DZR-NZP, and x-rays of USNM and FMNH skins. The tree shrews from DZR-NZP were stained for both cartilage and bone (Dingerkus and Uhler, 1977) while the Peromyscus leucopus were cleared and stained for bone only (Green, 1952) at the New England Regional Primate Research Center. Other specimens in the USNM collections had been cleared and stained for bone only. Nevertheless, cartilaginous templates were easily identifiable in these specimens. The sciurid specimens were not cleared and stained, but were examined grossly. The cartilages were clearly defined. Carpal nomenclature follows Romer (1954). Osteological specimens were used to examine carpal morphology and articular relationships.

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Scanning electron micrographs were made of hair samples from eleven taxa in order to evaluate hypotheses about the microstructure of the hair of gliding mammals. Hairs were pulled from the midline dorsum of one individual from each selected taxon (Table 2.2). Hairs were mounted on stubs and coated for use in the scanning electron microscope. Terminology for describing hair microstructure follows Brunner and Coman (1974). Taxa sampled in Brunner and Coman (1974) were not sampled again here. Glirulus japonicus was included because of suggestions that its lineage includes gliding forms (Mein and Rommagi, 1991).

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Table 2.2: Taxa examined for hair microstructure

Taxon	USNM #	Locomotor Category
Cynocephalus volans	USNM 104078	Gliding / Suspensory
Pteropus vampyrus	USNM 104726	Flying / Suspensory
Myotis lucifugus	USNM 297235	Flying / Suspensory
Ptilocercus lowii	USNM 77905	Arboreal
Acrobates pygmaeus	USNM 19583	Gliding / Arboreal
Hemibelideus lemuroides	USNM 238373	Arboreal
Glaucomys sabrinus	USNM 129707	Gliding / Arboreal
Sciurus carolinensis	USNM 293398	Arboreal / Terrestrial
Anomalurus peli	USNM 414450	Gliding / Arboreal
Idiurus macrotis	USNM 83626	Gliding / Arboreal
Glirulus japonicus	USNM 356013	Arboreal

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CHAPTER 3: BEHAVIOR AND ECOLOGY

Little is known about the behavior and ecology of the dermopterans, and this short chapter covers all that we currently know. Our lack of knowledge is largely because dermopterans are both nocturnal and highly cryptic. They also tend to be primarily canopy dwellers and have little or no economic value to humans. Consequently, even local peoples are often unaware that dermopterans are present in the forests around them, or in their plantations, in some abundance.

Most of what is known about dermopterans comes from the work of Wischusen (1990), field guides (Corbet and Hill, 1992; Harrison, 1951, 1964; Heaney and Rabor, 1982; Lekagul and McNeely, 1977; Medway, 1977; Payne et al., 1985; Rabor, 1977; Taylor, 1934), and various anecdotal reports (Beebe, 1913; Chapman, 1902; Harrison, 1949; Lim, 1967b; Wallace, 1867; Wharton, 1950). Wischusen's study is the only formal study ever published. However, Marlynn Mendoza and Carlo Custodio of the Philippine Protected Areas and Wildlife Bureau are in the process of publishing their extensive work on the dermopterans from the island of Bohol, but this work is not yet available. The information presented below comes from Wischusen (1990), and has been verified with Ms. Mendoza and Mr. Custodio. It is important to remember that most of the information presented here relates to the Philippine flying lemur or kagwang. Given the morphological distinctness of the two dermopteran taxa (see Chapter 4),

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aspects of the behavior and ecology of Cynocephalus may be quite different from that of the Sundaic genus, Galeopterus.

Dermopterans are not large animals although they are among the largest of the gliding mammals (Table 3.1). Body weights are difficult to come by in museum collections and the weights reported in the literature vary widely. Runestad and Ruff (1995) give weights for Cynocephalus of 990 g. and for Galeopterus of 1,354 g. Their weights for Galeopterus appear to be acceptable, the average weight of eight adult Galeopterus specimens at USNM is 1,408 g. However, their weights for Cynocephalus are almost certainly wrong. The average weight of two Cynocephalus at USNM is 1,260 g., and Wischusen (pers. com.) reports wild weights of up to 2,000 g. in specimens from Mindanao. Nowak (1991) gives a weight of 1,000-1,750 g. for both species. The error in Runestad and Ruff's measurements may result from the inclusion of juveniles, or specimens from the island of Bohol. Kagwang from Bohol are reportedly smaller than other Philippine specimens, and may represent a distinct species or subspecies (Wischusen, 1990; Mendoza and Custodio pers. com.). Animals from Leyte (pers. obs.) are also somewhat smaller. These observations are consistent with body size reduction in peripheral or isolated dermopteran populations (Chapter 4).

Kagwang are considered nocturnal but show peaks of activity just after sunset and just before sunrise. These peaks in activity correlate with peaks in foraging and feeding behavior. They are highly folivorous and

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concentrates on the young leaves of a few preferred tree species. They spend most of their time hanging motionless from branches or trunks (Table 3.2) and as much time feeding as locomoting.

Of the time they spend locomoting, 15% is spent gliding, and 82% of intertree transfers are accomplished by gliding. Females carrying young however, use significantly more suspensory behaviors and glide much less, but they do still glide. No other gliding mammals has been observed to glide while carrying the young, although some bats do fly while carrying the young. The only nongliding locomotor behaviors that have been noted are vertical climbing and bounding, and quadrumanous suspensory behaviors. Some authors (Nowak, 1991; Wharton, 1950) have proposed that dermopterans are incapable of terrestrial quadrupedalism, or incapable of supporting the body over the limbs. There appear to be, however, no anatomical preclusions to dermopterans performing conventional locomotor behaviors where the limbs support the body in compression. However, this may be extremely difficult for them.

Home range sizes average 9.91 ha for kagwang on Mindanao, but range from 2.15 to 25.56 ha depending on individuals and seasons. Nightly travel distances average 1381 m (± 363 m), and range from 1011 to 1764 meters. Distance traveled each night is significantly correlated with home range size. Contra most previous reports (Wallace, 1869; Wharton, 1950; Liat, 1967; Medway, 1978) kagwang appear to prefer dense foliage for day

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roosts over cavities. Their mottled coloration would provide excellent camouflage in such situations.

Dermopterans are unique among arboreal folivores in several ways. The three-toed sloth (*Bradypus variegatus*) and the koala (*Phascolarctos cinerus*) are two of the best studied arboreal folivores (see Eisenberg, 1978) and they seem to deal with the problems of extensive folivory in similar ways. They both have low metabolic rates and long digesta passage times, and both koalas and sloths spend long periods of time inactive. Folivorous primates are also notably less active than nonfolivorous primates. However, whereas koalas and sloths eat large amounts of both mature and immature leaves, the colugo preferentially feeds on young leaves (Wischusen, 1990). Koalas and sloths also have relatively long mean retention times of digesta (koalas ~156.5 hrs., Parra, 1978; sloths ~632 hrs. Cork and Warner, 1983) as compared to colugos (~14.4 hrs., Wischusen, 1990). In fact, the mean retention time of digesta in colugos is shorter than expected for a folivore of its size, even though their relative gut capacity is similar to other herbivores (Wischusen, 1990). It is not unreasonable to assume for the time being that gliding in colugos evolved as an energetically cheap means of accessing widely dispersed food resources (young leaves) for an animals that must minimize energy expenditure. An alternate possibility would be that gliding evolved in dermopterans not as an energetically cheap means of accessing food resources, but as a means of rapid travel between widely dispersed resources that must be constantly sampled for appropriate food items (i.e.,

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young leaves). Of course, such selective pressures may have also been operating in tandem.

All other aspects of colugo biology and behavior are unknown at this time. However, given the differences in craniodental and postcranial anatomy between the two living genera of colugos it would not be wise to extrapolate from the kagwang to the colugo except in the most general terms.

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Table 3.1: Mass of some gliding mammals.

Taxon	Common Name	Mass
Diprotodontia		
Acrobates pygmaeus	Feather-tail Glider	14 g.
Petaurus breviceps	Sugar Glider	112 g.
Petaurus norfolcensis	Squirrel Glider	230 g.
Petaurus australis	Fluffy Glider	537 g.
Petauroides volans	Greater Glider	1,300 g.
Dermoptera		
Cynocephalus volans	Kagwang	1,260 g.
Galeopterus variegatus	Colugo	1,408 g.
Rodentia		
Anomaluridae		
Idiurus macrotis	Pygmy Scaly-tailed Flying Squirrel	26 g.
Anomalurus pusillus		215 g.
Anomalurops beecrofti	Becroft's Scaly-tailed Flying Squirrel	405 g.
Anomalurus derbianus	Lord Derby's Scaly-tailed Flying Squirrel	483 g.
Anomalurus peli	Pell's Scaly-tailed Flying Squirrel	1,585 g.
Pteromyinae		
Petaurillus kinlochii	Pygmy flying squirrel	20 g.
Petinomys vordermanni	Vordemann's dwarf flying squirrel	36 g.
Petinomys setosus	Temminck's flying squirrel	39 g.
Hylopetes platyurus		41 g.
Hylopetes spadiceus	Red-cheeked flying squirrel	63 g.
Glaucomys volans	Southern flying squirrel	70 g.
Petinomys genibarbis	Whiskered flying squirrel	108 g.
Glaucomys sabrinus	Northern flying squirrel	140 g.
Pteromyscus pulverulentus	Smoky flying squirrel	266 g.
Eoglaucomys fimbriatus	Small Kashmir flying squirrel	567 g.
Petaurista elegans	Lesser giant flying squirrel	920 g.
Petaurista petaurista	Red giant flying squirrel	1,131 g.
Petaurista grandis		1,133 g.
Aeromys tephromelas	Large black flying squirrel	1,300 g.

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Table 3.2: Kagwang behavioral profile[1]

Behavior	Mean % of Total Observations
Hanging and Clinging	61%
Feeding	14%
Locomotion	13%
Grooming	9%
Other	3%

[1] Data from Wischusen (1990)

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CHAPTER 4: CRANIODENTAL MORPHOLOGY

Craniodental form and function were evaluated in the two species of dermopterans. The appropriate names for these two taxa are Cynocephalus volans (Linnaeus, 1758) for the Philippine flying lemur, and Galeopterus variegatus (Geoffroy, 1796) for the heterogeneous populations of the Sundaic flying lemurs. Cynocephalus probably has a hypertrophied version of the ancestral cynocephalid molar complex, and modified incisor and canine morphology. The hypertrophied metaconules of cynocephalids occlude with an expanded paracristid and a cusp-like shelf, the distocuspid. Cynocephalus also has a broader rostrum, a greater degree of postorbital constriction, and enhanced ectocranial ridges associated with a more robust masticatory musculature than Galeopterus. Cynocephalus appears adapted to a tougher or harder diet that requires a greater degree of shearing by the anterior dentition and crushing by the molariform dentition. These anterior shearing teeth (I3, C1, P3, c1, p3) are larger and more blade-like than those of Galeopterus, and the bite force is more anteriorly directed. The angle of the mandible is ventrally expanded in Cynocephalus, facilitating enhanced chewing force for the postcanine dentition while maintaining orientation of the temporalis muscle. Dwarfed forms of Galeopterus are found on many of the smaller islands of the Sunda shelf and in central Laos. They are not morphologically distinguishable from larger members of this species, other than in size, and do not warrant specific distinction. However, it may be

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desirable to designate four subspecies of G. variegatus; G. v. variegatus Chasen and Boden Kloss, 1929 from Java, G. v. temminckii Chasen and Boden Kloss, 1929 from Sumatra, G. v. borneanus Chasen and Boden Kloss, 1929 from Borneo, and G. v. peninsulae Chasen and Boden Kloss, 1929 from the Malay Peninsula and mainland Southeast Asia. Separate species rank for each of the dwarfed populations should not be recognized.

Dermopterans have been considered essentially monomorphic by most workers. With the exceptions of Szalay (1969) who noted generic differences in the teeth, and Szalay and Lucas (1993, 1996) who demonstrated postcranial distinctions between the two genera, one must go back to earlier works (Cabrera, 1925; Miller, 1906; Thomas, 1908) to find recognition of the differences between the taxa. Unfortunately, these early works give only a general account of craniodental differences among the dermopterans, and do not consider functional implications. Yet these craniodental differences are quite striking, and obviously related to adaptively significant aspects of the masticatory system (Stafford and Szalay, in press). In general, it appears that there is a megadont and morphologically distinct species, and a craniodentally less robust one. These are separated by Huxley's Line (Fig. 4.1). These differences are particularly striking because the megadont form, Cynocephalus, seems to be smaller of the two genera (Table 2.1), signaling distinctive but as yet undiscovered feeding strategies.

General cranial characters.--Three kinds of extant dermopterans can be recognized based on size and gross craniodental morphology. They are

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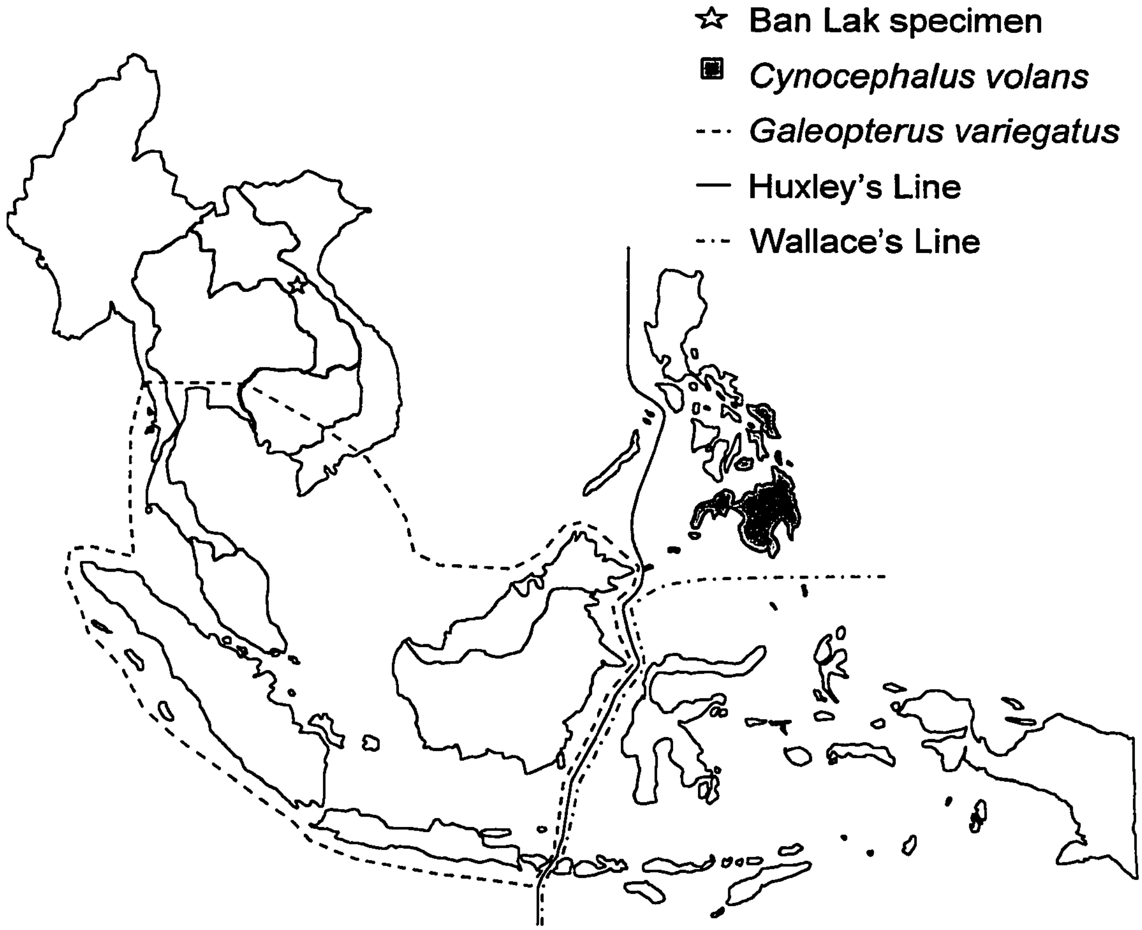

Figure 4.1: Distribution of extant dermopterans. The line encircling the distribution of Galeopterus variegatus reflects the extent of the Sunda shelf at a depth of 100 meters. The Bak Lak specimen appears to be an isolated population and does not warrant the extension of the range of Galeopterus to 20^0 north latitude.

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Cynocephalus volans from the Philippines (the kagwang), *Galeopterus variegatus* from Borneo, the Malay Peninsula and Southeast Asian mainland, Sumatra, and Java (the colugo), and smaller morphs of *G. variegatus* from Langkawi Island off the west coast of the Malay Peninsula, Bakung and Sebangka islands in the Lingga archipelago off the east coast of Sumatra, Aur Island off the east coast of the Malay Peninsula, Serasan Island in the Natuna Archipelago in the South China Sea, Sebuku Island off the southeastern coast of Borneo, and from central Laos (dwarfed colugos). In the remainder of this work, the Philippine dermopterans will be referred to by their generic name, *Cynocephalus*. *Galeopterus* will refer to both the large and small morphs of the Sundaic flying lemur. The larger and smaller forms of the Sundaic flying lemur will be referred to as colugos and dwarf colugos, respectively.

A dorsal view of the cranium (Fig. 4.2a-c) shows large differences between the two genera (Table 4.1, 4.2). Compared to *Galeopterus*, *Cynocephalus* has a broader rostrum, a smaller neurocranium, and a greater degree of postorbital constriction. The superior temporal lines converge posteriorly and form a short sagittal crest before joining the nuchal crest. This condition is never seen in *Galeopterus*, where the superior temporal lines rarely contact the nuchal crest and never form a sagittal crest. Also in *Cynocephalus*, the orbital processes of the frontal are larger and more robust, and the zygomatics are more laterally displaced and thinner dorsoventrally. These traits reflect a more open and capacious temporal fossa in

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Figure 4.2: Dermopteran skulls: a) Cynocephalus volans USNM 536048 dorsal view, b) Galeopterus variegatus USNM 49640 dorsal view, c) dwarf Galeopterus variegatus USNM 104600 dorsal view, outlines represent the extent of the temporal fossa, d) C. volans USNM 536048 left lateral view, e) G. variegatus USNM 49640 left lateral view, f) dwarf G. variegatus USNM 104600 left lateral view, dimension bars on the zygoma illustrate the differences in arch height; g) C. volans USNM 536048 ventral view, h) G. variegatus USNM 49640 ventral view, i) dwarf G. variegatus USNM 104600 ventral view; and mandibles of extant dermopterans, j) C. volans USNM 536048 left lateral view, k) G. variegatus USNM 49640 left lateral view, l) dwarf G. variegatus USNM 104600 left lateral view; m) C. volans USNM 536048 dorsal view, n) G. variegatus USNM 49640 dorsal view, o) dwarf G. variegatus USNM 104600 dorsal view; c = canine, scale bars = 1 cm.

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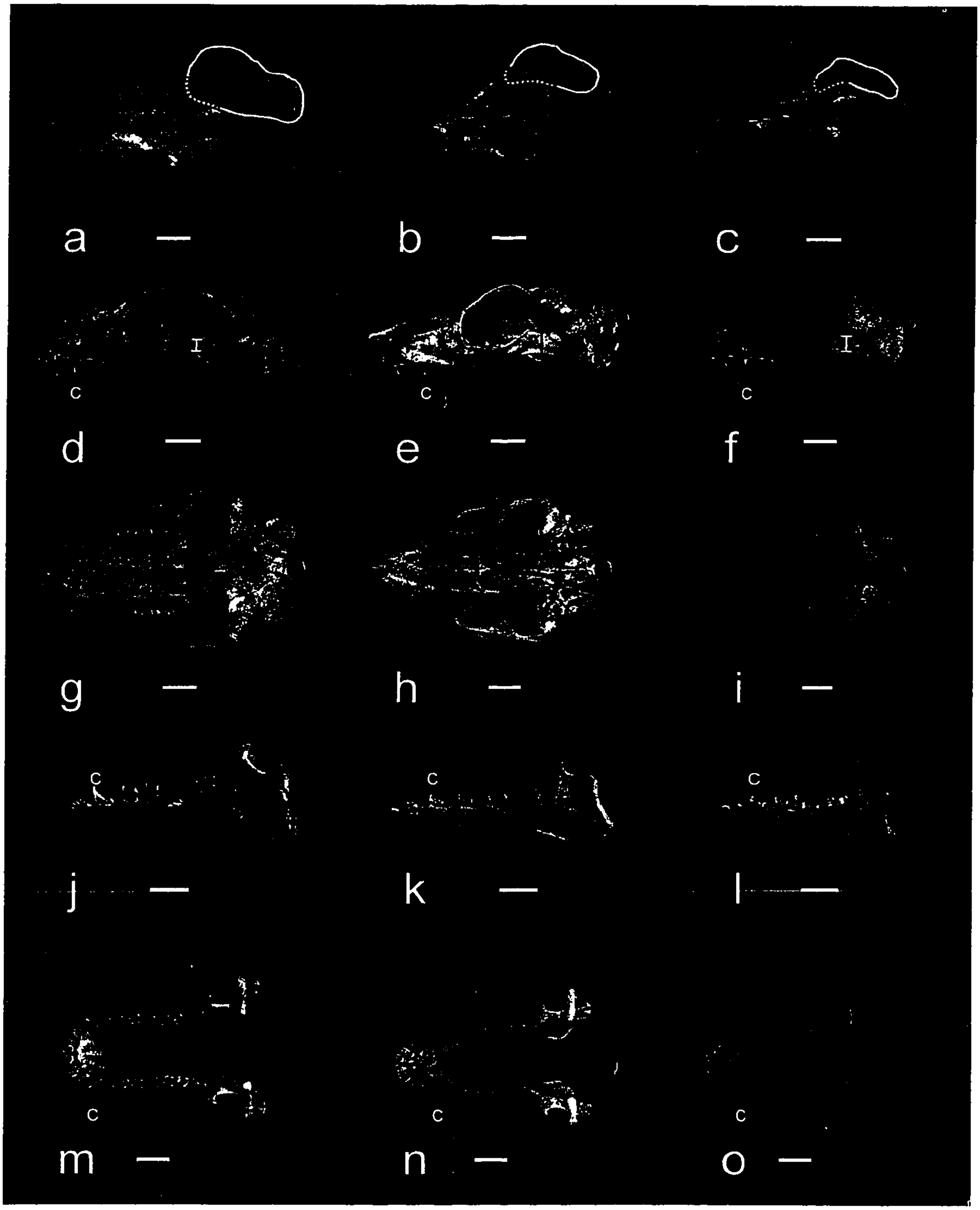

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TABLE 4.1: Average (±1 SD; range) craniodental measurements (in mm) in dermopterans.

Measure	*Cynocephalus volans* (*n* = 12)	*Galeopterus variegatus* (*n* = 14)	Dwarf *Galeopterus variegatus* (*n* = 3)	*C. volans* versus *G. variegatus*	*C volans* versus Dwarf *G. variegatus*	*G. variegatus* versus Dwarf *G. variegatus*
Estimators of body size in dermopterans						
Length of skull	70.02 (2.84; 66.80 - 74.99)	70.89 (2.74; 64.50 - 74.53)	59.52 (1.63; 58.14 - 61.32)	p = 1.000	p< 0.001	p< 0.001
Basal length	63.77 (3.19; 60.07-69.57)	65.11 (2.40; 59.50-67.98)	54.24 (1.71; 53.00 - 56.19)	p = 0.662	p < 0.001	p < 0.001
Craniodental measures in dermopterans, corrected for body size[1]						
Postorbital constriction	26.48 (1.76; 23.83 - 29.23)	33.66 (1.61; 31.41 - 36.38)	36.44 (2.58; 33.85 - 39.00)	P < 0.001	P < 0.001	P = 0.130
Rostral breadth	35.53 (1.76; 33.42 - 37.57)	31.82 (1.70; 29.59 - 35.17)	31.70 (0.84; 31.10 - 32.66)	P < 0.001	P = 0.002	P = 1.000
Minimum palate length	49.36 (1.22; 48.03 - 52.20)	51.62 (0.96; 50.54 - 53.58)	51.50 (0.71; 50.75 - 52.15)	P < 0.001	P = 0.012	P = 1.000

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Width of I2 gap	23.37 (1.08; 21.46 - 25.10)	21.05 (0.96; 18.80 - 22.56)	20.61 (0.61; 20.18 - 21.04)	P < 0.001	P = 0.004	P = 1.000
Height of coronoid process	8.71 (1.16; 7.18 - 10.63)	6.31 (0.91; 4.26 - 7.91)	4.60 (0.74; 3.83 - 5.30)	P<0.001	P<0.001	P=1.000
Width of I2	2.61 (0.27; 2.21 - 3.19)	4.23 (0.29; 3.79 - 4.86)	4.46 (0.37; 4.13 - 4.87)	P<0.001	P<0.001	P=0.470
Number of I2 tines	2.50 (0.59; 2.00 - 4.00)	3.36 (0.56; 3.00 - 5.00)	3.40 (0.55; 3.00 - 4.00)	P = 0.002	P = 0.081	P = 1.000
Width of I3	9.10 (0.43; 8.34 - 9.71)	8.24 (0.80; 7.26 - 9.79)	8.12 (0.95; 7.45 - 8.79)	P = 0.012	P = 0.212	P = 1.000
Height of I3	9.41 (0.41; 8.67 - 10.14)	5.10 (0.43; 4.40 - 5.94)	5.35 (0.04; 5.32 - 5.38)	P < 0.001	P < 0.001	P = 1.000
Number of I3 tines	0.00 (0.00; 0.00-0.00)	4.96 (0.74; 4.00 - 7.00)	4.50 (0.58; 4.00-5.00)	P <0.001	P < 0.001	P = 0.743
Length of C1	10.01 (0.66; 8.77 - 11.06)	9.63 (0.78; 8.28-11.15)	10.40 (1.57; 8.80 - 11.94)	P = 0.708	P = 1.000	P = 0.599
Height of C1	7.27 4.43-8.32 0.16	4.63 3.55-5.49 0.55	5.01 4.81-5.28 0.24	P<0.001	P=0.003	P=0.1.000

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Number of C1 tines	0.00 (0.00; 0.00-0.00)	6.08 (0.53; 5.00 - 7.00)	5.83 (0.76; 5.00 - 6.50)	P < 0.001	P < 0.001	P = 1.000
Length of P3	9.23 (0.05; 8.49 - 10.21)	7.38 (0.68; 5.85 - 8.65)	8.84 (0.53; 8.25 - 9.26)	P < 0.001	P = 1.000	P = 0.032
Breadth of P3	5.53 (0.11; 4.93 - 7.30)	4.41 (0.83; 3.45 - 6.16)	4.30 (0.44; 4.02 - 4.80)	P = 0.001	P = 0.038	P = 1.000
Length of P4	7.38 (0.28; 6.87 - 7.80)	5.64 (0.57; 4.99 - 6.72)	5.86 (0.41; 5.45 - 6.26)	P < 0.001	P < 0.001	P = 1.000
Breadth of P4	7.67 (o.42; 6.95 - 8.50)	6.12 (0.40; 5.43 - 6.73)	6.55 (0.52; 6.25 - 7.14)	P < 0.001	P = 0.002	P = 0.296
Length of M1	6.80 (0.39; 6.17 - 7.39)	4.91 (0.38; 4.16 - 5.67)	5.10 (0.43; 4.83 - 5.59)	P < 0.001	P < 0.001	P = 1.000
Breadth of M1	8.18 (0.40; 7.64 - 8.77)	6.15 (0.21; 5.87 - 6.80)	6.63 (0.57; 6.17 - 7.27)	P < 0.001	P < 0.001	P = 0.069
Mesial stylar area of M1	4.75 (0.65; 3.84 - 5.61)	2.53 (0.65; 1.33 - 3.44)	2.53 (0.53; 2.20 - 3.14)	P < 0.001	P = 0.005	P = 0.046
Distal stylar area of M1	5.47 (0.63; 4.60 - 6.50)	2.76 (0.58; 1.26 - 3.46)	2.54 (0.36; 2.30 - 2.97)	P < 0.001	P < 0.001	P = 1.000

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M1 Eocrista Length	20.70 (1.63; 18.46 - 22.65)	16.16 (1.13; 14.63 - 18.41)	16.23 (2.05; 14.17 - 18.27)5	P<0.001	P<0.001	P=1.000
Width of i1	4.09 (0.30; 3.83 - 4.68)	4.04 (0.38; 3.42 - 4.76)	4.17 (0.45; 3.85 - 4.48)	P = 1.000	P = 1.000	P = 1.000
Height of i1	5.03 (0.34; 4.51 - 5.58)	4.64 (0.38; 4.10 - 5.47)	5.24 (0.32; 5.01 - 5.46)	P = 1.000	P = 0.039	P = 0.120
Number of i1 Tines	9.36 (0.51; 9.00 - 10.00)	7.36 (0.77; 6.00 - 9.00)	6.50 (0.71; 6.00 - 7.00)	P < 0.001	P < 0.001	P = 0.310
Width of i2	6.06 5.42-6.91 0.43	6.07 5.30-6.86 0.45	5.66 5.30-6.01 0.50	P=1.000	P=0.478	P=0.455
Height of i2	5.01 (0.33; 4.26 - 5.57)	4.79 (0.29; 4.43 - 5.30)	5.69 (0.50; 5.38 - 6.01)	P = 0.222	P = 0.491	P = 0.003
Number of i2 Tines	11.91 (0.82; 11.00 - 13.00)	9.07 (0.62; 8.00 - 10.00)	7.50 (0.71; 7.00 - 8.00)	P < 0.001	P < 0.001	P = 0.023
Length of i3	6.64 (0.35; 6.32 - 7.47)	6.32 (0.35; 5.87 - 6.93)	6.51 (0.48; 5.96 - 6.80)	P = 0.098	P = 1.000	P = 1.000
Height of i3	3.62 (0.24; 3.27 - 4.05)	2.29 (0.31; 1.85 - 2.80)	2.68 (0.59; 2.47 - 3.09)	P < 0.001	P = 0.001	P = 0.103

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Number of i3 Tines	4.04 (0.62; 3.00 - 5.00)	5.42 (0.67; 4.50 - 7.00)	4.33 (0.58; 4.00 - 5.00)	P < 0.001	P = 1.000	P = 0.041
Length of c1	8.90 8.11-10.37 0.61	9.59 8.33-10.88 0.70	9.94 9.10-10.75 0.82	P=0.039	P=0.072	P=1.000
Height of c1	7.19 (0.84; 5.38 - 8.62)	4.31 (0.34; 3.59 - 4.91)	4.71 (0.38; 4.29 - 5.02)	P < 0.001	P < 0.001	P = 0.449
Number of c1 Tines	0.00 (0.00; 0.00 - 0.00)	5.50 (1.16; 3.50 - 7.00)	5.17 (0.29; 5.00 - 5.50)	P < 0.001	P < 0.001	P = 1.000
Length of m1	6.99 (0.44; 6.22 - 7.65)	5.33 (0.34; 4.99 - 6.13)	5.87 (0.18; 5.74 - 6.08)	P < 0.001	P < 0.001	P = 0.360
Width of m1	5.74 (0.33; 5.30 - 6.21)	4.72 (0.30; 4.19 - 5.13)	5.07 (0.26; 4.87 - 5.36)	P < 0.001	P = 0.013	P = 0.203
Area of m1 Trigonid	5.45 (0.59; 4.43 - 6.14)	2.80 (0.49; 2.13 - 3.70)	2.74 (1.04; 1.54 - 3.34)	P < 0.001	P < 0.001	P = 1.000
Area of m1 Talonid	11.87 (1.60; 9.10 - 14.14)	7.83 (1.28; 6.15 - 10.46)	7.81 (1.03; 6.85 - 8.90)	P < 0.001	P = 0.079	P = 0.275
Area of m1 distocuspid	1.77 (0.38; 1.33 - 2.46)	1.19 (0.20; 0.85 - 1.44)	1.22 (0.30; 0.96 - 1.55)	P = 0.001	P = 0.436	P = 0.463

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Length of molar tooth row (P4-M3)	25.39 (0.82; 23.98 - 26.44)	21.91 (1.22; 20.24 - 24.82)	22.74 (1.96; 21.17 - 24.94)	P < 0.001	P = 0.005	P = 0.783
Lever arm of masseter muscle (P4-glenoid fossa)	42.57 (0.68; 41.30 - 43.57)	34.61 (7.20; 17.77 - 39.59)	38.17 (1.58; 36.63 - 39.78)	P = 0.013	P = 1.000	P = 0.939
Depth of Mandible below m1	13.15 (0.91; 11.64 - 14.17)	11.75 (0.74; 10.44 - 12.93)	12.12 (0.88; 11.47 - 13.12)	P = 0.001	P = 0.221	P = 1.000
Depth of the mandible below c1	13.03 11.91-14.34 0.70	10.43 8.96-11.10 0.62	11.41 11.17-11.64 0.24	P < 0.001	P = 0.004	P = 0.050
Height of Ascending Ramus of Mandible	32.90 31.48-34.60 0.70	28.93 26.35-32.71 2.15	27.64 27.02-28.42 0.71	P<0.001	P<0.001	P=1.000

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[1] Linear measurements were corrected for body size by dividing each measurement by basal length. Area measurements were corrected for body size by dividing each measurement by basal length squared. Analysis of variance with a post hoc Bonferroni's test for significance were performed on natural log transformed data. The means, ranges, and standard deviations presented here have not been log transformed. Lengths and widths of teeth are the mesiodistal length and the buccolingual width. Height of teeth is from the cingulum to the tallest point on the tooth. See Figures 2.1 and 2.2 for illustration of measurements.

Cynocephalus, and indicate enhanced development of the posterior fibers of the temporalis muscle. This constellation would produce a more rostrally oriented bite force in Cynocephalus. Although sagittal cresting in Cynocephalus may reflect in part its smaller neurocranium, there is a distinct posterior expansion of the origins for the posterior fibers of the temporalis muscle out over the mastoid region (Fig. 4.2d-f).

The broader rostrum of Cynocephalus may be partially explained by the more rostrally oriented bite force in this taxon. This also is reflected in the more robust roots of I3 and C1 in Cynocephalus. However, the broad rostrum of Cynocephalus provides it with a larger nasal cavity than Galeopterus. Nasal cavity size has been proposed to correlate with environmental factors (i.e., temperature and humidity--Cabanac, 1986; Dean, 1988; Scott, 1954; Van De Graff and Fox, 1986; Wolpoff, 1968) but such conditions are not likely to differ significantly between the Philippine subregion, and the Sundaic and Indochinese subregions. However, Cynocephalus also has larger nasal conchae than does Galeopterus. The inferior nasal concha are especially relatively larger in Cynocephalus, and it is these inferior conchae that appear to be associated with swellings above the canines and incisors that produce the broader rostrum in Cynocephalus. Similarly, the Roman-nosed appearance of Cynocephalus in lateral view (Fig. 4.2d-f) appears to be related to expansion of the middle concha. Expansion of the conchae may indicate an enhanced sense of smell compared to Galeopterus, but the role of this character is unclear. Olfactory abilities may

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be related to different patterns of feeding or foraging in the two genera, to different mechanisms of social control, or differences in their reproductive physiologies. The vomeronasal organ has been studied in dermopterans (Bhatnagar and Wible, 1994), but the taxonomic assignment of the specimen used in this study is uncertain (K. Bhatnagar and J. Wible, pers. comm.). However, Bhatnagar and Wible (1994) found that dermopterans possess one of the relatively longest vomeronasal organs of any mammal. This may reflect the importance of olfactory clues for dermopterans. Reevaluation of this organ, with more precise taxonomic assignment of specimens, will provide valuable insights into the significance of differences in facial morphology among the genera.

A ventral view of the cranium (Fig. 4.2g-i) illustrates other differences among the genera. The relatively larger size of the anterior and postcanine dentitions in Cynocephalus are evident. Here we also see the relatively broader edentulous gap in Cynocephalus (Table 4.1). The palate is relatively longer in Cynocephalus than in the colugos, but not relatively longer than in the dwarf colugos. This may be the result of the relatively small sample of dwarf colugos. Attachments for the masseter muscle along the zygomatic arch are well developed in both genera. The rostral extent of the masseter reaches the mesial border of P4 in both genera, but this provides a longer lever arm for the masseter in Cynocephalus (Table 4.1). This is largely the result of the longer postcanine toothrow in Cynocephalus. However, the expansion of the temporal fossa, in conjunction with the compressed cranial

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base, results in the lengthening of the lever arm of the masseter. In Cynocephalus, the masseter also inserts more laterally on the cranium than in Galeopterus. In Galeopterus the orbital rims project laterally past the origin for the masseters, but in Cynocephalus the orbital rim extends to the lateralmost portions of the maxilla, jugal, and squamosal. The effect of this lateral displacement of the masseter may be to contribute an additional buccal component to movement of the mandible during the masticatory cycle in Cynocephalus.

The lateral view of the cranium (Fig. 4.2d-f) also shows functionally important differences. The rostrum of Cynocephalus is deeper dorsoventrally. This may reflect greater forces acting on the anterior dentition of Cynocephalus, as well as expansion of the nasal conchae. More posteriorly, the dorsoventral distance from the zygomatic arch to the molars is deeper in Cynocephalus, providing a longer distance over which the superficial masseter muscles can work. This appears to be a result of the ventral displacement of the molars in Cynocephalus. The more dorsally arched jugal in Cynocephalus also would provide the same benefit for the zygomaticomandibularis.

Continuing posteriorly, the orbital processes of the jugal and frontal provide more complete enclosure of the orbit in Cynocephalus. This may reflect greater chewing stresses being transmitted through this area in Cynocephalus. The external acoustic meatus of Cynocephalus is oval, being rostrocaudally compressed compared to Galeopterus. Similarly, the

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pneumatized portion of the mastoid is significantly reduced in Cynocephalus, to the point that the two taxa can be differentiated easily on this feature alone. This view also shows the greater spread of the posterior fibers of the temporalis muscle onto the nuchal region in Cynocephalus.

The mandible (Fig. 4.2j-l) is more robust in Cynocephalus than in Galeopterus. Depth of the mandible below m1 and c1 are statistically different among genera (Table 4.1). This supports the hypothesis that Cynocephalus has a more robust and posteriorly oriented Muscle temporalis, and enhanced masseter musculature, compared to Galeopterus. This produces a stronger bite force directed anteriorly to the incisor-canine complex and a stronger bite force in the molar toothrow. Cynocephalus also has a larger tubercle for attachment of the digastric muscles.

Cynocephalus has a higher coronoid process and a taller ascending ramus (Fig. 4.2j-l, Table 4.1) than Galeopterus. The higher coronoid process of Cynocephalus may simply be related to a larger temporalis in this taxon. However, a higher coronoid process also will shift the line of action of the temporalis dorsally, away from the fulcrum (the glenoid fossa), giving the muscle a longer moment arm, providing a greater mechanical advantage, and giving a stronger anterior bite force.

The ascending ramus of the mandible is also taller in Cynocephalus than in Galeopterus, providing a longer moment arm for the masseter muscle and a stronger bite force on the molariform teeth. This is achieved in an interesting manner, highlighting the mosaic nature of the dermopteran

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craniodental system. The ramus has become deeper through a ventral expansion of the angle of the mandible (Fig. 4.2j-l). This increases distance over which the masseter can act and provides a stronger bite force at the molar toothrow. However, this does not disturb the orientation of the temporalis muscle in relation to the dentition. Raising the ramus itself dorsally would shift the point of maximum mechanical advantage for the temporalis even more anteriorly. It also would require a ventral migration of the maxillary dentition to maintain occlusal relationships. Such a shift would alter functional relationships that may concentrate chewing forces at the I3, c1, C1 complex in *Cynocephalus*.

Although *Galeopterus* has a shorter ascending ramus of the mandible, the angle of the mandible generally projects more posteriorly behind the mandibular condyle than in *Cynocephalus* (Fig. 4.2j-o), although this character is variable. In *Cynocephalus* the angle of the mandible flares laterally and is even with the lateralmost projection of the mandibular condyle. This would allow the medial pterygoid muscles to effect greater lateral motion of the mandible than in *Galeopterus*, in which the angle of the mandible is never so laterally flared. Conversely, posterior expansion of the angle in *Galeopterus* would allow the medial pterygoid to protrude (translate anteriorly) the mandible to a greater extent than in *Cynocephalus*, especially as the teeth come more fully into centric occlusion.

The anterior dentition: incisors, canines, and third premolars.—The anterior dentition of colugos has been the subject of some interest (Aimi and

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Inagaki, 1988; Rose, 1973, 1975; Rose and Walker, 1981). Results of these studies have been contradictory and largely concerned with whether or not the highly specialized incisors of dermopterans are used in grooming. Rose and Walker (1981) reported no microscopic wear facets on lower incisors of either Cynocephalus or Galeopterus, but Aimi and Inagaki (1988) found evidence of grooming in Galeopterus. Whether or not dermopterans use their pectinate incisors for feeding, grooming, both, or neither, none of these studies have noted morphological differences among the anterior dentitions of the genera (Figs. 4.3a-d, Table 4.1).

Both genera have two upper incisors separated by an edentulous gap (Fig. 4.2g-i), similar to what is seen in cervids. Both genera also have three procumbent, pectinate lower incisors (Figs. 4.3a-b). In both genera, I3 is larger than, but similar in shape to the genus-specific C1. Most importantly, the similarity of I3 and C1 to one another, and their differences among genera is remarkable. Furthermore, while a general in line similarity holds for c1 and p3 in Galeopterus, these teeth are more distinctive from one another in Cynocephalus (Figs. 4.3c-d).

The I2 in Cynocephalus is relatively narrower than in Galeopterus (Table 4.1, Figs. 4.3c-d), and generally has only two tines as opposed to the normal three tines in Galeopterus. The relative mesial-distal lengths of I3 are the same among genera, but in Cynocephalus I3 are relatively taller (Table 4.1). More importantly, I3 in Cynocephalus is blade-like compared to Galeopterus. In Galeopterus I3 is serrated, and so is the canine behind it. This condition

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Fig. 4.3: Dentition of extant dermopterans: a) *Cynocephalus volans* USNM 536048 dorsal view of lower anterior dentition; b) *Galeopterus variegatus* USNM 49640 dorsal view of lower anterior dentition to same scale as a, c) *C. volans* USNM 536048 left lateral view of anterior dentition prior to full occlusion, d) *G. variegatus* USNM 49640 right lateral view of anterior dentition prior to full occlusion to same scale as c reversed for comparison, e) *C. volans* USNM 536048 occlusal view of upper right molariform dentition, f) *G. variegatus* USNM 49640 occlusal view of upper left molariform dentition to same scale as g reversed for comparison, g) *C. volans* USNM 536048 occlusal view of lower right molariform dentition, h) *G. variegatus* USNM 49640 occlusal view of lower left molariform dentition to same scale as g reversed for comparison.

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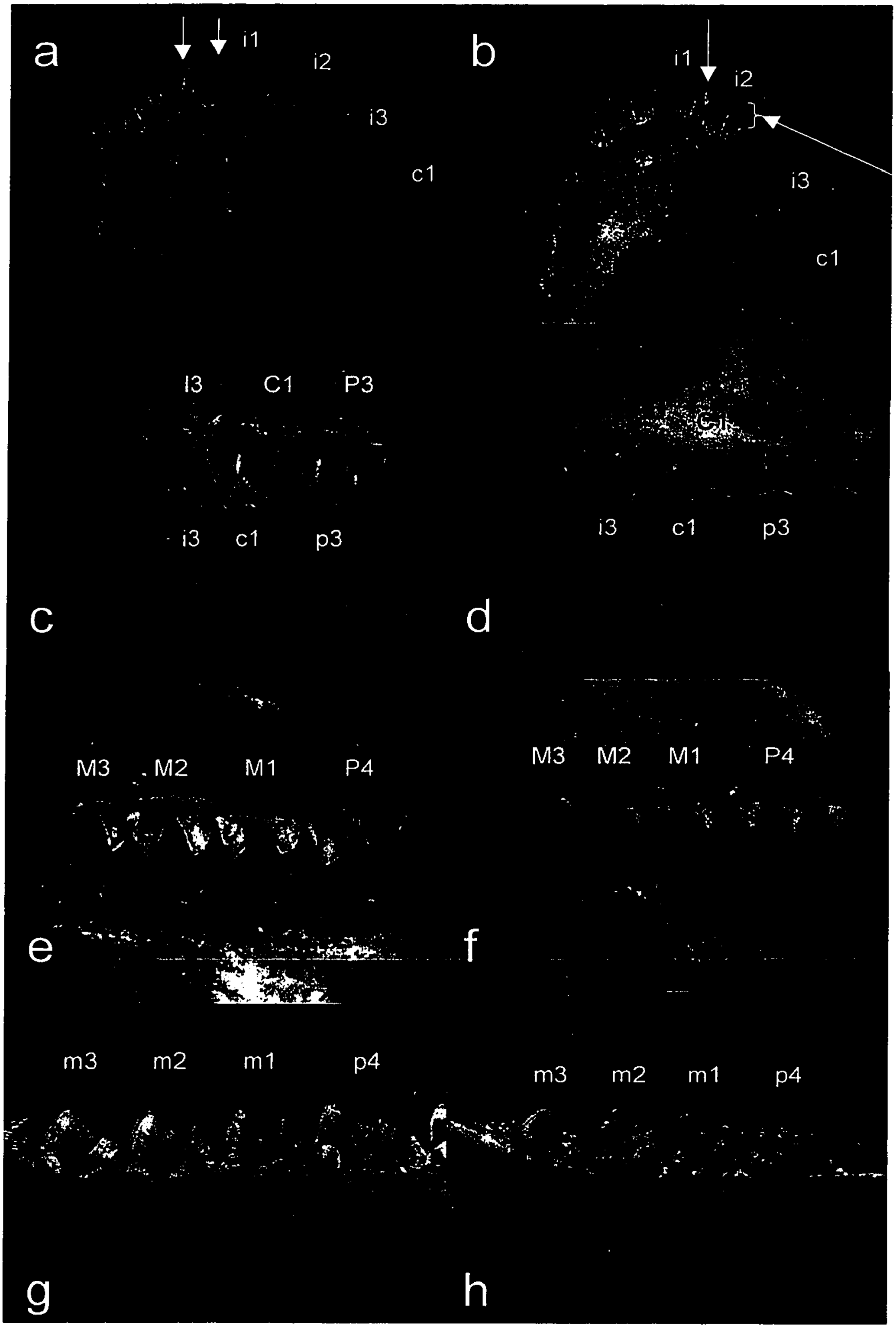

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on I3 is represented as a series of accessory cuspules (usually four) along the crest of the tooth (one anterior to the main cusp and three posterior to it). In Cynocephalus, there are only two small cuspules on a blade-like I3 that is more trenchant and taller than the canine itself. These are located at the base of the tooth, one mesially abutting I2 and one distally abutting C1 (Fig. 4.3c). These cusps were not counted as tines because they appear to be outgrowths of the base of the tooth rather than structures associated with the crest of the tooth as seen in Galeopterus. Between I3 and C1 in Galeopterus there is a diastema. This is never seen in Cynocephalus.

There are also differences among genera in i1-3 and c1 morphology (Figs. 4.3a-b). Height and width of i1 are the same among genera, but there are differences in the number of tines making up the tooth. Cynocephalus has 9-10 tines while Galeopterus only has 6-9. On i2, Cynocephalus has 11-13 tines, whereas Galeopterus has 7-10. There also are differences in robusticity of the tines. In Cynocephalus each of the tines are generally the same size and shape (Fig. 4.3a). However, the outer tines of i1 and i2 are more robust than the others. This holds only for the i1 of Galeopterus, in i2 the distal 3-4 tines also are more robust than the other tines.

Morphology of i3 shows similar differentiation. This tooth is taller in Cynocephalus and has fewer tines, 3-5, while Galeopterus has 4-7 tines. The fact that this distinction is only statistically significant in relation to the large-bodied colugos may be related to the small sample size of dwarfed colugos. In Galeopterus there is a diastema between i2 and i3. This gap

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rarely is seen in Cynocephalus and always is narrower. The i3 also is more mediolaterally oriented in Cynocephalus. In Galeopterus, this tooth is more parallel to the canines, premolars, and molars.

In both genera, the two medial lower incisors occlude with an edentulous palate, and the degree to which these teeth are used in feeding or grooming is the subject of some debate. Evidence presented by Aimi and Inagaki (1988) shows that incisors may be used for grooming in Galeopterus. I also have examined this specimen (USNM 49640) and concur with their observations and conclusions. In addition, all specimens of Galeopterus examined for this study had dirty incisors with a pale-colored, flaky substance encrusting the space between the tines of i1 and i2. All Cynocephalus examined had clean incisors. In no case was any kind of material found embedded between incisor tines. In addition, incisor tines of Cynocephalus are so fragile that they may not, in fact, be used, a curious abandonment of an adaptation if this inference is confirmed. Preliminary observations of Cynocephalus in the Philippines have not revealed a single instance of use of i1 or i2.

There also appears to be strong functional emphasis between I3 and C1 and the occluding c1. In Galeopterus, pectination extends farther back to influence both upper and lower canines and the mesial portions of p 3/3. Relative canine height is different among genera (Table 4.1). Within each genus, I3 and C1 are very similar morphologically. Also, within each genus, C1 is very similar to c1. In both genera, the canines are double rooted, as

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are the I3s. As with I3, the canines of Galeopterus are serrated and the canines of Cynocephalus are not. In Cynocephalus the anterior end of C1 buccally overlaps I3, and is buccally overlapped by P3. The result is that C1 in Cynocephalus is slightly rotated out of alignment with the axis of the postcanine dentition. In Galeopterus, C1 is strictly in line with this axis, and there is no overlap.

Although not generally considered as part of the anterior dentition, p 3/3 are considered here because they function with the anterior dentition as part of the shearing or shredding complex. The molariform fourth premolars are considered with the molar tooth row because they function as part of the shearing-crushing complex.

General shape of the P3 is not greatly different in the two genera (Figs. 4.3c-d). In both, P3 is a buccolingually narrow tooth with paracone and metacone, although a small protocone may be present. Galeopterus usually also has a small cuspule along the preparacone crista. In terms of relative size of P3, dwarf colugos (Galeopterus) occupy an intermediate position between large colugos and Cynocephalus. P3 is mesiodistally longer in Cynocephalus than in the large colugos (Table 4.1). However, this tooth is not significantly longer when compared with dwarf colugos. The dwarf colugos are not significantly different from their larger conspecifics in these measures. While relative size relationships are continuous, there are clear morphological differences among the genera. In Cynocephalus, the eocrista (= ectoloph) is more W-shaped, and the lingual area of the tooth where the

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protocone should be located is more extensive than in Galeopterus. In Galeopterus, a short diastema separates P3 from C1, while in Cynocephalus the anterior edge of P3 overlaps the posterior edge of C1 buccally, exactly as C1 buccally overlaps I3 in this genus. Similarly, the mesialmost part of the p3 paracristid passes lingual to the distal accessory cuspule of c1 in Cynocephalus.

The p3 has a blade-like trigonid in both genera, but only in Galeopterus is the trigonid serrated. The paracristid in Cynocephalus is more attenuated than in Galeopterus. The main cusp on the p3 trigonid is the protoconid but the homology of the remaining trigonid cusps in Galeopterus is uncertain. The talonid is deeper in Cynocephalus and has the hypoconid and entoconid distal to the rudimentary basin.

Deciduous canines and premolars.—Morphological patterns of the deciduous versus replacement dentitions of canines and premolars are also distinctive and may shed light on the polarity of the craniodental differentiation. Deciduous canines and premolars of Galeopterus are morphologically similar to their successors (i.e., serrated). In Cynocephalus, the deciduous dentition also closely resembles the scalloped and serrated teeth of Galeopterus. This may indicate that the morphology of incisors, canines, and premolars in Galeopterus represents the ancestral condition, and that Cynocephalus morphology is derived in these respects. Alternately, the serrated canines of Galeopterus may be a derived retention of a juvenile pattern.

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Occlusion, wear, and dental function in the anterior dentition.—In both genera, i1 and i2 occlude with an edentulous premaxillary pad and no wear was found on them (Table 4.3). In both genera, I2 occludes with the buccal face of the mesial one-half of i3. The distal one-half of i3 occludes with the lingual face of the mesial one-half of I2 (Fig. 4.3c-d). In *Cynocephalus*, the posterior crest of I3 occludes along the lingual side of the mesial crest of c1. In *Galeopterus*, most of this contact is with the mesialmost serrations on c1.

Wear patterns on i3 are distinct between the genera (Table 4.3). The i3 of *Galeopterus* is more heavily worn than that of *Cynocephalus*. What little wear there is on i3 in *Cynocephalus* appears to be produced by the lingual aspect of the mesial crest of I3. However, in *Galeopterus* wear of the distalmost tine of i3 is produced by the apex of I3. Wear on the next most-distal tine in *Galeopterus* is produced as this tine comes into contact with the mesial cuspule on the mesial crest of I3. In *Cynocephalus*, i3 occludes lingually and only near the base of I3 mesially. This produces a characteristic V-shaped wear facet on the mesiolingual face of the I3 of *Cynocephalus* that is not seen in *Galeopterus*.

Morphology, wear facets, and occlusal relationships of I3 clearly show that this tooth is more suited for shearing in *Cynocephalus* than in *Galeopterus*. This may explain why it is relatively less worn in *Cynocephalus*. In *Galeopterus*, the main area of occlusion of I3 seems to be with i3. The wide gap between i3 and c1 prevents I3 from occluding with c1 until late in the chewing cycle (Figs. 4.3c-d). In *Cynocephalus*, the distal

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aspect of I3 comes into contact with the mesial crest of c1 early in the chewing cycle. The mesial crest of I3 does not contact i3 until later in the cycle. Similarly, the distal accessory cuspule on I3 and the mesial accessory cuspule on C1 provide a shearing contact for the apex of c1 in Cynocephalus that is not present in Galeopterus.

In both genera, the mesial crest of c1 occludes with the distal crest of I3, and the distal crest of c1 occludes with the mesial crest of C1. Again, the pattern of this occlusion is different. In Cynocephalus the lower canine fits closely between I3 and C1, and produces wear on the lingual face of the crests of these teeth (Figs. 4.3c-d; Table 4.3). In Galeopterus, the lower canine appears to contact only the upper canine in initial stages of the chewing cycle. It does not contact I3 until the molar teeth are almost in centric occlusion. In initial stages of contact between upper and lower canines, serrations on these teeth interdigitate (Fig. 4.3d). This accounts for lingual wear on the upper canines and buccal wear on the lower canines in this genus. Furthermore, there is a sizable gap between c1 and p3 in Galeopterus. In Cynocephalus the c1 distal-accessory cuspule fits firmly against the buccal face of the p3 paracristid. Thus, during the chewing cycle, c1 provides an additional cutting surface for C1 that is not present in Galeopterus. This is an effective scissors-like cutting mechanism in Cynocephalus. The condition seen in Galeopterus (i.e., interdigitating serrations) appears better suited to shredding or puncturing food between these serrations.

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Table 4.2: Craniodental differences among extant dermopteran genera.

	Cynocephalus	Galeopterus
Rostrum	Broader mediolaterally, deeper dorsoventrally.	Narrower mediolaterally, shallower dorsoventrally.
Nasal concha	Larger	Smaller
Neurocranium	Smaller	Larger
Postorbital constriction	Narrow	Broader
Superior temporal lines	Converge posteriorly, form sagittal crest, join nuchal crest.	Do not converge posteriorly, no sagittal cresting, never join nuchal crest.
Orbital processes of frontal	Robust	Gracile
Zygomatics	Laterally placed, narrow dorsoventrally, dorsally arched.	More medial, thicker dorsoventrally, not dorsally arched.
Cranial base	Compressed rostrocaudally.	Not compressed.
Mastoid region	Dorsoventrally flat, not pneumatized.	Projects ventrally, heavily pneumatized.
External acoustic meatus	Oval	Round
Coronoid process	Taller	Shorter
Angular process of mandible	Ventrally and laterally expanded.	Caudally extended.

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I2	Smaller, 2 tines.	Broader, 3 tines.
I3	Taller, bladelike.	Shorter, serrated.
C1	Taller, bladelike.	Shorter, serrated.
P3	Longer, more trenchant.	Shorter, less trenchant.
i1	9-10 tines.	6-9 tines.
i2	11-13 tines.	7-10 tines, distal 3-4 tines more robust.
i3	Taller, 3-5 tines.	Shorter, 4-7 tines.
c1	Taller, bladelike.	Shorter, serrated.
p3	Trigonid bladelike, talonid deeper.	Trigonid serrated, talonid shallower.
P4 - M3	Longer eocrista, tightly folded centrocrista, accessory buccal cuspules, no interstitial spaces.	Shorter eocrista, more open centrocrista, no accessory buccal cuspules, may have interstitial spaces.
p4 - m3	Large trigonid, large talonid, large distocuspid, no interstitial spaces.	Much smaller trigonid, smaller talonid, smaller distocuspid, may have large interstitial spaces.

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Table 4.3.: Dental wear in extant dermopterans.

	Cynocephalus	Galeopterus
I2	Little to no wear, even in latest stages when molars are almost flat.	Small amount of apical wear on posterior two tines and along distal crest of most distal tine.
I3	Early wear at apex and along distal crest; distal crest wear on the lingual side even in latest stages; in later stages wear along mesial crest. V-shaped wear facet on lingual side of tooth near base of mesial crest in later stages (facet produced by distal tines of i3). Wear at base of distal crest in later stages quite extensive.	Early wear along distal serrations usually along lingual side, apical in some specimens; wear along mesial serrations later (these facets may also be on the lingual side of the serrations, or may be more apical). Apical wear on main cusps not until very advanced stages. V-shaped facet seen in Cynocephalus not present in Galeopterus.
C1	Early wear along mesial and distal crests of tooth. As in I3, wear restricted to lingual face of crests; facets continuous across apex of tooth even in early wear; no evidence of more extensive apical wear.	Wear along mesial and distal serrations, restricted to the lingual face of the serrations. In early stages wear present only on most mesial and most distal serrations. Central cusp worn only in most heavily worn teeth.

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P3	Early wear on mesial end of preparacone crista, distal end of postmetacone crista and at vertex of both cristae; later wear across entire ectoloph. Apical wear not present on either paracone or metacone; paracone more heavily eroded than metacone.	Early wear on preparacone crista, postmetacone crista and at vertex of both cristae. Wear on the preparacone and postmetacone cristae accompanied by paracone and metacone apical wear even at earliest stages. Wear tends to be heaviest mesially in later stages but differential degree of paracone-metacone erosion is not nearly as pronounced as in *Cynocephalus*.
P4	Early wear only along ectoloph, continuous; no indication of greater wear of cusps than crests; no wear evident on metaconule, paraconule, protocone, or associated crests. Initial paraconule wear appears apical and mesial to crest; initial wear of metaconule appears along mesial aspect as well; initial wear of protocone along postprotocone crista and includes some apical wear.	Early wear only along ectoloph, continuous; greater wear of cusps than crests, no wear evident on metaconule, paraconule, protocone, or associated crests. Initial wear of paraconule appears apical and mesial to crest; initial wear of the metaconule appears along mesial aspect as well; initial wear of protocone along postprotocone crista and includes some apical wear.
M1	Early wear only along ectoloph, continuous; no evidence of greater wear of cusps than crests; no wear evident on metaconule, paraconule, protocone, or associated crests. Initial wear of paraconule appears apical and mesial to cusp; initial	Early wear along the ectoloph; continuous; evidence for greater wear of cusps than crests; slight wear on metaconule, paraconule, and protocone, and associated crests. Initial wear of paraconule appears apical and mesial to cusp; initial wear of

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	wear of metaconule appears along premetaconule crista; initial wear of protocone is apical and along postprotocone and preprotocone cristae. In late wear tooth almost totally flat except for W shaped remnant of ectoloph. Overall impression: tooth wearing evenly from lingual aspect of buccal side.	metaconule appears almost directly mesially, and not along premetaconule crest; initial wear of protocone apical and along postprotocone and preprotocone cristae. In late wear postprotocone crest heavily eroded. Tooth never worn totally flat; advanced wear produces greater separation between mesial and distal stylar shelf components with relatively less apical wear compared to <u>Cynocephalus</u>. Overall impression: tooth wearing from midline mesially, and from midline lingually.
M2	Patterns of wear same as on M1; M2 relatively more worn than M1.	Patterns of wear same as on M1; M2 relatively more worn than M1.
M3	Patterns of wear same as on M1 and M2; M3 relatively more worn than M2.	Patterns of wear same as on M1 and M2; M3[3] relatively more worn than M2.
i1	No wear observed.	No wear observed.
i2	No wear observed.	No wear observed.
i3	No wear early, but begins along distal crest of most distal tine; wear proceeds until apical wear on most posterior tine. Thereafter, apical wear begins to appear on tines beginning with most posterior and progressing to most mesial. Posterior tines	Wear early, beginning along distal crest of most distal tine; wear proceeds until apical wear on most posterior tine. Thereafter, apical wear begins to appear on tines beginning with the most posterior and progressing to most mesial. Eventually,

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	always more heavily worn than ones mesial to them.	all tines appear equally worn.
c1	Earliest wear low along distal crest near distal accessory cuspule; begins along mesial crest before apical wear visible; in latest stages considerable apical wear. Wear directly along crests, not lingual or buccal to them.	Earliest wear on all serrations simultaneously, and on apex of main cusp at same time. In later wear serrations worn away. Wear usually on buccal side of serrations.
p3	Initial wear at apex of protoconid and some along protocristid; early wear also on cristid obliqua; later wear on paracristid, apices of hypoconid and entoconid, and along postcristid.	Initial wear on apices of all serrations, and later apices of all cusps; early wear also on cristid obliqua; later wear on paracristid. No postcristid wear at any stage.
p4	Early wear on paracristid, protocristid, cristid obliqua, and postcristid; apical wear first on distal aspect of hypoconid. Eventually all cusps heavily worn.	Early wear on protoconid, hypoconid, and hypoconulid; also slight wear along paracristid and cristid obliqua; little or no wear distal to hypoconulid; postcristid wear appears later; apical wear first on distal aspect of the hypoconid. Eventually all cusps worn.
m1	Patterns of wear same as on p4; m1 relatively more worn than p4.	Patterns of wear same as on p4; m1 relatively more worn than p4.
m2	Patterns of wear same as on p4 and m1; m2 relatively more worn than m1.	Patterns of wear same as on p4 and m1; m2 relatively more worn than m1.

m3	Patterns of wear same as on p4, m1, and m2; m3 relatively more worn than m2.	Patterns of wear same as on p4, m1, and m2; m3 relatively more worn than m2.

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The p3 trigonid occludes with the distal crest of C1 and the preparacone crista of P3. This complex (Fig. 4.3c-d) is considered with the anterior dentition because it also appears to function mainly for shearing in Cynocephalus and mainly for shredding in Galeopterus due to the blade-like trigonid in Cynocephalus and the serrated trigonid of Galeopterus. Again, in Cynocephalus C1 and P3 are closely appressed to each other and this provides an additional cutting surface for the p3 protoconid. Galeopterus has a gap between C1 and P3, and the p3 protoconid appears to occlude only with preparacone crista of P3. The greater degree of paracone wear of P3 in Galeopterus suggests tighter occlusion between the paracone and the p3 talonid in Galeopterus than in Cynocephalus. The more lingual position of the postprotoconid crista in Cynocephalus prevents this kind of wear, and provides the protocone in Cynocephalus an increase in its shearing rather than crushing function.

Fourth premolar and molars.—Molariform teeth of both genera are generally characterized by a dominant and highly dilambdodont eocrista (= paracrista + postparacrista + premetacrista + metacrista) and large conules on upper teeth. There are correspondingly large crista obliqua and postcrista on the lower teeth (Figs. 4.3e-h; Table 4.2). There has been enlargement of the metacone and metaconule as compared to other archontans and many other mammals. However, metacone enlargement, together with extreme lingual displacement of the hypoconulid against the entoconid (= entoconid twinning), is a phenomenon that occurs independently in a number of

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lineages (e.g., Metatheria, Tupaiidae, Mixodectidae, and Microsyopidae). A hypocone is totally absent in both dermopteran genera, but the enlarged and distally displaced metaconule may be functionally equivalent and linked to the distocuspid-paraconid shelf complex in the Cynocephalidae.

Proportions of the toothrow from p 4/4 to m 3/3 are different among the genera. In the megadont Cynocephalus, tooth size decreases slightly from p 4/4 to m 3/3, whereas in Galeopterus there is generally a slight increase from p 4/4 to m 3/3 (in Cynocephalus P4≈M1≈M2>M3, and p4>m1≈m2>m3; in Galeopterus P4>M1≈M2≈M3, and p4>m2≈m3>m1). This character, however, is variable within Galeopterus. Some specimens show more equally sized molariform teeth, while others show a distinct increase in tooth size posteriorly. However, upper molariform teeth are both mesiodistally longer and buccolingually broader in Cynocephalus than in Galeopterus. The eocrista is also relatively longer in Cynocephalus as a result of its more tightly folded centrocrista, and hypertrophy of the paracone and metacone. These factors also produce a more extensively developed ectoloph in Cynocephalus. As a result of the differences in the ectoloph, the V-shaped notch formed by the centrocrista in Cynocephalus forms an acute angle in contrast to that of Galeopterus where the postparacrista and premetacrista meet buccally in a rounded and U-shaped notch. Cynocephalus also has small, but distinct, accessory cuspules on its buccal cingulum. In keeping with the hyper-developed ectoloph, the paraconules and metaconules of

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Cynocephalus also are relatively (and absolutely) larger than those of Galeopterus.

Lower molariform teeth show different relative proportions of different areas of the tooth (Fig. 4.3e-f; Fig. 4.4, Tables 4.1, 4.2). Cynocephalus has a relatively larger trigonid than Galeopterus. In Cynocephalus, trigonid area is about one-half of talonid area. In Galeopterus, trigonid area is only about one-third of talonid area. Relative trigonid, talonid, entoconid, and basal area are all also relatively larger in Cynocephalus. Consequently, the trigonid of Galeopterus is mesiodistally constricted and appears shrunken compared to the talonid in Cynocephalus. Whether or not the diminutive trigonid of Galeopterus represents the ancestral dermopteran or cynocephalid condition is an important question. Unfortunately, Dermotherium major [Ducrocq, 1992], a purported dermopteran from the Eocene of Thailand, is of little help here. The fossil is a mosaic of characters found in both extant taxa, but it is twice as large as any living dermopteran and poorly preserved.

In both extant genera, the protoconid is the tallest cusp on p4 and m1, while the metaconid is the tallest cusp on m2 and m3. The paraconid is much smaller in Galeopterus. In Cynocephalus the sweeping paracristid has expanded mesially to form a shelf that abuts against another small shelf or cusp, an area delimited by the postcristid distal to the hypoconulid and entoconid (the distocuspid) of the tooth in front of it. This largely explains the large trigonid in this genus. This paraconid shelf is largest on p4 and gradually decreases in size from m1 to m3. The paraconid in Galeopterus

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Fig. 4.4.—Dental nomenclature: Ccr, centrocrista; Crob, cristid obliqua; Distocuspid; End, entoconid; Entcd, preentoconid cristid; Eocrista; Hyd, hypoconid; Hyld, hypoconulid; Me, metacone; Mecl, metaconule; Med, metaconid; Pa, paracone; Pacl, paraconule; Pactd, paracristid; Pad, paraconid; Pmecr, postmetacone crista; Poctd, postcristid; Ppacr, preparacone crista; Pprcr, preprotocone crista; Pr, protocone; Prcd, protocristid; Prd, protoconid; Ptprcr, postprotocone crista; Tldb, talonid basin; Tldn, talonid notch; Trb, trigon basin; Trdb, trigonid basin.

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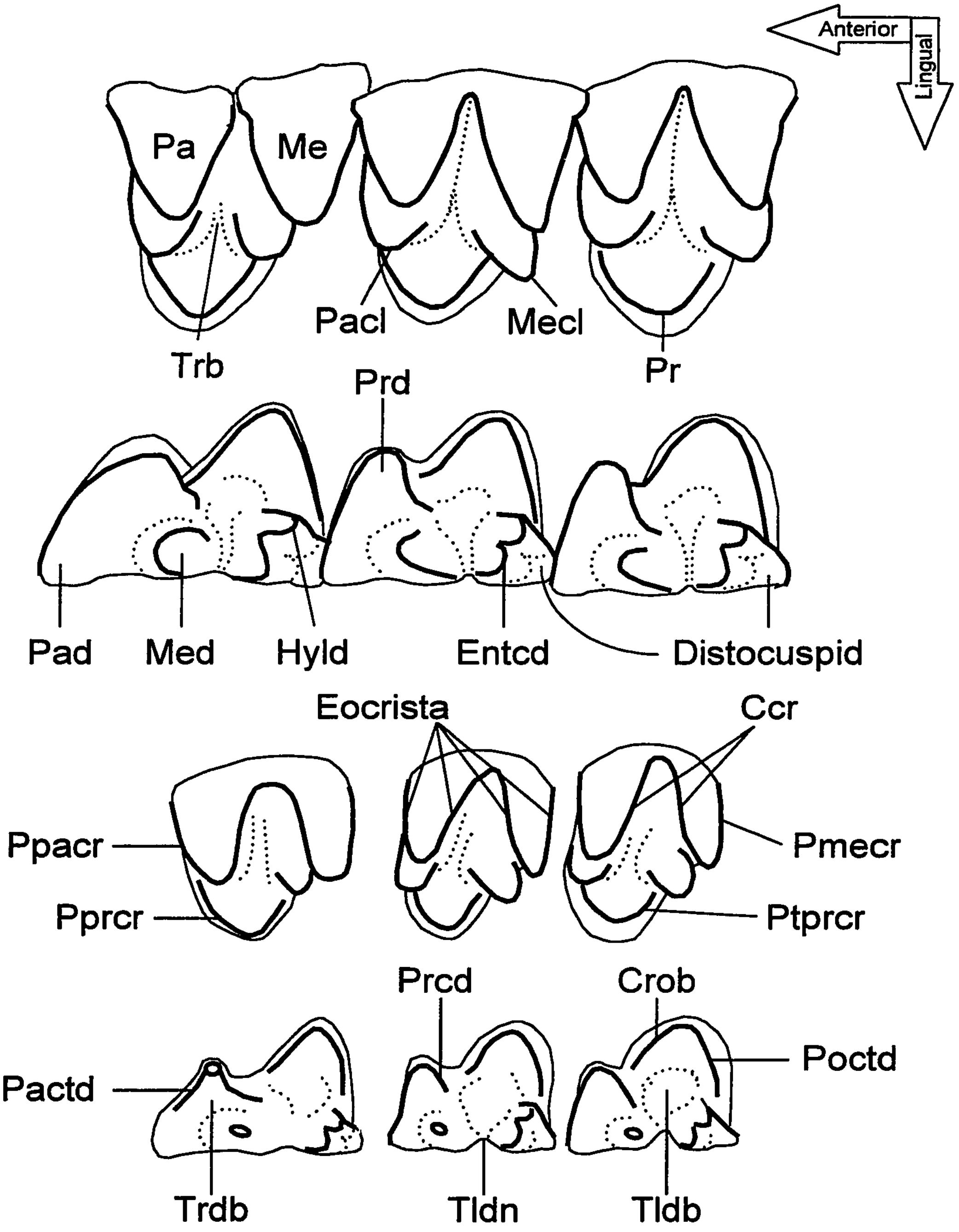

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follows a similar pattern, being largest on p4 and smallest on m3. In Galeopterus, the cristid obliqua joins the base of the protoconid slightly more buccally than in Cynocephalus. In Cynocephalus, the cristid obliqua joins the protoconid more lingually and ascends the distal face of the trigonid. This provides relief on the distal face of the trigonid in Cynocephalus that may abrade against the distal aspects of the paracone and paraconule during chewing.

The talonid (like the trigonid) is relatively larger in the megadont Cynocephalus than it is in Galeopterus. However, the talonid is relatively much larger compared to the trigonid in Galeopterus. In both genera, the talonid has a lingually displaced hypoconulid, twinned with the entoconid. The talonid notch between the metaconid and entoconid is slightly distinctive in the genera; it is more open mesiodistally in Galeopterus, forming a slightly more acute angle in Cynocephalus.

In both genera, the hypoconulid is lingually displaced and appressed to the entoconid. These structures are together raised well above the floor of the talonid basin. The distal extension of these coalesced cusps forms the distocuspid, delimited simply by an extension of the postcristid. In Cynocephalus there is extensive contact between the distocuspid and the paraconid shelf of the next tooth. Galeopterus has a much smaller distocuspid and there often is no contact between this structure and the paraconid of the next tooth. In Cynocephalus the postcristid is well defined and passes distal to the hypoconulid to delimit the distocuspid. In

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Galeopterus the postcristid is less well defined and becomes the distocuspid closer to the hypoconulid.

Occlusion, wear, and dental function in the postcanine dentition.—Rose and Simons (1977) provided the only published details of dermopteran wear facets. They described a dentition that is more heavily reliant on shearing (buccal phase, or phase 1) than crushing (lingual phase, or phase 2). Their study concentrated only on molar wear facets of Cynocephalus as compared to plagiomenids, and did not report on Galeopterus. Rose and Simons (1977) concluded that dental morphology, wear, and function of Cynocephalus are similar enough to plagiomenids to warrant the inclusion of Plagiomenidae within Dermoptera. They also suggested, as did Simpson (1937) and others, that the Mixodectidae lie close to the ancestry of dermopterans (see also Szalay and Lucas, 1996).

A comparison of molar occlusion (Fig. 4.5a-f) and wear of the two genera (Table 4.3) indicates that the patterns of wear described by Rose and Simons (1977) are generally characteristic of both genera, with a few important exceptions. There may be also differences in the relative degree of wear of different facets among genera. Cynocephalus shows heavier wear and greater development of the lingual phase crushing facets than Galeopterus. Yet, it is clear that the molariform dentition of Cynocephalus emphasizes shearing compared to Galeopterus. This accounts for the hypertrophied eocrista (and eocristid, the crests of the trigonid and the cristid obliqua) that

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Figure 4.5: Occlusal diagrams of dermopterans, upper and lower left p 4/4 - m 2/2. Upper teeth are shown as transparent in order to visualize crown occlusal contacts. Cynocephalus volans a), and G. variegatus b), at the beginning of buccal phase occlusion; C. volans c), and G. variegatus d), at the beginning of the lingual phase of occlusion; and C. volans e), and G. variegatus f), in centric occlusion.

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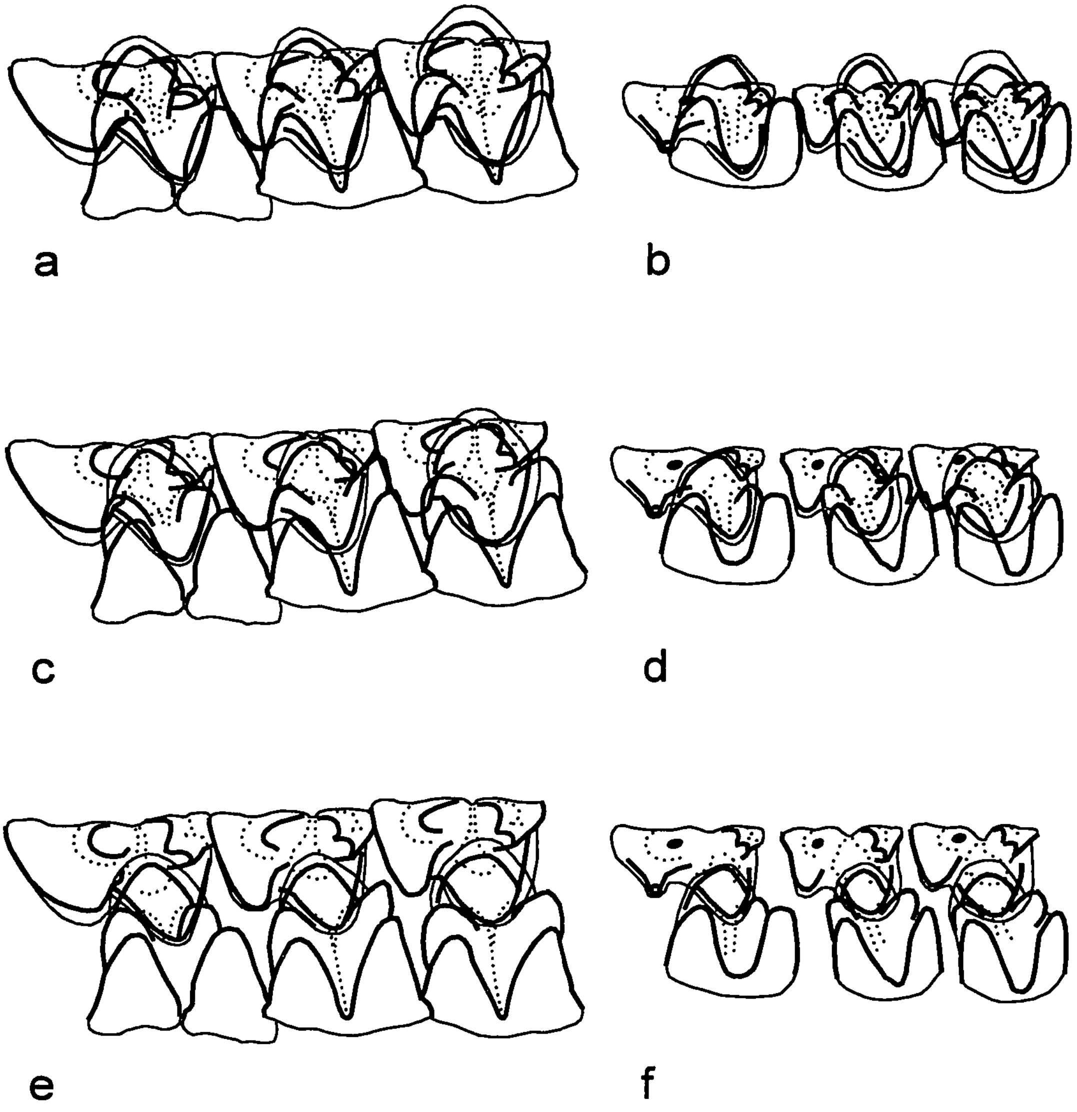

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provides Cynocephalus with relatively longer shearing crests than it does Galeopterus (Table 4.1). The hypertrophied and distally displaced metaconule in Cynocephalus occludes with the distocuspid and provides a more extensive crushing surface than it does in Galeopterus. The expanded paraconid shelf does not appear to function as a crushing surface with the metaconule until the advanced stages of wear. Instead, it provides an expanded shearing surface between the postmetacrista and the paracristid. Likewise, the prominent cristid obliqua in Cynocephalus provides greater shearing with both the postparacone crista and the preprotocone crista. It also is slightly more lingually situated and provides relief along the distal trigonid face. The mesially extended preparaconule crista provides important and increased shearing edges in conjunction with the postvallid. The postmetaconule crista cuts against the cristid obliqua in the later stages of wear. The posthypoconid cristid in Cynocephalus also provides a well-developed shearing surface for the premetacrista.

Although obviously stamped with the same general heritage as the teeth of Cynocephalus, the molariform dentition in Galeopterus seems to emphasize protocone-talonid crushing. However, this crushing occurs in a way that does not produce the strong lingual-phase crushing facets seen in Cynocephalus (Rose and Simons, 1977). In Galeopterus, the metaconule does not contact the distocuspid area until the later stages of wear. Similarly, shearing surfaces are not developed in this taxon to the extent seen in Cynocephalus (Table 4.1). Although the cristid obliqua does shear

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against the postparacone and preprotocone cristae in Galeopterus, the length of the shearing crests available are relatively less than in Cynocephalus. This is because Galeopterus has a relatively broader and more open talonid basin than Cynocephalus, partly as a result of its relatively small trigonid. In Galeopterus, the cristid obliqua joins the talonid more mesio-buccally, the distal face of the talonid is more mesially inclined, and the mesial face of the distocuspid is more distally inclined. Also, the postprotoconid crista does not extend down the mesial face of the talonid to provide an additional shearing crest.

In general, wear appears to be heavier in Cynocephalus than in Galeopterus, but molar tooth wear also differs in other ways (Table 4.3). The upper molariform teeth of Cynocephalus wear from the protocone buccally (i.e., tongue to cheek). In later stages of wear, the paraconid, metaconid, and protocone will be completely obliterated but a distinct W-shaped ectoloph (heavily worn) will be present. In Galeopterus, rarely do molariform teeth reach such advanced stages of wear, and in Galeopterus the teeth wear from the midline mesiodistally (i.e. from inside-out). Here, as wear progresses, there is a greater separation of the mesial and distal components of the stylar shelf. This suggests a greater degree of bucolingual movement as the hypoconid moves through the trigon basin in Galeopterus. This contradicts the hypothesis of greater lateral movement in the mandible of Cynocephalus based on morphology of the angle of the mandible. In Cynocephalus it appears that a more extensive orthal

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component of the buccal phase of the masticatory cycle brings the teeth into centric occlusion. After reaching centric occlusion, lingual motion of the mandible would serve to crush and grind recently sheared material and produce the heavy phase two facets seen in <u>Cynocephalus</u>. This may explain the laterally expanded angle of the mandible in <u>Cynocephalus</u>. More subtle aspects of molariform wear (Table 4.3) support this hypothesis. Early wear in both genera is present along the whole eocrista. Lack of noticeable wear on the tips of metacone and paracone in <u>Cynocephalus</u> indicates a strict vertical shear of the crests past each other. The more pronounced apical wear on the paracone and metacone of <u>Galeopterus</u> can be explained by a greater distomesial component in its masticatory cycle.

It appears that in <u>Galeopterus</u> in initial stages of occlusion the hypoconid contacts the metacone, and the protoconid may contact the paracone. The mandible then shifts mesially as the hypoconid drops into the trigon basin. Alternately, if the mandible were displaced so far laterally that the lower canine was positioned lateral to the upper canine, the hypoconulid and protoconid could produce these wear facets. It is impossible to produce such an arrangement in <u>Cynocephalus</u> without completely dislocating the mandible. In <u>Galeopterus</u>, however, posterior displacement of the angle of the mandible could produce distal to mesial translation of the mandible and produce these wear facets.

A comment on the purported fossil dermopteran from Thailand is required. If <u>D. major</u> proves to be a dermopteran then its inclusion in the family

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Cynocephalidae may be appropriate (Ducrocq et al., 1992). However, the dermopteran affinities of this specimen (TF 2580) are uncertain. The specimen is poorly preserved, and only m3 preserves any diagnostic features. Furthermore, some features listed as characteristic of Dermoptera are more widespread than these authors acknowledge. For example, a "...hypoconulid lingually displaced and close to the entoconid..." is also characteristic of many other eutherian taxa. There also are inconsistencies in the description of TF 2580. For example, the specimen is said to resemble Cynocephalus in having a "...rather deep talonid basin..." (Ducrocq et al., 1992: 374), but later in the same paragraph it is said to differ from Cynocephalus in having a "...shallow talonid basin..." (Ducrocq et al., 1992: 374). The description is also problematic because the authors have misidentified the extant dermopteran taxa they figure. In their figure (Ducrocq et al., 1992: figure 3), figure A is G. variegatus not C. volans, and figure B is C. volans not G. variegatus. This confusion extends to the description of the fossil. For example, the strong paraconid purported to link TF 2580 to extant Sundaic dermopterans is a character of the Philippine kagwang C. volans. Similarly, the size of the fossil is more similar to Cynocephalus, which is the larger of the two extant taxa, and not to Galeopterus as the authors propose. An emended and expanded description of this fossil is much needed.

One might want to ask which of the two extant genera exhibit morphology more similar to the cynocephalid ancestor? To consider the entire craniodental morphology of one genus more primitive or derived than

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the other in general, is entirely too simplistic. Pectinate incisors, serration of the canines and third premolars in Galeopterus and in the deciduous teeth of Cynocephalus, hypertrophied metacone, metaconule, and eocrista, close association of the distal talonid cusps, and the distinct distocuspid all indicate a highly derived cynocephalid ancestor. It is important to remember that this set of initial conditions constrained evolution of the two extant lineages.

Stafford and Szalay (in press) have suggested the following analytical perspective on the phylogeny of the extant dermopterans. Initially it appears that Cynocephalus possesses the more derived suite of characters. For example, the deciduous canine and premolar dentition of Cynocephalus is similar to that of adult Galeopterus. Also, the greater number of incisor tines in Cynocephalus hint at a more derived condition. Although these factors may indeed be derived characters in Cynocephalus, one must consider the functional and adaptive implications of such a premise. For example, the distocuspid may have arisen to maintain occlusal contact between molariform teeth. Thus, it is part of a functional complex that includes the metacone and metaconule and appears to have been mediated by selection rather than happenstance. Although the distocuspid is present in Galeopterus, intermolar contact is minimal or may not occur at all, and this may reflect a derived reduction in tooth size in that genus. Consequently, the relatively large teeth of Cynocephalus that maintain intermolar contact may be nearer to the ancestral cynocephalid condition. Wide intermolar

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interstitial spaces certainly are not the norm among mammals. TF 2580 has intermolar interstitial spaces, but poor preservation of this fossil, and variable distribution of this character in Galeopterus make this character difficult to polarize, especially if TF 2580 postdates the split between the extant genera (highly unlikely).

Reduction in tooth size may not be the only derived condition in the Sundaic form. The unusually small trigonid of Galeopterus may be derived compared to the ancestral condition and may largely explain the large interstitial spaces in this genus. Ectoloph hypertrophy is tied to increased cutting functions and to a triangular and trenchant trigonid, as seen in Cynocephalus. A specific component of this complex is centrocrista hypertrophy that is linked to cristid obliqua and postcristid hypertrophy. Hypoconid size is directly linked to both cristid obliqua development, postcristid development, and to the size of the talonid. I believe the ancestral condition from which the two extant dermopterans are derived was characterized by these adaptations. This would explain the hypertrophied talonid that is still seen in both genera. Therefore, trigonid reduction in Galeopterus appears to be derived. Granted, this makes for a complex evolutionary scenario, but both genera may have derived dental attributes that are reflected in, and correlated with, cranial traits.

The ancestral cynocephalid morphotype both constrained and facilitated subsequent adaptive transformations in the lineages leading to the extant genera. Talonid function, characterized by a hypertrophied paracristid, cristid

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obliqua, postcristid, and ectoloph, may have already been well entrenched in the dermopteran morphotype (predating the cynocephalid one). Perhaps morphology of the molariform teeth of Galeopterus, as suggested by wear patterns, may be explained by a departure from a more shear-oriented molariform dentition similar to that of Cynocephalus. While it appears certain that Cynocephalus is derived compared to Galeopterus in its increased number of incisor tines and canine and third premolar conformations, Galeopterus may have undergone cheek-tooth size reduction and particularly trigonid reduction and a shift toward molar crushing tied to a specific diet. The valid family name for extant dermopterans is Cynocephalidae, not Galeopithecidae. The type genus is Cynocephalus, and the family must therefore take its name from this (ICZN, 1985, Article 35.c), hence Cynocephalidae. Simpson (1945) was correct in that in 1925 the codification of the name Galeopithecus over Cynocephalus provided a clear case for overriding priority in the name of stability (Gardner and Robbins, 1998 give a parallel example regarding fur seals). He was also correct (Simpson, in Opinion 1077, 1977) that this is no longer the case. The Commission rendered a decision on the family name of extant dermopterans in 1977 (Opinion 1077), concluding that Cynocephalidae was the valid name. Galeopithecus has not been widely used since 1945, when Simpson adopted Cynocephalus (Corbet and Hill, 1992; Nowak, 1991; Wilson and Reeder, 1993; Yates, 1984). Consequently, it is not now in the best interest of stability to continue using the names Galeopithecus or Galeopithecidae.

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CHAPTER 5: THE VERTEBRAL COLUMN

The vertebral column of gliding mammals has not been studied, but there has been a large body of work on mammalian vertebral columns in general (Hatt, 1932; Slijper, 1946; Schultz, 1961; Ankle, 1972; Rose, 1975; Gaudin and Biewener, 1992; Long et al., 1997; Shapiro, 1993, 1995; Johnson and Shapiro, 1998). These works provide the context within which to interpret the functional morphology of the dermopterans and other gliding and suspensory mammals.

The vertebral column has often been modeled as a bridge (Thompson, 1917; Gregory, 1937; Slijper, 1946; Figs. 5.1, 5.2) although there has been some disagreement over which type of bridge best models the mammalian vertebral column. There has also been some disagreement over how to best model the vertebral column during locomotion or when the animal is not supported by both limbs (Slijper, 1946). Slijper (1946) specifically argues that bipedal mammals *and bats* can be modeled as beams supported at one end (Fig. 5.3). This analogy also holds true for the cervical vertebrae regardless of orientation, because these vertebrae always support the cranium. Quadrupedal mammals can be modeled as a suspension bridge or as a bow bridge. However, there are problems with these interpretations.

Specifically, the situation regarding dermopterans and sloths may be very different from other mammals, even lorids. These animals are largely under-branch quadrumanous suspensors. Dermopterans do load the spine in cranio-caudal compression when vertically climbing/clinging, and they also load the

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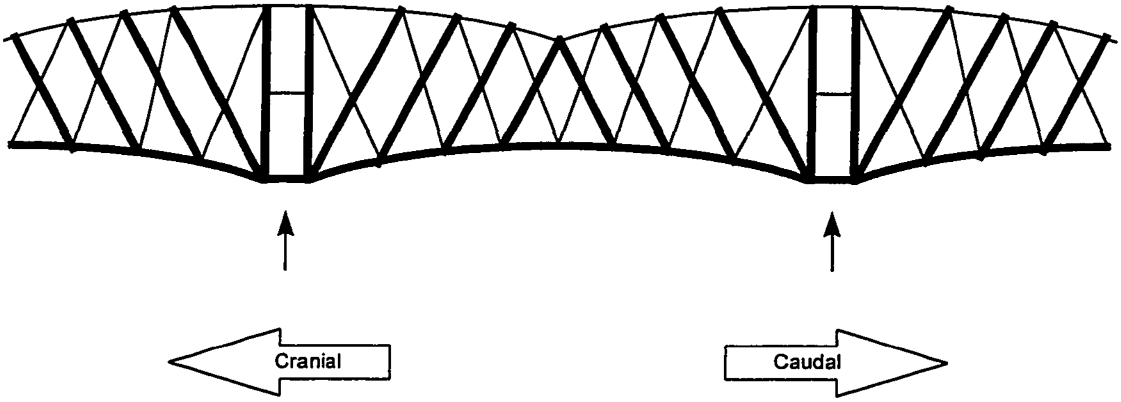

Figure 5.1: Inverted parabolic cantilever bridge. Modified from Thompson (1917, 1942), and Slijper (1946). Solid arrows represent forces acting at the acetabulum and at the gleno-humeral joints when the limbs are loaded in compression (i.e., quadrupedalism, gliding). Thick lines are elements in compression (centra and neural spines), thin lines are in tension (supraspinous ligament and interspinous ligaments).

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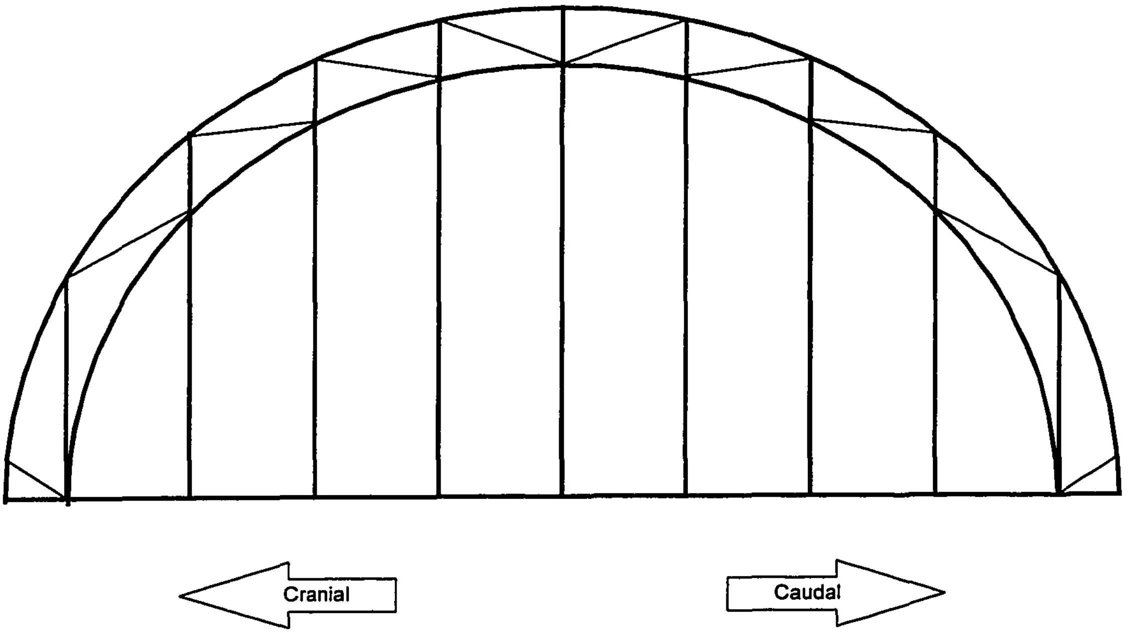

Figure 5.2: Parabolic bowstring bridge. Modified from Slijper (1946).). Thick lines are elements in compression, thin lines are in tension.

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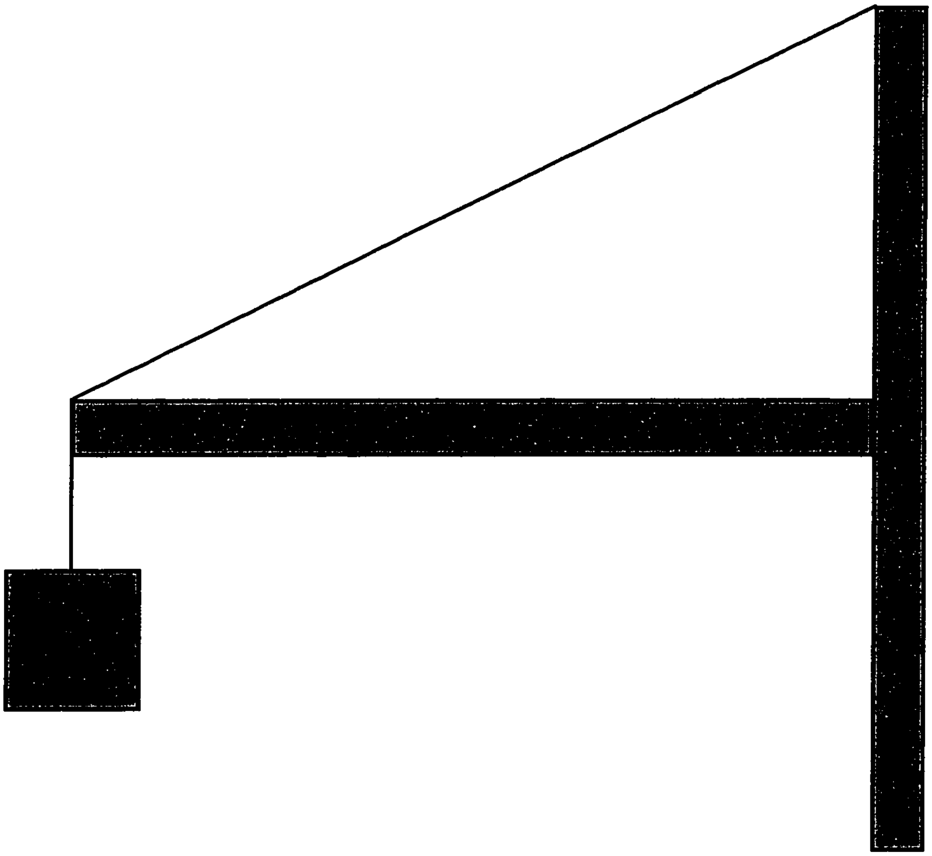

Figure 5.3: Beam supported at one end only and supported by a stretched cord. Modified from Slijper (1946).

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spine with dorsal compression at the gleno-humeral joint and at the acetabulum during gliding. Still, the physical constraints on the vertebral column of largely under-branch suspensory organisms are likely much different from other mammals that typically load the limbs in compression.

SKELETAL TRUNK LENGTH

Throughout this study, skeletal trunk length has been used as a measure of body size. This poses a problem if skeletal trunk length is subjected to different selective pressures among the taxa studied here. Unfortunately, there are few weights associated with the postcranial specimens and this makes it impossible to evaluate the relationship between skeletal trunk length and mass. However, there are many more study skins with associated weights available and these specimens also have head and body weights associated with them. Therefore it is possible to evaluate the relationship between head and body length and mass in the studied taxa, and indirectly evaluate how good of an estimator of body size skeletal trunk length may be. Runestad and Ruff (1995) used cross sectional properties of limb bones to estimate body size in their study of limb proportions. Although they conclude that these measures are reliable indicators of body size, there are problems with the body weights that they use in their study. Also, predominantly suspensory animals may be subject to much different selective and environmental pressures on the limb bones than animals that load these limbs in compression.

Figures 5.4a and 5.4b show the relationships between head and body length and mass in gliding and nongliding taxa. However, least squares regression

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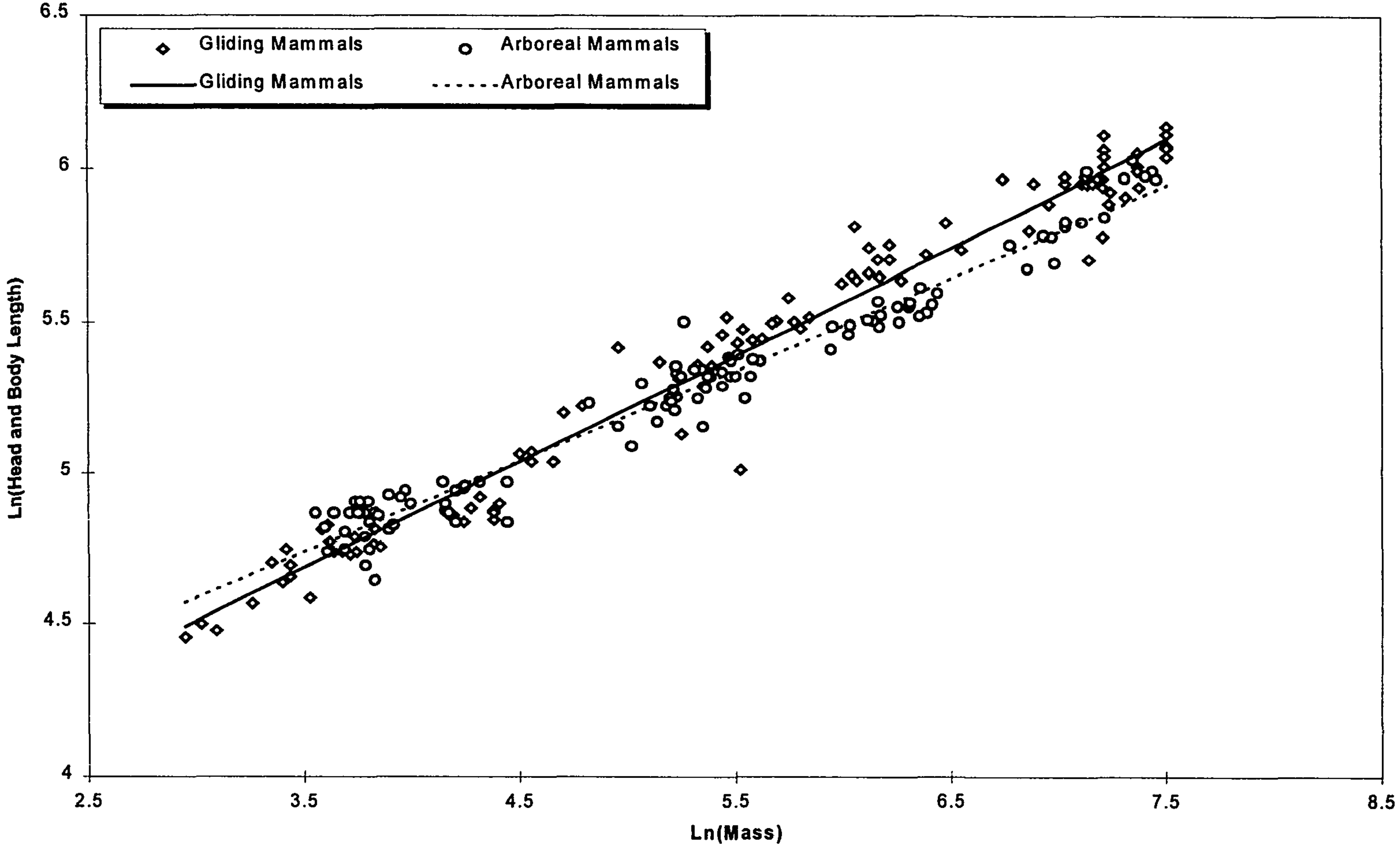

Figure 5.4a: Head and Body Lengths in Some Mammals. Statistics of regression lines are presented in Table 5.1.

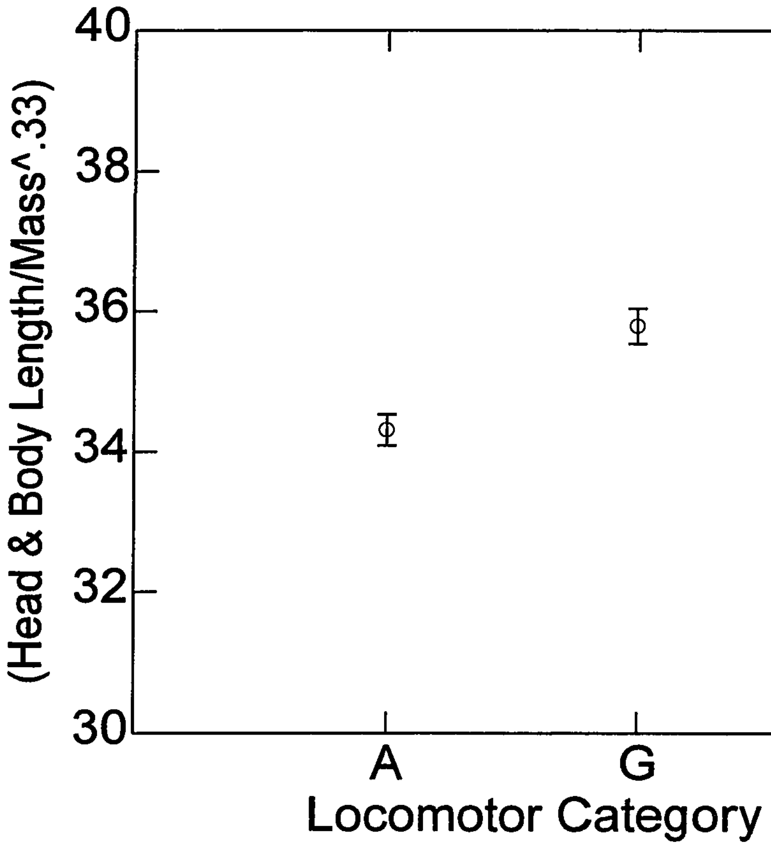

Figure 5.4b: Relative head and body lengths in Some Mammals.

A = Arboreal, G = Gliding taxa.

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Table 5.1: Head and body length statistics. Regression lines are illustrated in Fig. 5.4a.

Least Squares Regression Statistics

		95% Confidence Intervals				
	Y Intercept	Lower	Upper	r-squared	t[1]	P
Arboreal Taxa	3.676	3.617	3.735	0.96	123.706	<0.001
Gliding Taxa	3.455	3.384	3.525	0.97	97.115	<0.001

		95% Confidence Intervals				
	Slope	Lower	Upper	Isometry	F[2]	P
Arboreal Taxa	0.303	0.292	0.314	0.33	12.583	0.001
Gliding Taxa	0.352	0.340	0.364	0.33	24.474	<0.001

Bonferroni Test[3]

	Pairwise Mean Differences			Pairwise Comparison Probabilities	
	Arboreal	Gliding		Arboreal	Gliding
Arboreal	0.000		Arboreal	1.000	
Gliding	2.077	0.000	Gliding	0.003	1.000

---

[1] T-test tests the hypothesis that observed y-intercepts are not significantly different from zero at the $p \leq 0.001$ level. Differences among y-intercepts are considered significantly different when the 95% confidence intervals of the intercept do not overlap.

[2] F-test tests the hypothesis that observed slopes of regression lines are not significantly different from isometry. Slopes are considered significantly different from isometry when $p \leq 0.001$. Differences among slopes are considered significantly different when the 95% confidence intervals of the intercept do not overlap.

[3] ANOVA with Bonferroni's test for pairwise differences was carried out on (head & body length / $\text{mass}^{.33}$). these ratios were considered significantly different when $p \leq 0.001$.

indicates that the slopes of the regression lines for gliding and nongliding taxa are different from each other (Table 5.1). The slopes of these lines are also significantly different from predicted isometry, but are nevertheless quite close to this value. It is possible that the differences in the slopes of the two lines are also affected by the dermopterans to an undue extent. Head and body length includes the cervical vertebrae in its measure, and dermopterans have unusually long necks. When dermopterans are removed from the analysis the results do not change. Gliding mammals are still slightly positively allometric, and nongliding mammals are still slightly negatively allometric Consequently, differences in relative limb proportions, or other indices that incorporate skeletal trunk length, must be cautiously interpreted. However, Given the large differences found in most such indices the slight differences in scaling of skeletal trunk length with respect to mass may be of little importance.

It is also possible that the relatively longer head and body lengths in larger gliding mammals do reflect adaptive differences. Longer head and body lengths may reflect increased cord of the wing and this may be important in maintaining lift over the wing at high angles of attack (see Chapter 11). If this is so, it is difficult to explain why smaller gliders would have relatively shorter head and body lengths, and consequently shorter wing cords, than nongliding taxa of the same body size. Smaller gliders do tend to have higher aspect ratios than larger gliding mammals (Chapter 11) but the differences among gliding mammals in aspect ratios are not great.

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In spite of the factors mentioned above, it appears that head and body length (and by inference skeletal trunk length) are reasonable surrogates for mass in estimating body size of the taxa studied here.

THE CERVICAL REGION

Dermopterans have long necks. Because the propatagium in many flying mammals attaches at the base of the skull, or further rostrally, the relative length of the neck to a large extent determines the cord of the propatagium, and increases the cord of the patagium as a whole. Such expansion of the patagium would serve to increase the surface area of the wing, to decrease aspect ratio, and allow the animal to reach high angles of attack at low speeds (see Chapters 10 & 11). The propatagium is important to any flying mammal because this structure largely determines the flow of the slipstreams over the rest of the wing. It does this because it is the first part of the wing to contact the slipstreams. At low speeds, if the propatagium can be flexed downward (ventrally), this will increase the camber of the wing and producing greater lift. This will reduce stalling speed, although an increase in camber would also produce greater profile drag. At high angles of attack, if the propatagium can be flexed downward, it presents an initial area of low angle of attack to the slipstreams and helps to direct them over the wing, preventing breakaway of the slipstreams, and thereby avoiding stalling. Conversely, at high speeds and low angles of attack if the propatagium can be maintained coplanar with the rest of the patagium it will serve to decrease profile drag and thereby improve glide distance.

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Increasing the cord of the propatagium also increases the chord of the whole wing. This leads to an increase in Reynold's number and also helps to prevent separation of the slipstreams from the wing at high angles of attack. For any one of these reasons one might expect gliding mammals with propatagia that extend onto the cervical region to have longer necks than their nonflying relatives. Flying squirrels have a well defined propatagium (Johnson-Murray, 1977; Thewissen and Babcock, 1993) that extends onto the cranium, and anomalurids also appear to have a well defined propatagium. However, the extent of the propatagium in marsupial gliders is difficult to define. Johnson-Murray (1987, p. 110) notes that "...the propatagium is limited in size..." in marsupials, and describes a different origin for the M. sphincter colli profundus pars patagialis in gliding marsupials. In the gliding marsupials this muscle originates "[f]rom the ventral midline of the neck..." rather than from the "...mid-ventral line ventral to the sternebrae..." as it does in Pseudocheirus and Hemibelideus. However, it is difficult to determine whether or not a distinct propatagium exists in gliding marsupials.

Bats also have an extensive propatagium and interesting and highly specialized necks. However, in bats the propatagium does *not* extend onto the neck or cranium. It only extends to the shoulder, and terminates at the glenohumeral joint. The propatagium may fulfill a different role in bat flight as compared to the role it has in gliding mammals, or it may be controlled differently. Specifically, in bats the propatagium may help to maintain lift and prevent flow separation throughout the widely different angles of attack

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encountered during the wing beat cycle. This may also explain the relatively long first metacarpal in bats (see Chapter 8). Without the ability to control propatagial camber by flexing the neck, they may control it by movement of the pollex. Stafford and Thorington (1998) provide an analysis of the possible role of this feature in bats (see also Chapter 8).

Given the above statements one would expect gliding mammals with a propatagium extending onto the cervical region to have elongate necks compared to their nongliding relatives. One would not necessarily expect bats to have elongate necks because the propatagium only extends to the glenio-humeral joint, and in fact, some authors (Walton and Walton, 1970; Fenton and Crerar, 1984) have noted that bats actually have relatively short necks. If dermopterans are closely related to bats (cladistically or functionally) we might expect to find some of the characters noted for bats by Fenton and Crerar (1984) in dermopterans. Conversely, one would expect dermopterans to have long necks, similar to other gliding mammals with extensive propatagia (i.e., flying squirrels and anomalurids).

Figures 5.5a and 5.5b illustrate the relative neck lengths of the taxa used in this study (Table 5.2). Contra previously published claims (Walton and Walton, 1970; Fenton and Crerar, 1984), bats do not have relatively short necks. They have relatively long necks. The dermopterans also have relatively long necks, as do the three-toed sloths. The bats and the dermopterans have elongated their necks through an elongation of all the component vertebrae. Bradypus, however, has increased the number of vertebrae to nine, and increased the

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Table 5.2: Bonferroni pairwise comparison probabilities for relative neck length[1]

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1. *Acrobates*	1																				
2. *Anomalurus*		1																			
3. *Bradypus*	***	***	1																		
4. *Choloepus*			***	1																	
5. *Cyclopes*			***		1																
6. *Cynocephalus*	***	***		***	***	1															
7. *Galeopterus*	***	***		***	***		1														
8. *Glaucomys*			***			***	***	1													
9. *Hemibelideus*			***			***	***		1												
10. *Hylopetes*			***			***	***			1											
11. *Iomys*			***			***	***				1										
12. Loridae			***			***	***					1									
13. Megachiroptera	***	***	**	***	***		***	***	***	***	***	***	1								
14. Microchiroptera	***	***		***	***			***	***	***	***	***		1							
15. *Petaurista*			***			***	***						***	***	1						
16. *Petauroides*			***			***	***						***	***		1					
17. *Petaurus*			***			***	***						***	***			1				
18. *Pseudocheirus*			***			***	***						***	***				1			
19. *Sciurus*			***			***	***						***	***	*				1		
20. *Trogopterus*			***			***	***						***	***						1	
21. *Tupaia*			***			***	***						***	***							1

---

[1] *, $p \leq 0.01$; **, $p \leq 0.001$; ***, $p \leq 0.0005$

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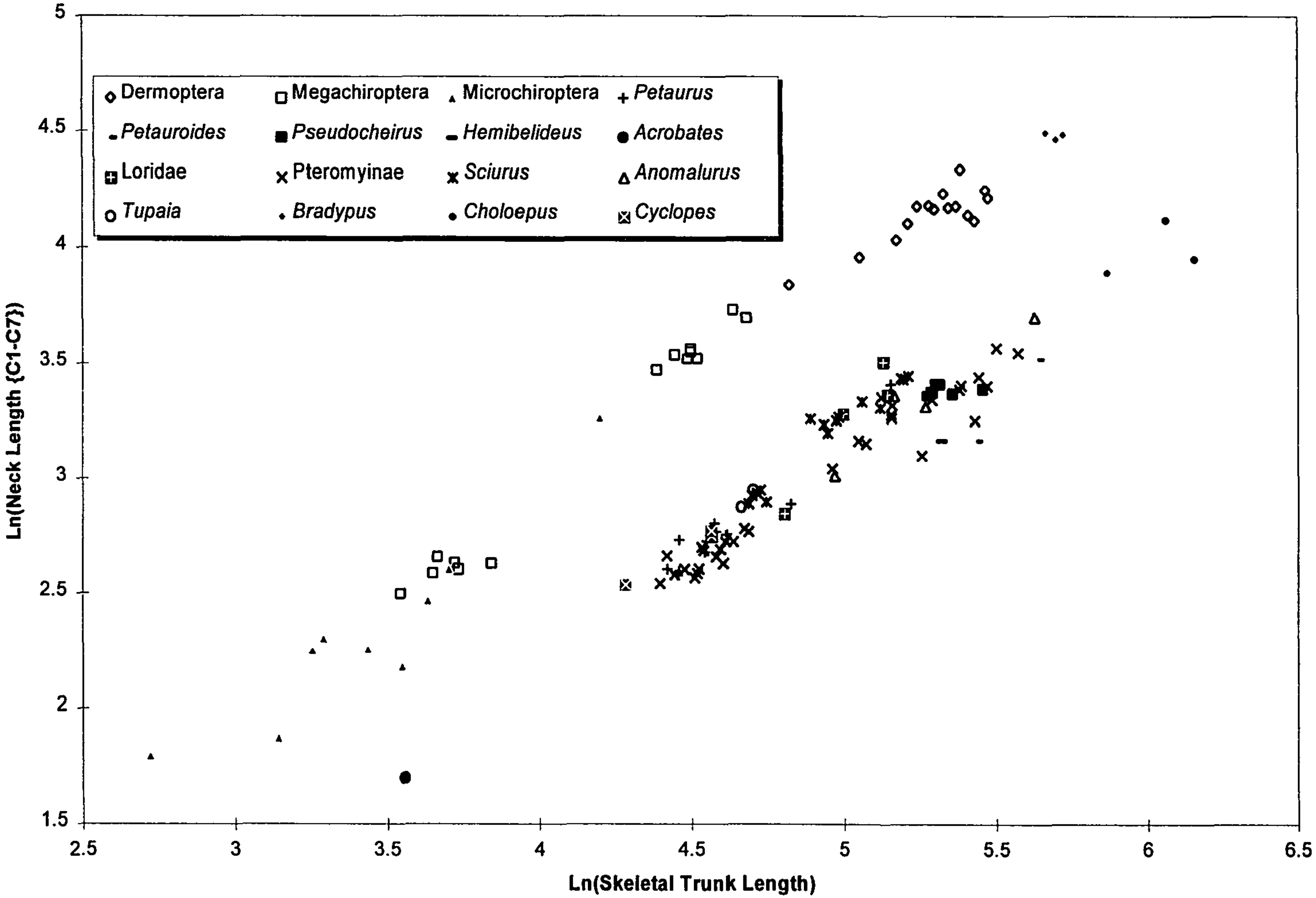

Figure 5.5a: Neck length in some mammals.

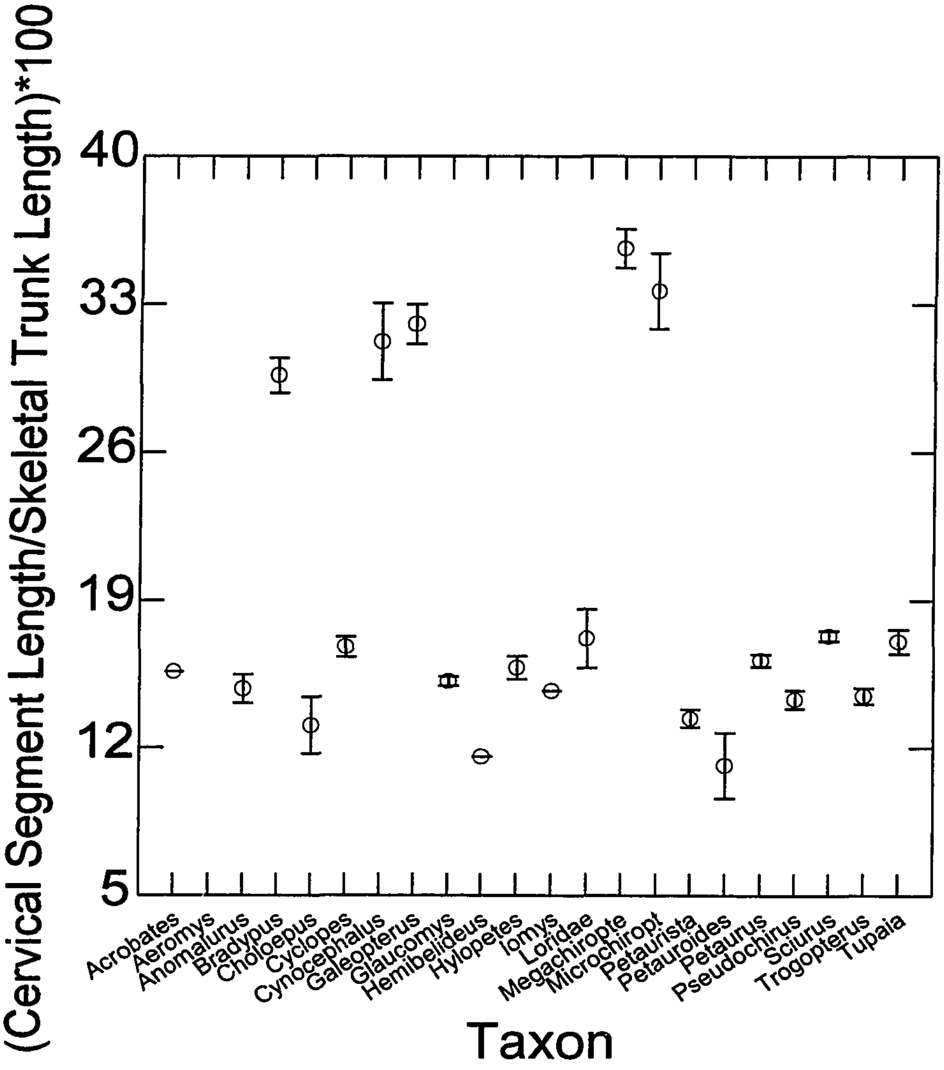

Figure 5.5b: Relative neck length in some mammals. Error bars equal one standard error of the mean.

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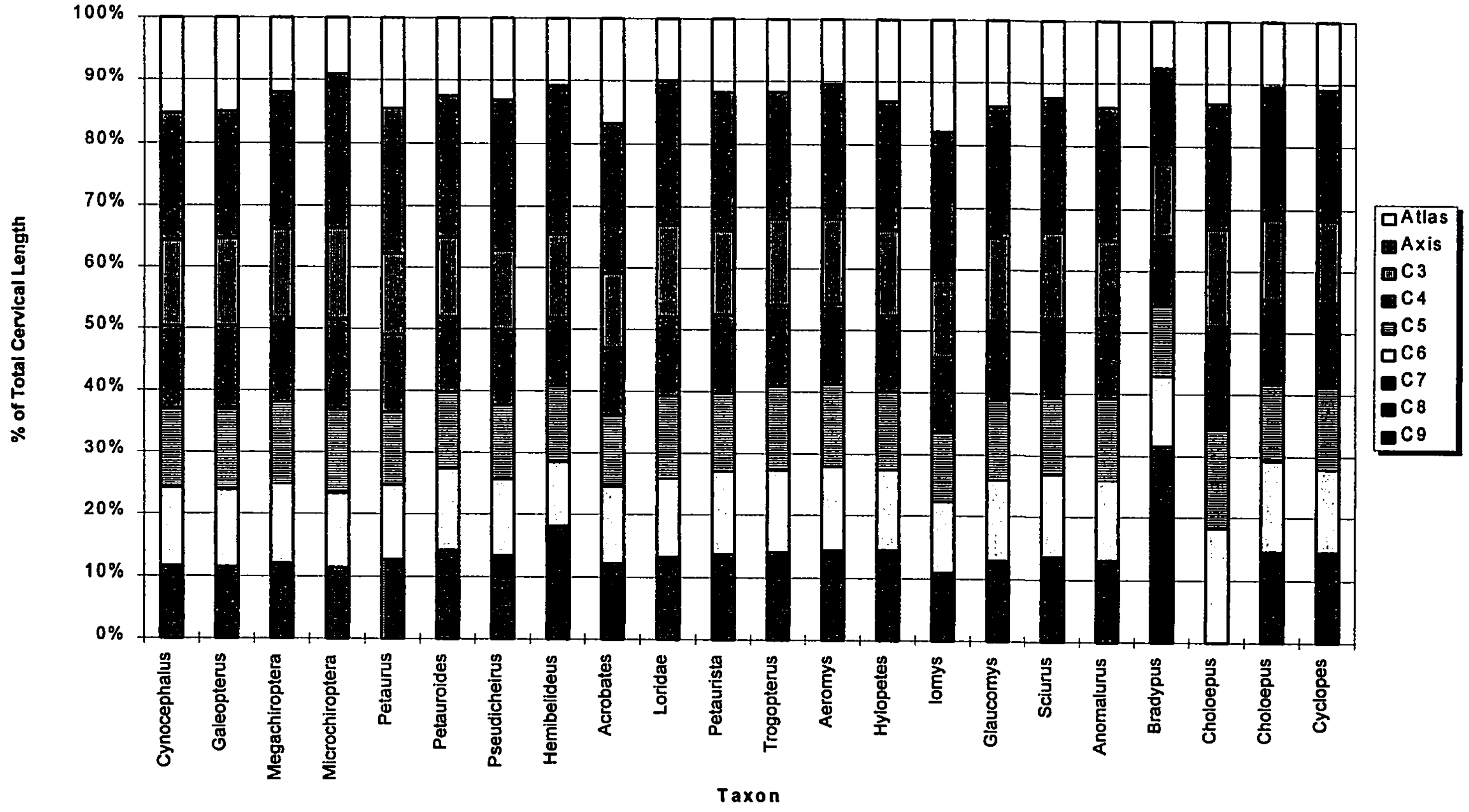

Figure 5.6: Cervical vertebrae length in some mammals. Note that the relative lengths of individual vertebrae are not as different among taxa as one might expect based on differences in relative neck length.

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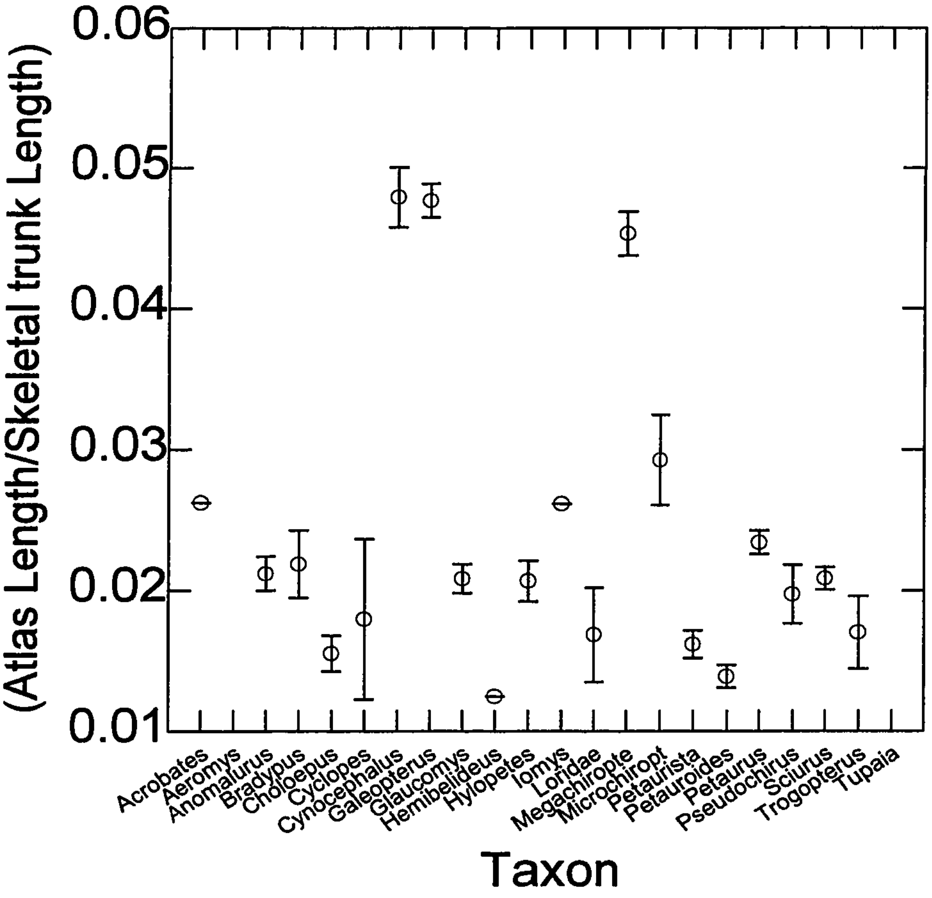

Figure 5.7a: Relative Atlas Length in Some Mammals. Error bars equal one standard error of the mean.

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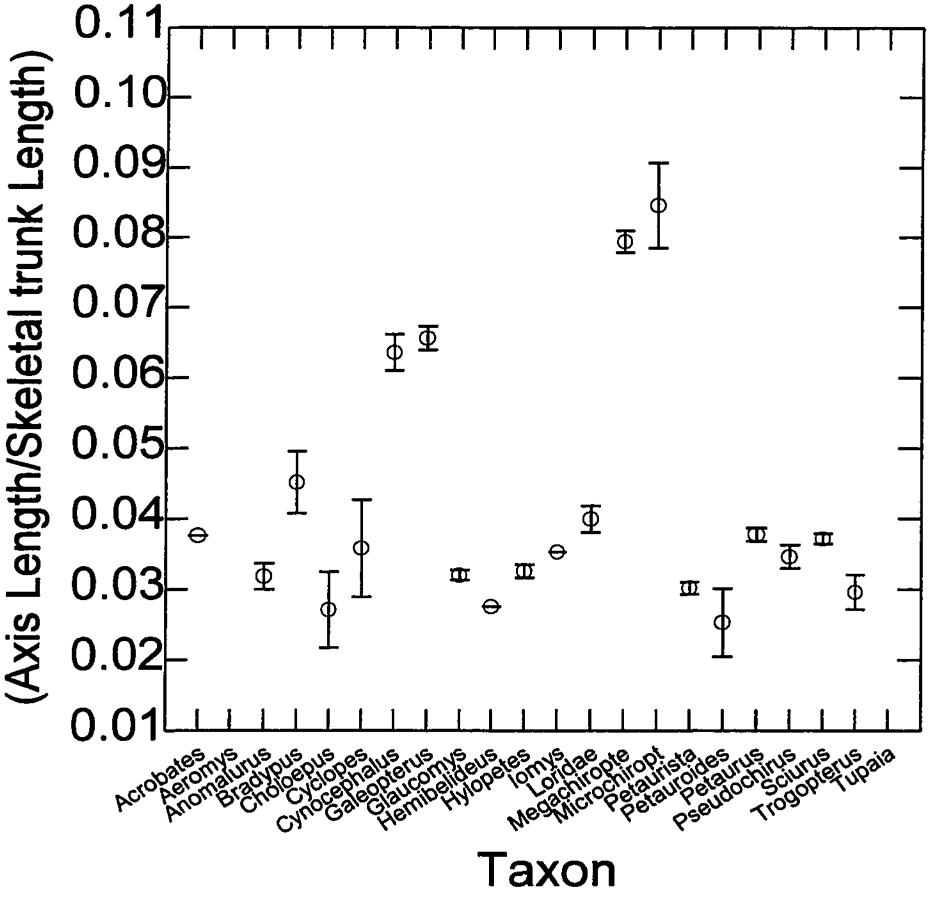

Figure 5.7b: Relative Axis Length in Some Mammals. Error bars equal one standard error of the mean.

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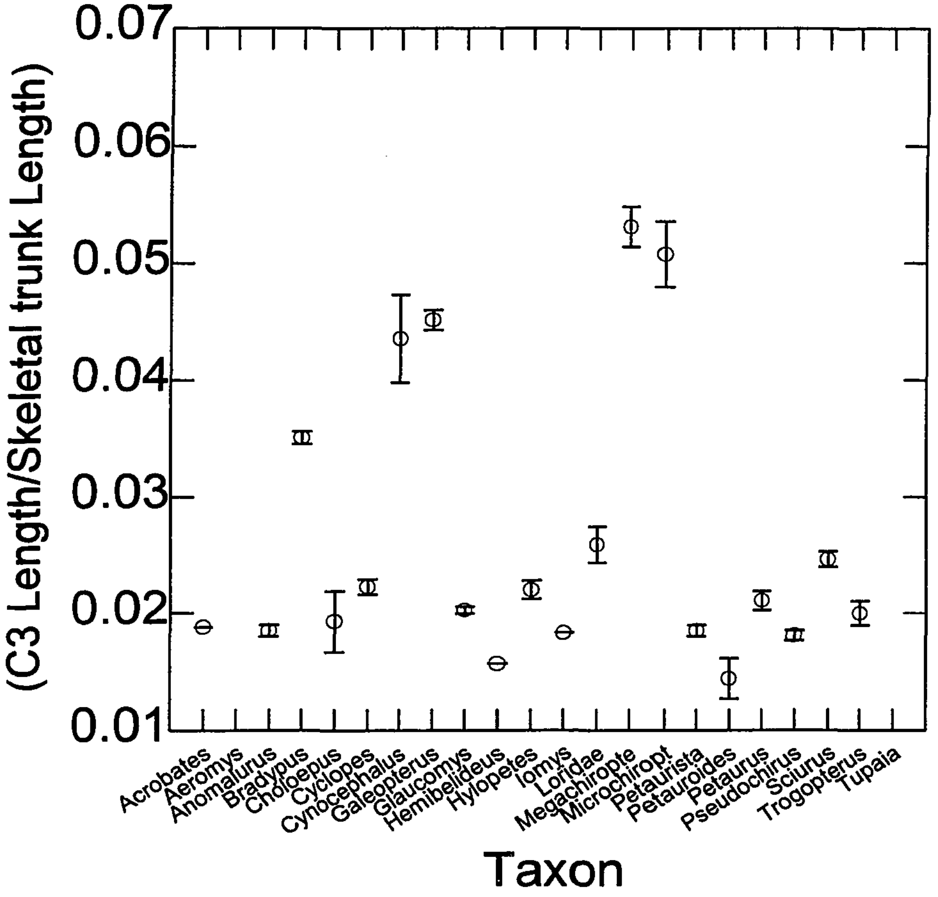

Figure 5.7c: Relative C3 Length in Some Mammals. Error bars equal one standard error of the mean.

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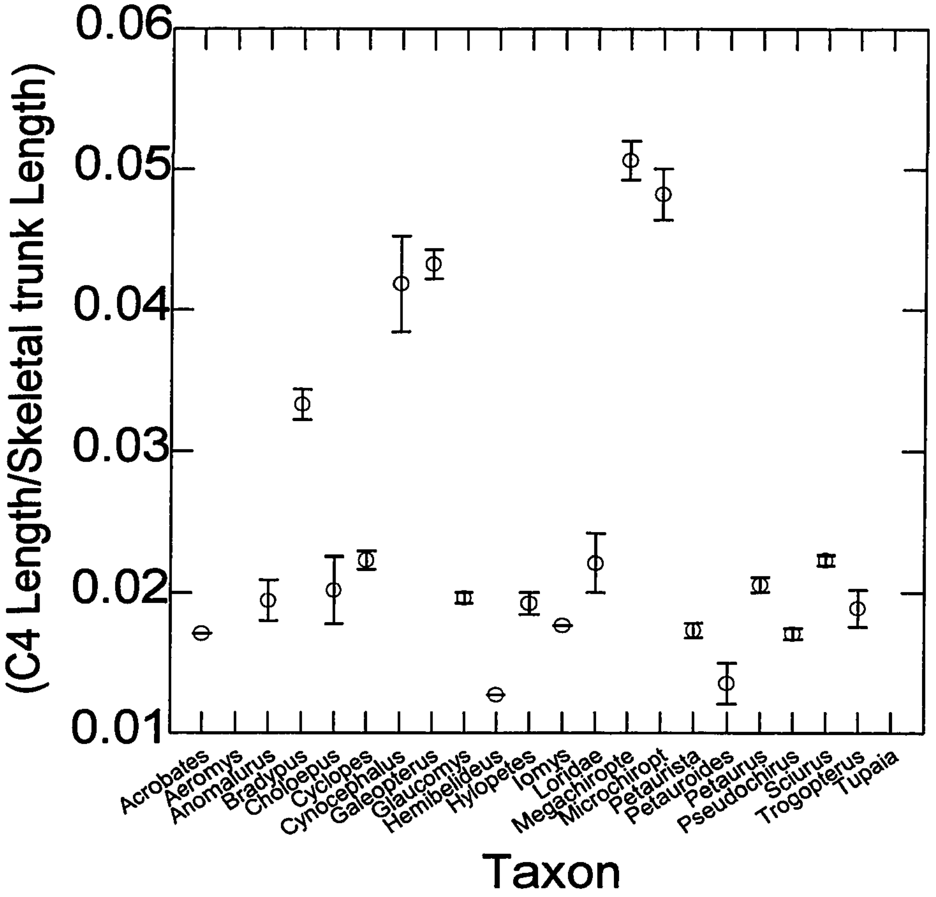

Figure 5.7d: Relative C4 Length in Some Mammals. Error bars equal one standard error of the mean.

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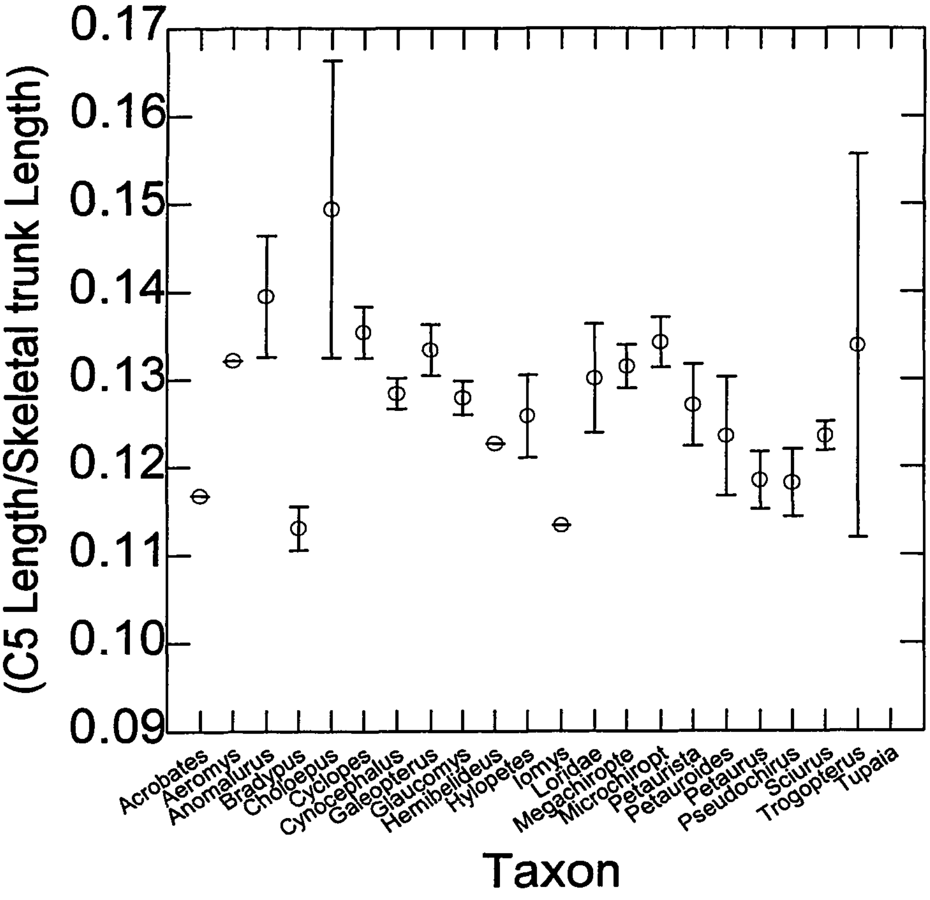

Figure 5.7e: Relative C5 Length in Some Mammals. Error bars equal one standard error of the mean.

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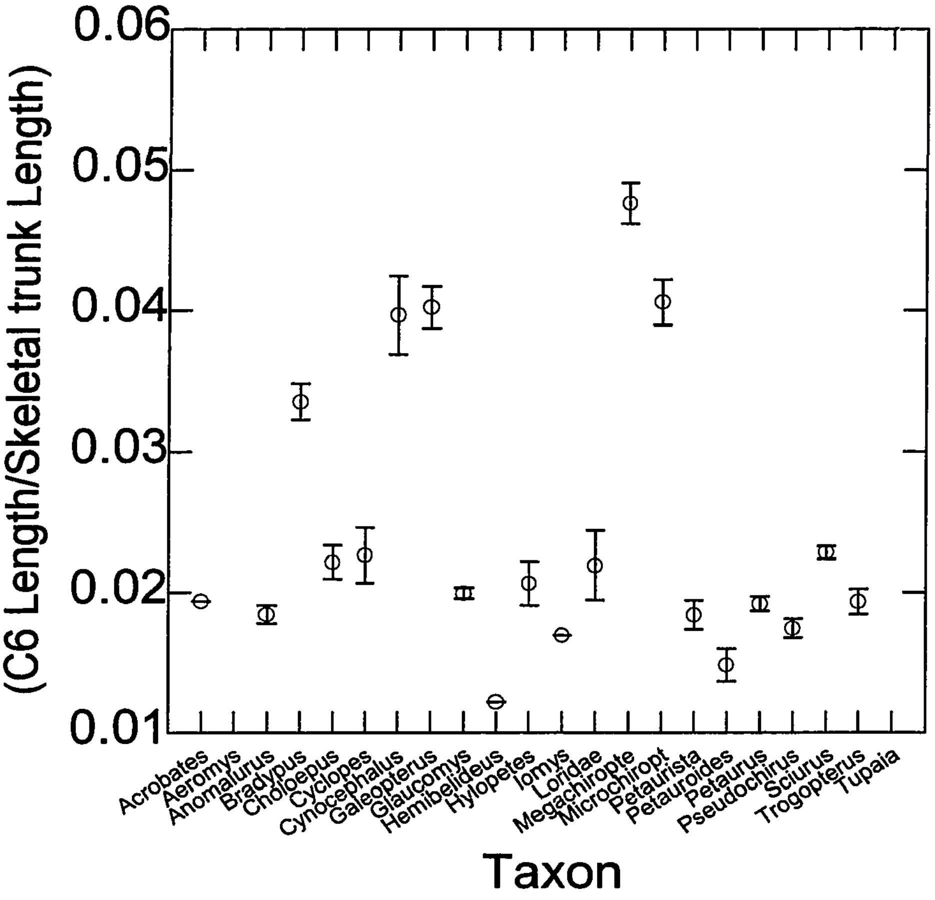

Figure 5.7f: Relative C6 Length in Some Mammals. Error bars equal one standard error of the mean.

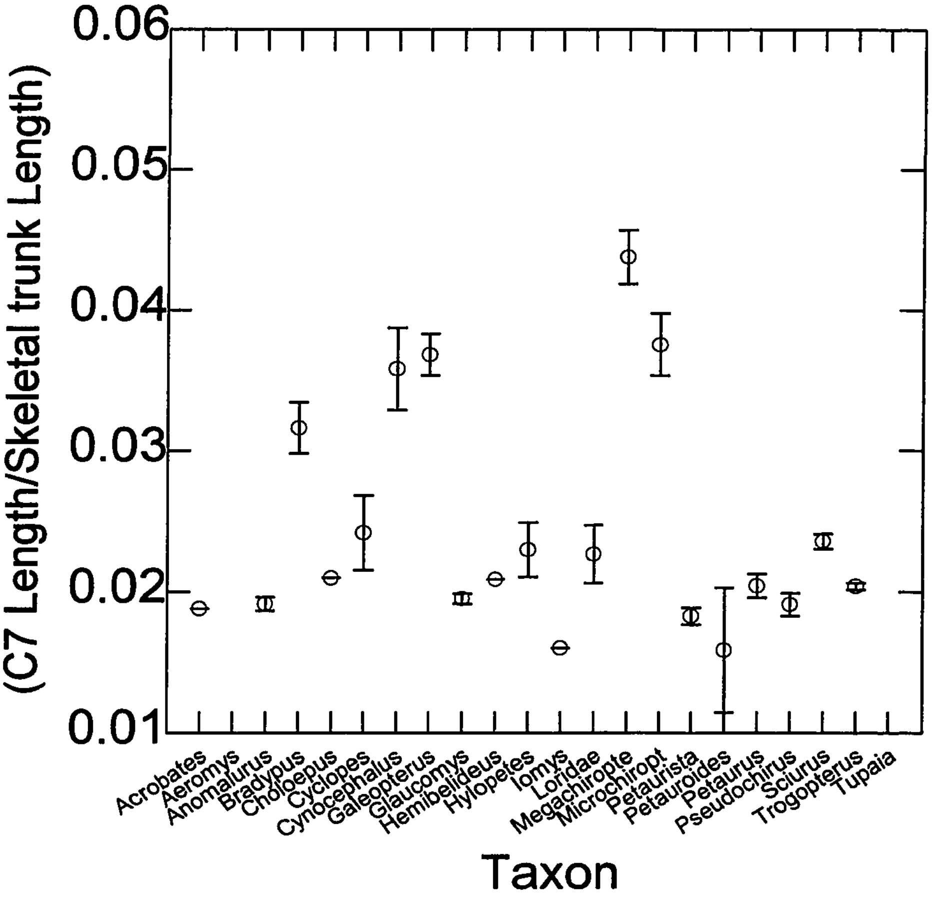

Figure 5.7g: Relative C7 Length in Some Mammals. Error bars equal one standard error of the mean.

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Table 5.3: Bonferroni pairwise comparison probabilities for relative length of cervical vertebrae[1]

Atlas

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1. Acrobates	1																			
2. Anomalurus		1																		
3. Bradypus			1																	
4. Choloepus				1																
5. Cyclopes					1															
6. Cynocephalus		***	***	***	***	1														
7. Galeopterus	**	***	***	***	***		1													
8. Glaucomys						***	***	1												
9. Hemibelideus						***	***		1											
10. Hylopetes						***	***			1										
11. Iomys											1									
12. Loridae						***	***					1								
13. Megachiroptera		***	***	***	***			***	***	***		***	1							
14. Microchiroptera						***	***						***	1						
15. Petaurista						***	***						***	***	1					
16. Petauroides						***	***						***			1				
17. Petaurus						***	***						***				1			
18. Pseudocheirus						***	***						***					1		
19. Sciurus						***	***						***						1	
20. Trogopterus						***	***						***							1

Axis

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1. Acrobates	1																			
2. Anomalurus		1																		

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3. Bradypus			1																	
4. Choloepus				1																
5. Cyclopes					1															
6. Cynocephalus		***		***	***	1														
7. Galeopterus	*	***	***	***	***		1													
8. Glaucomys						***	***	1												
9. Hemibelideus						***	***		1											
10. Hylopetes						***	***			1										
11. Iomys							**				1									
12. Loridae						***	***					1								
13. Megachiroptera	***	***	***	***	***	*	***	***	***	***	***	***	1							
14. Microchiroptera	***	***	***	***	***	***	***	***	***	***	***	***		1						
15. Petaurista						***	***						***	***	1					
16. Petauroides						***	***						***	***		1				
17. Petaurus						***	***						***	***			1			
18. Pseudocheirus						***	***						***	***				1		
19. Sciurus						***	***						***	***					1	
20. Trogopterus						***	***						***	***						1

C3

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1. Acrobates	1																			
2. Anomalurus		1																		
3. Bradypus		***	1																	
4. Choloepus			***	1																
5. Cyclopes					1															
6. Cynocephalus		***		***	***	1														
7. Galeopterus	***	***		***	***		1													
8. Glaucomys			***			***	***	1												

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9. Hemibelideus			*			***	***		1											
10. Hylopetes			*			***	***			1										
11. Iomys						***	***				1									
12. Loridae						***	***					1								
13. Megachiroptera	***	***	***	***	***	*	***	***	***	***	***	***	1							
14. Microchiroptera	***	***	***	***	***			***	***	***	***	***		1						
15. Petaurista			***			***	***						***	***	1					
16. Petauroides			***			***	***						***	***		1				
17. Petaurus			***			***	***						***	***			1			
18. Pseudocheirus			***			***	***						***	***				1		
19. Sciurus			*			***	***						***	***					1	
20. Trogopterus			*			***	***						***	***						1

C4

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1. Acrobates	1																			
2. Anomalurus		1																		
3. Bradypus	*	***	1																	
4. Choloepus			***	1																
5. Cyclopes			*		1															
6. Cynocephalus	***	***		***	***	1														
7. Galeopterus	***	***	*	***	***		1													
8. Glaucomys			***			***	***	1												
9. Hemibelideus			***			***	***		1											
10. Hylopetes			***			***	***			1										
11. Iomys			*			***	***				1									
12. Loridae			*			***	***					1								
13. Megachiroptera	***	***	***	***	***	**	***	***	***	***	***	***	1							
14. Microchiroptera	***	***	***	***	***			***	***	***	***	***		1						

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15. Petaurista			***			***	***						***	***	1					
16. Petauroides			***			***	***						***	***		1				
17. Petaurus			***			***	***						***	***			1			
18. Pseudocheirus			***			***	***						***	***				1		
19. Sciurus			***			***	***						***	***					1	
20. Trogopterus			***			***	***						***	***						1

									C5											
Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1. Acrobates	1																			
2. Anomalurus		1																		
3. Bradypus	*	***	1																	
4. Choloepus			***	1																
5. Cyclopes			*		1															
6. Cynocephalus	***	***		***	***	1														
7. Galeopterus	***	***	*	***	***		1													
8. Glaucomys			***			***	***	1												
9. Hemibelideus			***			***	***		1											
10. Hylopetes			***			***	***			1										
11. Iomys			*			***	***				1									
12. Loridae			*			***	***					1								
13. Megachiroptera	***	***	***	***	***	*	***	***	***	***	***	***	1							
14. Microchiroptera	***	***	***	***	***			***	***	***	***	***		1						
15. Petaurista			***			***	***						***	***	1					
16. Petauroides			***			***	***						***	***		1				
17. Petaurus			***			***	***						***	***			1			
18. Pseudocheirus			***			***	***						***	***				1		
19. Sciurus			***			***	***						***	***					1	
20. Trogopterus			***			***	***						***	***						1

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C6

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1. Acrobates	1																			
2. Anomalurus		1																		
3. Bradypus		***	1																	
4. Choloepus			*	1																
5. Cyclopes					1															
6. Cynocephalus	***	***		***	***	1														
7. Galeopterus	***	***		***	***		1													
8. Glaucomys			***			***	***	1												
9. Hemibelideus			***			***	***		1											
10. Hylopetes			***			***	***			1										
11. Iomys			*			***	***				1									
12. Loridae			*			***	***					1								
13. Megachiroptera	***	***	***	***	***	*	***	***	***	***	***	***	1							
14. Microchiroptera	***	***		***	***			***	***	***	***	***	***	1						
15. Petaurista			***			***	***						***	***	1					
16. Petauroides			***			***	***						***	***		1				
17. Petaurus			***			***	***						***	***			1			
18. Pseudocheirus			***			***	***						***	***				1		
19. Sciurus			***			***	***						***	***					1	
20. Trogopterus			*			***	***						***	***						1

C7

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1. Acrobates	1																			
2. Anomalurus		1																		

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3. Bradypus		*	1																	
4. Choloepus				1																
5. Cyclopes					1															
6. Cynocephalus		***				1														
7. Galeopterus	*	***			**		1													
8. Glaucomys			**			***	***	1												
9. Hemibelideus									1											
10. Hylopetes						*	***			1										
11. Iomys						*	*				1									
12. Loridae						*	***					1								
13. Megachiroptera	***	***	**	***	***		*	***	***	***	***	***	1							
14. Microchiroptera	*	***			***			***		***	***	***		1						
15. Petaurista			*			***	***						***	***	1					
16. Petauroides			*			***	***						***	***		1				
17. Petaurus			*			***	***						***	***			1			
18. Pseudocheirus			*			***	***						***	***				1		
19. Sciurus						***	***						***	***					1	
20. Trogopterus						*	***						***	***						1

---

[1] *, $p \le 0.01$; **, $p \le 0.001$; ***, $p \le 0.0005$

lengths of vertebrae 3 through nine. Figure 5.6 shows that although bats and dermopterans do have long necks, the individual vertebrae maintain the typical mammalian proportions with respect to each other. However, all of the vertebrae, with the exception of C5, are elongated in Dermoptera, Chiroptera, and Bradypus.

Relative atlas and axis length also separates the volitantians from all other mammals Figs. 5.7a,b, Table 5.3). Bats and dermopterans both have relatively long atlases compared to other mammals. What is surprising is that Bradypus does not have a long atlas or axis and falls among the other mammals. The relative lengths of these components in Choloepus is actually slightly lower than all other mammals. With regard to C3 length (Fig. 5.7c) we see a similar pattern to what we seen for cervical length. The volitantians and Bradypus fall well above all other mammals, the lorids are slightly above all other mammals here, but so are Sciurus. This pattern generally holds for C4-C7 as well (Figs. 5.7d-g).

Fenton and Crerar (1984) have illustrated other differences in the cervical vertebrae between megachiropterans and microchiropterans as well. They hypothesize that these differences relate to the ability flex the head either dorsally or ventrally. They correlate these differences with roosting postures in mega- and microchiropterans. Megachiropterans typically roost in exposed locations suspended from the hindlimbs with the wings folded around themselves, and with the head ventrally flexed against the chest (Fig. 5.8). Such a posture is very similar to the roosting posture used by colugos (Fig. 5.9) and to the defensive posture used by lorids (Fig. 5.10). Conversely the

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microchiropterans roost generally in more protected sites and typically suspend with the head flexed dorsally against the back (Fig. 5.11). Fenton and Crerar (1984) found the following difference between megachiropteran and microchiropteran necks;

1. the neural arches in megachiropterans were thicker superio-inferiorly than in microchiropterans,
2. microchiropterans lack neural spines on all but the second cervical vertebrae,
3. the articulations of the centra in microchiropterans are angled relative to the plane of the spinal chord,
4. that microchiropterans possess a ventral locking mechanism on the cervical vertebrae,
5. and that in megachiropterans the articulations between anterior and posterior zygapophyses are parallel to the axis of the vertebrae in the dorsal plane. In microchiropterans these articulations are angled with respect to the dorsal plane.

Fenton and Crerar (1984) propose that these characters allow the microbats to dorsiflex their necks to a greater degree than megachiropterans. Unfortunately, their functional analysis is very limited and how some of these characters affect dorsiflexion of the neck is unclear.

<u>Thickness</u> <u>of</u> <u>neural</u> <u>arches</u>.—Bats, dermopterans, <u>Bradypus</u>, and anomalurids generally have thicker neural arches on the cervical vertebrae than

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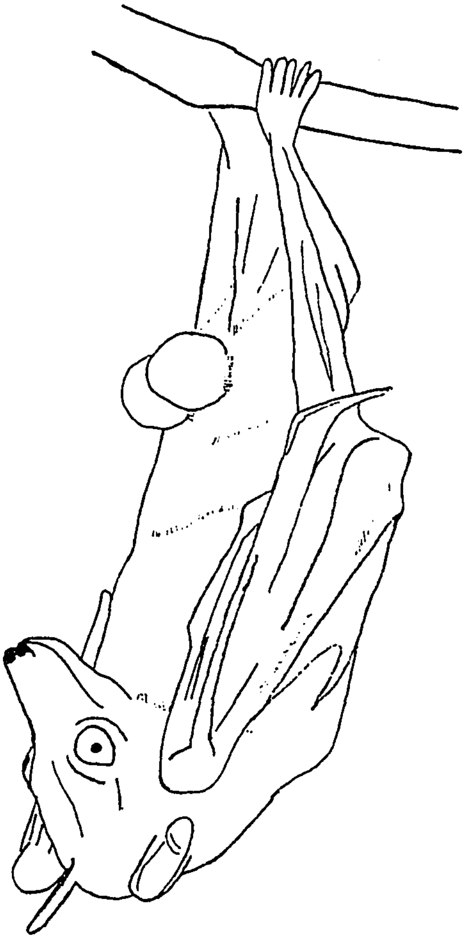

Figure 5.8: Straw-colored fruit bat, Ediolon helvum, in typical roosting posture (modified from Wilson, 1997)

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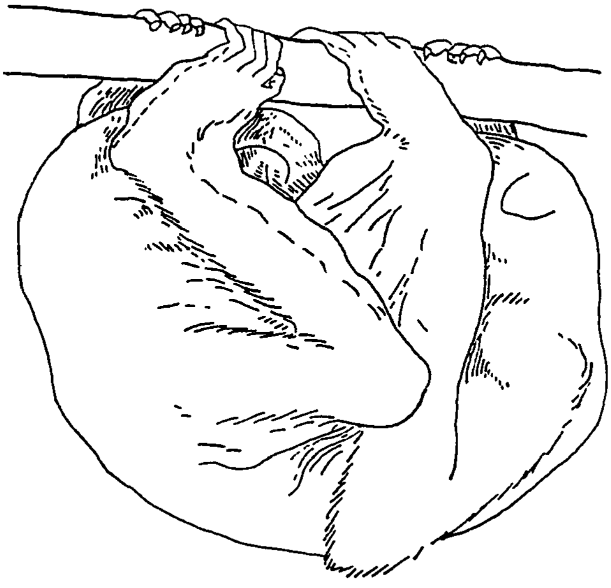

Figure 5.9: Dermopteran in typical roosting posture (redrawn from Pocock, 1926).

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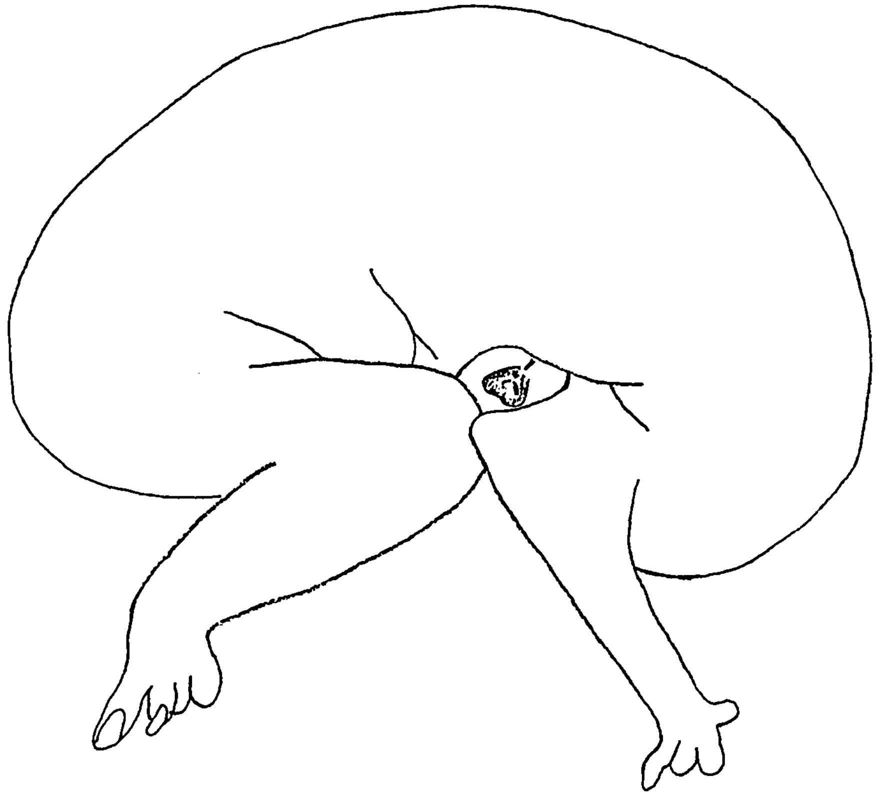

Figure 5.10: <u>Arctocebus</u> in typical defensive posture (redrawn from Charles-Dominique, 1977). The nose is visible under the right armpit.

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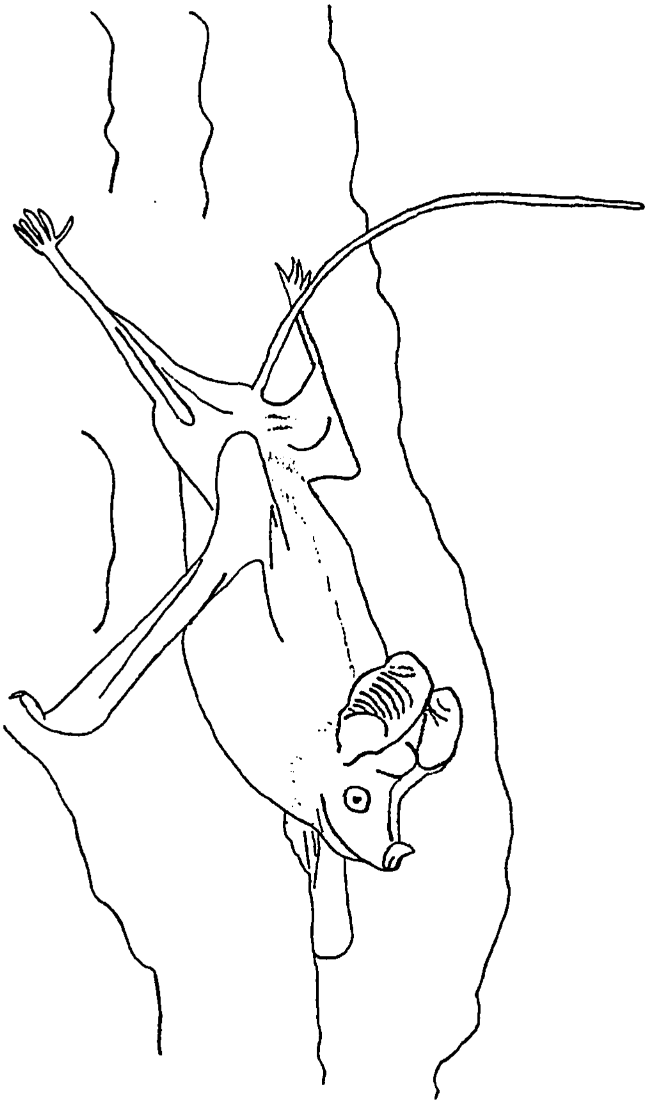

Figure 5.11: Hardwicke's mouse-tailed bat, Rhinopoma hardwickei, in typical roosting posture (redrawn from Wilson, 1997)

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most other mammals. As with most chiropteran characters, this one is highly variable among genera and families. The microchiropterans generally have relatively thinner neural arches then either the Megachiroptera or the dermopterans, but in many cases they are still relatively thicker than the neural arches of many other mammals. The degree of thickness of the neural arch is variable within the megachiropterans as well, and some megachiropterans (i.e., Rousettus) have relatively thinner neural arches than some microchiropterans (i.e., Macroderma). Further, other taxa (tree shrews, sciurids) have neural arches that are relatively thin and also very similar to those of many bats.

Fenton and Crerar (1984) believe that the thinner neural arches of microchiropterans allow them to more fully dorsiflex their necks. There appear to be certain problems with this interpretation. First, dorsiflexion of the cranium largely occurs at the atlanto-occipital and in some taxa at the atlanto-axial joints, not at the cervical intervertebral joints. Second, the cranio-caudal distance between superior and inferior zygapophyses would also have an effect here. Since this distance appears to be closely related to centrum length and not neural arch length, the lengths of individual vertebrae may be a better determinant of C3-C7 mobility. Shorter segments would be able to circumscribe a tighter radius of curvature for any given angle of movement between vertebrae than taxa with relatively longer segments. Although the neural arches may act as stops to dorsiflexion of the neck it seems that the morphology of the intervertebral articular facets may provide a more reliable predictor of neck flexion abilities (see below). Consequently, there is no evidence based on neural

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arch thickness supporting the hypothesis that microchiropterans have relatively greater abilities to dorsiflex the neck compared to megachiropterans.

Neural spines.—Dermopterans have a small neural crest on the atlas, an extremely well developed crest on the axis, and distinct neural spines on C3-C7 (Table 5.4). The development of the neural spine on the axis is very similar in size and shape to that seen in the megachiropterans and in the anomalurids. Megachiropterans may have neural spines or crests on vertebrae C2 and C7. No megachiropteran had a distinct neural spine or crest on the atlas. The degree of neural spine development on C3-C6 is variable in megachiropterans although most lack a definite spine on C6. However, C6 may have a slight neural crest. All microchiropterans have a neural spine on the axis. No neural spines were observed on the atlas or C3-C7 in any microchiropteran.

Of the marsupials studied here Acrobates, Petaurus and Hemibelideus have neural spines only on the axis. Pseudocheirus and Petauroides have a large spine on the axis and a smaller spines on C3-C7. The spine on C7 is very small and may be absent. Among the rodents, Sciurus have spines on the axis and may also have a spine on C7.

The pteromyines show the same condition except that the spines are not as robust. Anomalurids have neural spines or crests on vertebrae C2, C6, and C7. No anomalurid had a distinct neural spine on the atlas. The degree of neural spine development on C3-C5 is variable but usually these vertebrae possess only a slight neural crest. Tupaia is very similar to the anomalurids. The xenarthrans examined here all have nerual spines on all of the cervical

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Table 5.4: Neural spine or crest development in the cervical vertebrae.

Taxon	Locomotion[1]	Atlas[2]	Axis	C3	C4	C5	C6	C7
Acrobates	AQ, G		☯					
Hemibelideus	AQ		☯					
Petauroides	AQ, G		☯	☯	☯	☯	☯	⌖
Petaurus	AQ, G		☯					
Pseudocheirus	AQ		☯	☯	☯	☯	☯	⌖
Xenarthra	SU, SC		☯	☯	☯	☯	☯	☯
Anomaluridae	AQ, G		☯	⌖	⌖	⌖	☯	☯
Pteromyinae	AQ, G		☯					⌖
Sciurus	AQ		☯					⌖
Tupaia	AQ		☯	⌖	⌖	⌖	☯	☯
Loridae	SC		☯	☯	☯	☯	☯	☯
Megachiroptera	F, Su		☯	⌖	⌖	⌖	⌖	☯
Microchiroptera	F, Su		☯					
Dermoptera	Su, G	☯	☯	☯	☯	☯	☯	☯

☯ Well developed neural crest or spine always present.

⌖ Neural crest or spine may be present or absent and show a variable degree of development.

vertebrae except for the atlas. In the lorids all taxa have neural spines on C2-C7, but in Loris these spines are reduced.

The ubiquitous presence of a neural spine on the axis in all of the taxa studied is likely due to the insertions of the suboccipital muscles here (M. rectus capitis dorsalis major, M. rectus capitis dorsalis minor, M. obliquis capitis caudalis). These muscles dorsiflex the cranium and rotate the atlanto-occipital joint. Neural spines on C3-C6, however, may be related to providing attachments for M. rhomboides pars cervicalis, M. splenius capitis, M. splenius cervicis, M. trapezius, M. spinalis cervicis, and Mm. interspinales.

The first four of these muscles originate from the median fibrous raphe of the neck. This raphe is in turn connected to the spinous processes via the Ligamentum nuchae. The splenius muscles are involved with dorsiflexion of the cranium while the trapezius and rhomboides are associated with movements of the scapula. Those taxa with spinous processes on all cervical vertebrae may possess more robust musculature, or the lever arms for these muscles may have been increased. Unfortunately, the distribution of this character among the taxa studied here makes interpretation of the role of this character difficult. In the gliding taxa it is easy to postulate that the presence of these spines allows for greater dorsiflexion of the cranium and also for greater dorsiflexion of the scapula. In the first case, dorsiflexion of the cranium could have a role in orienting the eyes to the flight path as opposed to the branch that the animal is walking on. The flight path may be directly along the long axis of the body while an arboreal substrate is often ventral to this midline. Similarly, a more dorsally

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oriented orientation for the rhomboides and trapezius may be important in orienting the patagium in gliding position, especially with respect to maintaining a positive dihedral (see Chapter 11). However, given the distribution of these characters it is equally plausible to ascribe to them some role in suspensory or slow climbing locomotion.

M. spinalis cervicis, and Mm. interspinales are associated with the dorsiflexion of the caudalmost cervical vertebrae. This may explain the absence of spinous processes on C6 and C7 in microchiropterans. Some microchiropterans have fused the last cervical and first thoracic vertebrae together. Again functional and biorole interpretations of these characters are difficult at best.

Plane of articulation between centra.—In microchiropterans the plane of the intercentra articulations is generally angled with respect to the transverse plane. The articular surface of the centra is more cranial dorsally, and it slopes caudally ventrally (Fenton and Crerar, 1984). This condition is largely due to the caudal extension of the ventral portion of the centra. In many microchiropterans this elongation is so marked that it takes the form of a distinct process. Such is the case in Otomops martensseni but this species also has keeling occurring along the ventral cervical vertebrae that is associated with these processes.

Again, as most characters among microchiropteran families, this character is highly variable (Table 5.5). Although most microchiropterans have a caudally projecting ventral process on the cervical centra (some are bilobate, and some are not), the majority of the intercentra articulation is generally horizontal. Most microchiropterans also have a slight caudal projection of the intercentra articular

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surface dorsally. This provides them with a saddle-shaped dorsal articular surface, but this is not uncommon among mammals. In many taxa the ventral processes project so far caudally the vertebra are distinctly “T” or “Y” shaped in ventral view, while others are more conservative in their shape. In megachiropterans there is only a very slight, if any, angulation of the intercentra articular surfaces from the transverse plane, and these articulations are definitely not saddle shaped.

However, in dermopterans the plane of the intercentra articulations is markedly angled with respect to the transverse plane, as much as in some microchiropterans, but there is no saddle shaping of this joint. The articular surface of the centra is more cranial dorsally, and it slopes caudally as it moves ventrally.

The plane of articulation between centra in the other mammals studied here was either highly angled with respect to the dorsal plane (i.e., Bradypus,), only moderately angled (i.e., C2-C4 in Sciurus) or coplanar with it (i.e., Petaurus, Pseudocheirus, Hemibelideus, Petauroides, Anomalurus, Glaucomys, Cyclopes). In none of these other taxa is the plane of the centra as highly angled as in some microchiropterans, but some taxa closely approximate the condition seen in the dermopterans and megachiropterans, and many do have saddle shaped articular surfaces.

Ventral interlocking of adjacent centra.—Most Microchiroptera possess a caudal process projecting from the ventral aspect of vertebrae C2-C7 which

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Table 5.5: Summary of intervertebral articulations in the cervical vertebrae of some mammals.

Taxon	Neural Arch	Intercentra Articulation	Ventral Process	Zygapophyseal Articulation
Acrobates	Thin	Transverse & Flat	No	Dorsal & Vertical
Hemibelideus	Thin	Transverse & Flat	No	Dorsal & Vertical
Petauroides	Thin	Transverse & Flat	No	Dorsal & Vertical
Petaurus	Thin	Transverse & Flat	No	Dorsal & Vertical
Pseudocheirus	Thin	Transverse & Flat	No	Dorsal & Vertical
Xenarthra	Thick	Transverse & Flat[1]	No[2]	Dorsal & Vertical
Anomaluridae	Thin	Transverse & Flat	No	Subdorsal & Vertical
Pteromyinae	Thin	Transverse & Flat	No	Dorsal & Vertical
Sciurus	Thin	Transverse & Flat	No	Dorsal & Vertical
Tupaia	Variable[3]	Transverse & Flat	No	Dorsal & Vertical
Loridae	Thick[4]	Transverse & Flat	No	Subdorsal[5] & Vertical
Megachiroptera	Variable	Transverse & Flat	No	Dorsal & Vertical
Microchiroptera	Variable	Angled & Saddle-shaped	Variable Shapes	Variable
Dermoptera	Thick	Angled & Flat	Bilobate	Dorsal & Vertical

---

[1] Bradypus has angled articulations.

[2] Bradypus ventral processes that may appear slightly bilobate.

[3] Within individuals C2-C4 show interarch contact, while C4-C7 do not.

[4] Loris has thin neural arches.

articulates with a facet on the cranial aspect of the centra of the vertebrae below it. This character is highly variable within the Microchiroptera, being extensively developed in some families (i.e., Otomops) and completely absent in others (i.e., Artibeus). Dermopterans also possess moderately developed, bilobate processes that project caudally from the ventral aspect of vertebrae C2-C5. These processes articulate with facets on the ventral aspect of the centra of the next lower vertebrae. Bradypus also have a notable ventral processes that projects caudally from the centra. Megachiropterans do not have any caudally projecting ventral processes. The distinctness of this character is problematic because it is very likely correlated with the patterns of intercentra articulation described above. However, while the saddle shaped articular surface of microchiropterans coupled with ventrally projecting processes may correlate with cervical flexion, in the other mammals that posses this feature, it may be linked with cervical stability.

Articulation of anterior and posterior zygapophyses.—In megachiropterans the articulations between anterior and posterior zygapophyses are parallel to the axis of the vertebrae in the dorsal (i.e., coronal) plane while in microchiropterans these articulations are angled with respect to the dorsal plane, tilted either dorsally or ventrally (Fenton and Crerar, 1984). Fenton and Crerar (1984) propose that these characters allow the microbats to dorsiflex their necks to a greater degree than megachiropterans, and are related to roosting posture.

Again, this can be said to be generally true of bats, but the high degree of variability in this character (as noted by Fenton and Crerar, 1984) in

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microchiropterans makes this character difficult to interpret. These authors note that "This particular feature was variable within the Microchiroptera; the shallowest angle observed here was in the molossid, *Otomops martiensseni*. However, the anterior zygapophyses in this taxon are not shallow at all. In fact, they are in the transverse plane, perpendicular to the long axis of the spinal column. However, a cross sectional survey of microchiropteran does support the conclusions of these authors that some microchiropterans approach the megachiropteran condition.

Dermopterans show a condition very similar to that of the megabats, with the zygapophyses in the dorsal plane and not largely angled from the vertical. In some megachiropterans, however, the orientation of the zygapophyses is more nearly in the sagittal plane than in the dorsal plane. This condition is also seen in *Tupaia*. However, vertically oriented zygapophyses that are largely in the dorsal plane are common in mammals. They are also found In *Pseudocheirus*, *Hemibelideus*, *Petauroides*, *Petaurus*, *Cyclopes*, and *Sciurus*. The zygapophyses of *Glaucomys*, *Acrobates*, *Peromyscus*, *Cavia*, and *Bradypus* appear to be more angled in relation to the dorsal plane than other nonchiropteran mammals, and in some cases are very similar to the microchiropteran condition. In many of these taxa however, the angular orientation of the zygapophyses from the vertical increases as one moves caudally down the cervical segment. It is also important to note that in this sample, zygapophyseal angulation appears correlated with neural arch

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thickness. Taxa with relatively thick neural arches seem to have zygapophyseal articulations that are very vertical and largely in the dorsal plane.

Again, the taxonomic distribution of this character makes it difficult to evaluate (Table 5.5). There is no information available detailing which microchiropterans habitually dorsiflex the neck and which do not. However, Sciurus do habitually dorsiflex the neck yet their zygapophyses are in the dorsal plane and very vertical. Their neural arches are also quite thin. However, Glaucomys have angled zygapophyses and thin neural arches. Likewise, gliding mammals may or may not have vertically oriented zygapophyses.

THE THORACIC REGION

Dermopterans do not have a relatively elongate thoracic region of the vertebral column (Fig. 5.12, Table 5.6) compared to most other mammals. This is surprising because they do have relatively broad ribs (Wyss, 1983 and references therein), although not nearly as broad as some bats, xenarthrans, or primates. It is the bats and some xenarthrans that have relatively long thoracic columns. Among the other mammals studied here, there are no consistent correlations of thoracic column length. The dermopterans, lorids, and Petaurus are at the upper range of all other mammals, but so are Tupaia and Pseudocheirus. The pteromyines and Anomalurus fall along the lower end of the distribution. Sciurus is intermediate with respect to length of the thoracic segment of the vertebral column. The elongation of the thoracic segment in chiropterans and xenarthrans may related to the extremely high loading of this area during powered flight and digging respectively. These activities may not at

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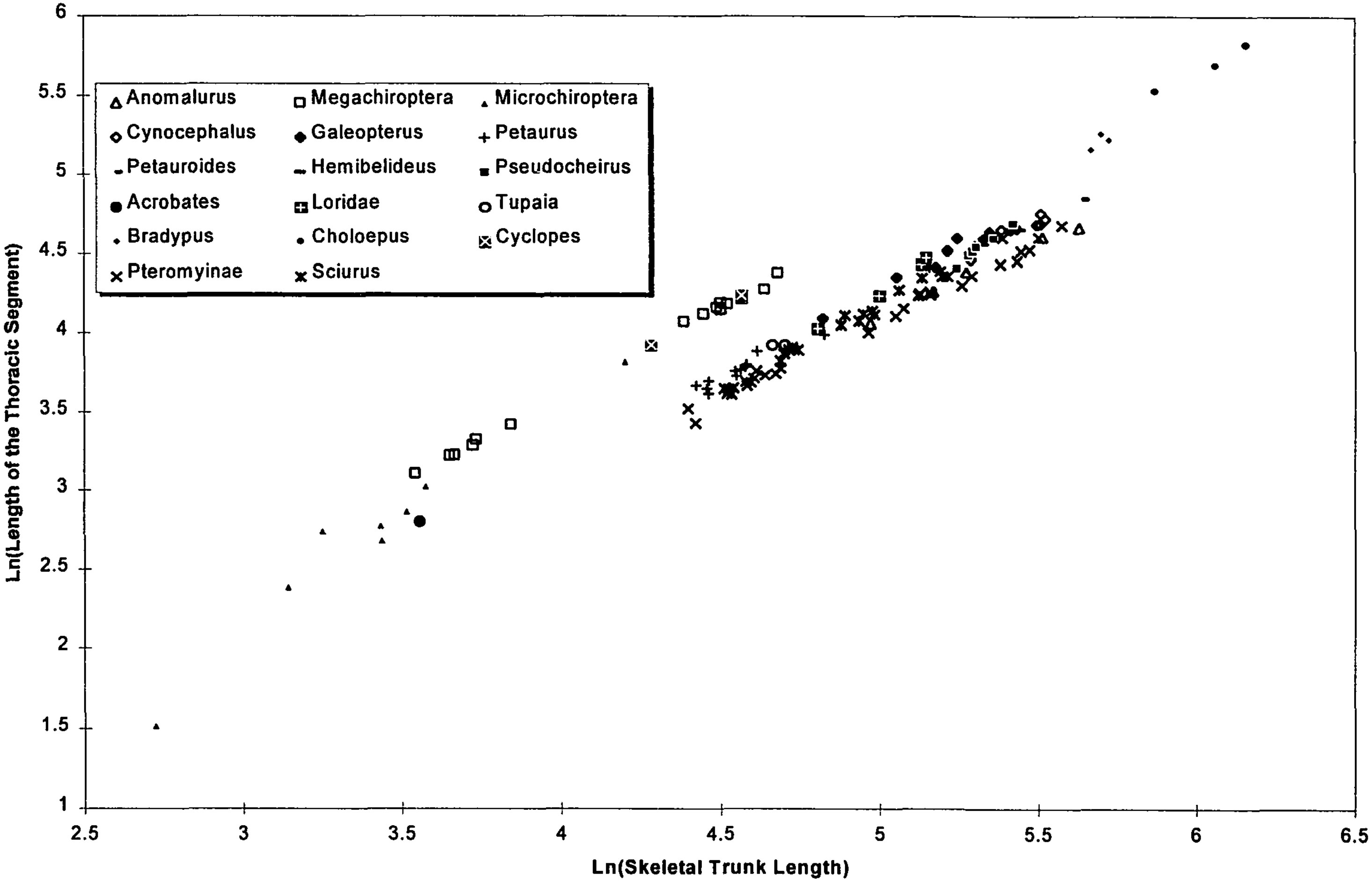

Figure 5.12a: Length of the thoracic segment of the vertebral column in some mammals.

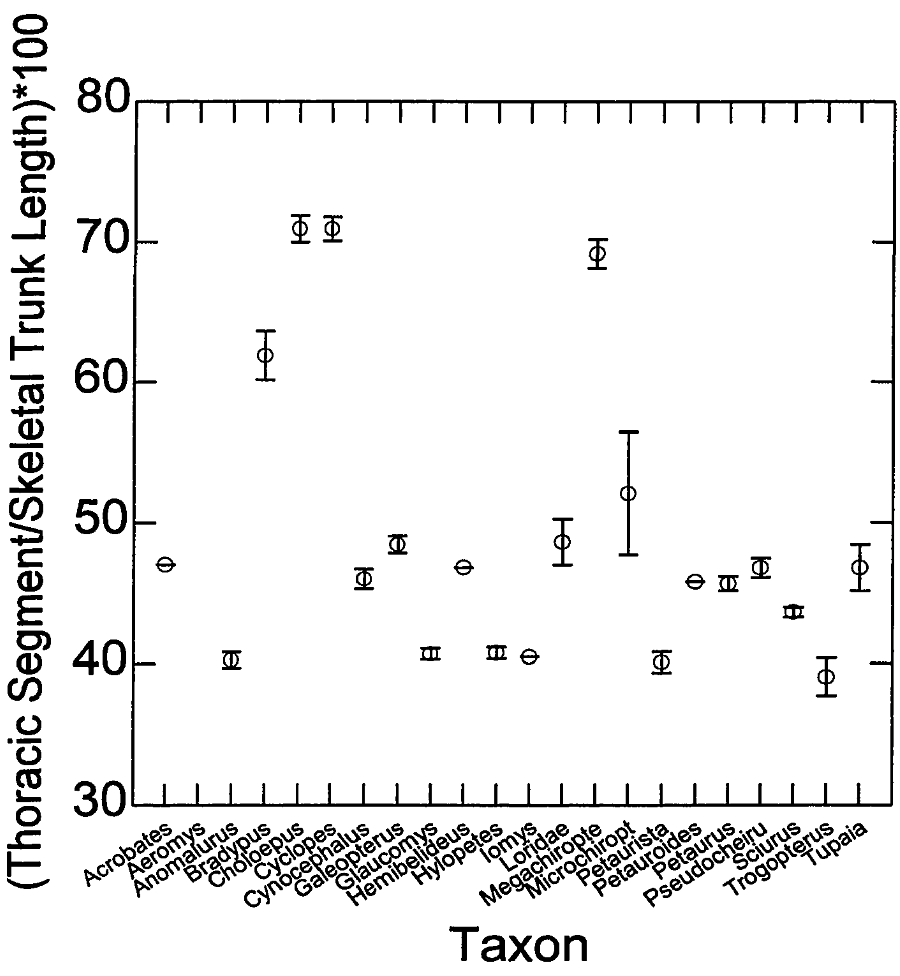

Figure 5.12b: Relative length of the thoracic portion of the vertebral column in some mammals. Error bars equal one standard error of the mean.

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first seem all that similar to produce such strikingly convergent morphologies, but the added rigidity that the longer thoracic segment would provide these taxa may be particularly important as the forelimbs are ventrally adducted. Such movements occur during the down-stroke of the chiropteran wing and may also occur (with a more caudally directed component) during digging by xenarthrans.

Jenkins (1970) provides a detailed description of the functional morphology of expanded ribs in Primates and Xenarthra. His conclusions are equally applicable to the Chiroptera and Dermoptera. He finds that expanded ribs correlate with robust intercostal muscles. This is somewhat counterintuitive because when the ribs are thinner, stronger muscles would be required to maintain the rigidity of the thoracic segment of the vertebral column. Expanded or imbricating ribs enhance the rigidity of the thoracic column on their own, and Jenkins suggests that the association of expanded ribs with well developed intercostal musculature reflects "...a mechanical adaptation to withstand unusual stresses." (Jenkins, 1970 p. 296). Jenkins ascribes these characters to the fossorial habits of the xenarthrans, but also discusses the locomotor implications of these characters with respect to lorids. Bates (1863), Van Tyne (1929), Reynolds (1931), Enders (1935), and von Hagen (1939) have all noted that Cyclopes extend the body horizontally from a vertical support, supported only by the hindlimbs and the prehensile tail (i.e. cantilevering). Lorids have been noted to use similar positional behaviors (Ishida et al., 1992; Preuschoft et al., 1995).

Suspensory locomotion

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Table 5.6: Bonferroni pairwise comparison probabilities for relative lengths of vertebral segments[1]

	Thoracic																				
Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1. Acrobates	1																				
2. Anomalurus		1																			
3. Bradypus	***		1																		
4. Choloepus	***	***		1																	
5. Cyclopes	***	***			1																
6. Cynocephalus			***	***	***	1															
7. Galeopterus		***	***	***	***		1														
8. Glaucomys			***	***	***	*	***	1													
9. Hemibelideus			***	***	***				1												
10. Hylopetes			***	***	***		***			1											
11. Iomys			***	***	***						1										
12. Loridae			***	***	***							1									
13. Megachiroptera	***	***				***	***	***	*	***	***	***	1								
14. Microchiroptera		***	***	***	***			***		***			***	1							
15. Petaurista			***	***	***	***	***					***	***	***	1						
16. Petauroides			***	***	***								***			1					
17. Petaurus			***	***	***		***						***	***			1				
18. Pseudocheirus			***	***	***								***	*	**			1			
19. Sciurus			***	***	***		***						***	***					1		
20. Trogopterus			***	***	***		**						***	***						1	
21 Tupaia			***	***	***								***								1

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									Lumbar												
Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1. <u>Acrobates</u>	1																				
2. <u>Anomalurus</u>		1																			
3. <u>Bradypus</u>		***	1																		
4. <u>Choloepus</u>	***	***		1																	
5. <u>Cyclopes</u>	***	***			1																
6. <u>Cynocephalus</u>			***	***	***	1															
7. <u>Galeopterus</u>		*	***	***	***		1														
8. <u>Glaucomys</u>			***	***	***		***	1													
9. <u>Hemibelideus</u>				***	***				1												
10. <u>Hylopetes</u>			***	***	***					1											
11. <u>Iomys</u>			***	***	***						1										
12. Loridae			**	***	***							1									
13. Megachiroptera	***	***				***	***	***	***	***	***	***	1								
14. Microchiroptera		***		***	***					***			***	1							
15. <u>Petaurista</u>			***	***	***								***	***	1						
16. <u>Petauroides</u>			***	***	***								***			1					
17. <u>Petaurus</u>			***	***	***								***				1				
18. <u>Pseudocheirus</u>			***	***	***								***					1			
19. <u>Sciurus</u>			***	***	***								***	***					1		
20. <u>Trogopterus</u>			***	***	***								***	*						1	
21 <u>Tupaia</u>			**	***	***								***								1

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	Sacral																				
Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1. <u>Acrobates</u>	1																				
2. <u>Anomalurus</u>		1																			
3. <u>Bradypus</u>	***	**	1																		
4. <u>Choloepus</u>	***	***		1																	
5. <u>Cyclopes</u>	***	***			1																
6. <u>Cynocephalus</u>			***	***	***	1															
7. <u>Galeopterus</u>		***	***	***	***		1														
8. <u>Glaucomys</u>			***	***	***	*	***	1													
9. <u>Hemibelideus</u>			***	***	***				1												
10. <u>Hylopetes</u>			***	***	***		***			1											
11. <u>Iomys</u>			***	***	***						1										
12. Loridae			***	***	***							1									
13. Megachiroptera	*	***				***	***	***	***		***	***	1								
14. Microchiroptera		***	***	***	***			***		***			***	1							
15. <u>Petaurista</u>			***	***	***	***	***					***	***	***	1						
16. <u>Petauroides</u>			***	***	***								***			1					
17. <u>Petaurus</u>			***	***	***		***						***	***			1				
18. <u>Pseudocheirus</u>			***	***	***								***	*	**			1			
19. <u>Sciurus</u>			***	***	***		***						***	***					1		
20. <u>Trogopterus</u>			***	***	***		**						***	***						1	
21 <u>Tupaia</u>			***	***	***								***								1

---

[1] *, $p \leq 0.01$; **, $p \leq 0.001$; ***, $p \leq 0.0005$

in the dermopterans could also explain the expanded ribs in these animals, although they have never been reported to use cantilevered postures.

In all of the mammals studied here the plane of articulation between thoracic central is strictly transverse. Thoracic spinous process morphology, however, is incredibly diverse (Slijper, 1946). Dermopterans have spinous processes on all thoracic vertebrae. These processes are not particularly tall, and they are very blade like. They extend the entire length if the neural arch and are never higher than long. They closely resemble the neural spines of some megachiropterans, but the morphology of dermopteran neural spines is very consistent from one vertebrae to the next. Interestingly, the neural spines of dermopterans also rise almost perpendicular to the long axis of the vertebral column. This is contrary to the biomechanical models of Thompson (1917), Gregory (1937) and Slijper (1946) that model the spinous processes as load bearing elements. In these models the neural spines converge near the thoraco-lumbar junction as a consequence of the loads to which they are subjected. That dermopterans do not show this anticliny may indicate that they are subject to different functional constraints. A comparison with other gliding and suspensory mammals may shed some light on this situation.

Spinous process morphology is also highly variable among chiropterans. Many chiropterans have bifurcating spinous processes on the thoracic vertebrae, but the spinous processes are usually very low and shield like, and in the dorsal rather than in the sagittal plane. However, many taxa that have this type of spinous process may also have thoracic spinous processes closely resembling

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those of dermopterans in the thoracic segment as well. Some chiropteran taxa, however, have no discernible spinous processes on the thoracic vertebrae at all.

Cyclopes, Bradypus, and Choloepus also have relatively low spinous processes. However, in none of these taxa are the spinous processes oriented as vertically as in the dermopterans. In all the xenarthran taxa studied the thoracic spinous processes are distinctly caudally orientated. Also, in both Bradypus and Cyclopes the height of the spinous processes decreases caudally, and they disappear in the lumbar region. This is the exact opposite from what we saw in the bats, where there were either very low, or no spinous processes cranially, but spinous processes appear as you move caudally. In all of the other mammalian taxa studied here the spinous processes of the thoracic column are all much taller than they are long, and are angled caudally.

Neural arch morphology is also extremely variable among mammals. In dermopterans the neural arches are very broad and shield like. Combined with the cranio-caudally elongate spinous processes, this would greatly restrict dorsiflexion of the thoracic spinal column. Megabats have a similar condition, as do many microchiropterans. However, as usual, this character is highly variable among microchiropterans. The xenarthrans also show this character, although it is highly modified by the presence of xenarthrous intervertebral articulations. The anomalurids also have shield like neural arches, but the degree of overlap between adjacent arches decreases caudally.

The other mammals studied here also show a high degree of variability in the degree of contact between adjacent thoracic neural arches. Acrobates has large

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spaces between thoracic neural arches. Pseudocheirus, Hemibelideus, and Petauroides, have somewhat smaller spaces, and Petaurus has no space between adjacent thoracic neural arches. Squirrels have some overlap between adjacent thoracic neural arch, but only near the thoracic-lumbar transition, and there is no apparent difference between the tree squirrels and the arboreal squirrels that were studied here. Furipterus deserve special mention here because of the highly derived nature of their thoracic and lumbar vertebrae. In this taxon, not only are C7 and T1 fused, but so are T7-L4.

THE LUMBAR REGION

Dermopterans do have relatively short lumbar regions although again not nearly as short as the bats and xenarthrans (Fig. 5.13a,b, Table 5.6). It is interesting though that the dermopterans do group with the lorids in this case. The bats do not group with the xenarthrans in this case, but are somewhat intermediate between xenarthrans and all other mammals.

The lumbar vertebrae allow for mostly flexion and extension, and for lateral flexion of the vertebral column. The long lumbar provides greater leaping velocity for leaping animals (Fleagle, 1988; Martin, 1990, Preuschoft et al., 1979), and a short lumbar region provides rigidity in the skeleton of suspensory animals using a lot of bridging behaviors. This explains the short lumbar column in arboreal xenarthrans. Such rigidity may also be important for animals that

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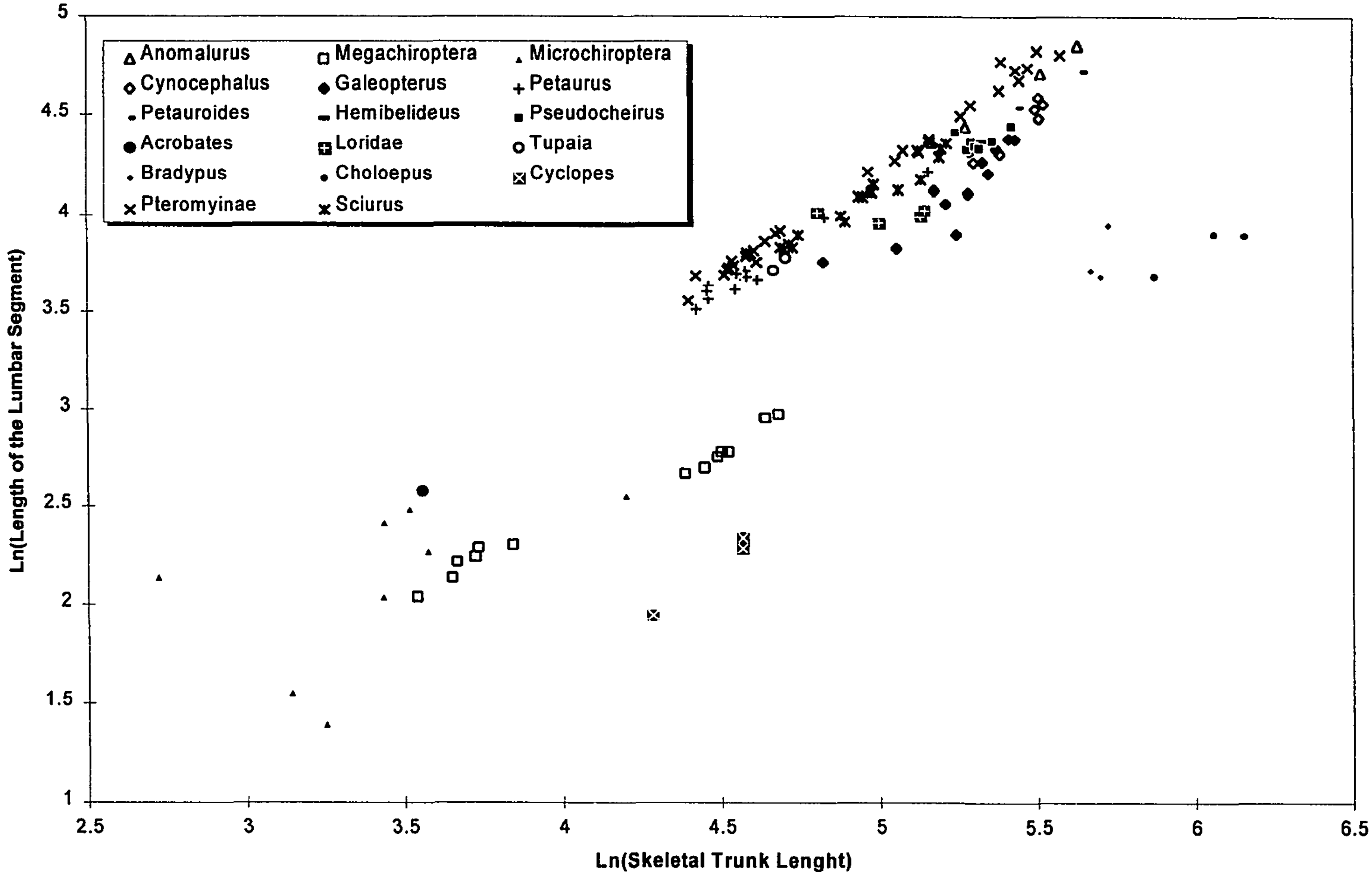

Figure 5.13a: Length of the lumbar segment of the spine in some mammals.

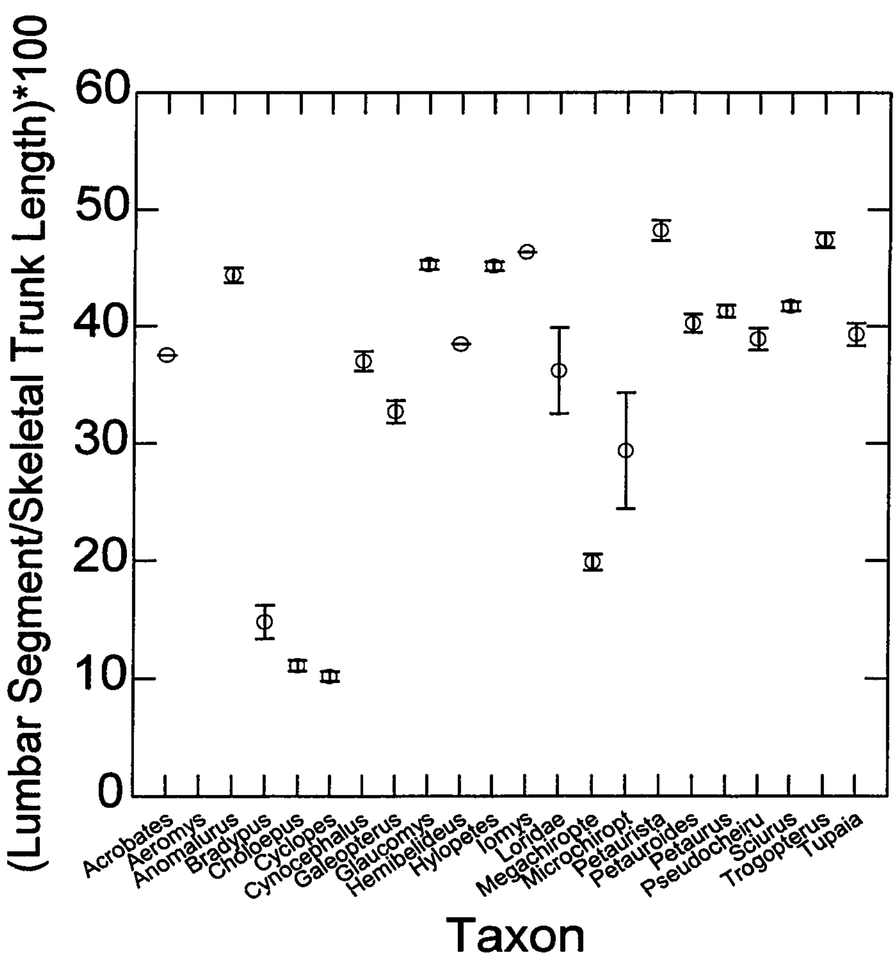

Figure 5.13b: Relative length of the lumbar segment of the spine in some mammals. Error bars equal one standard error of the mean.

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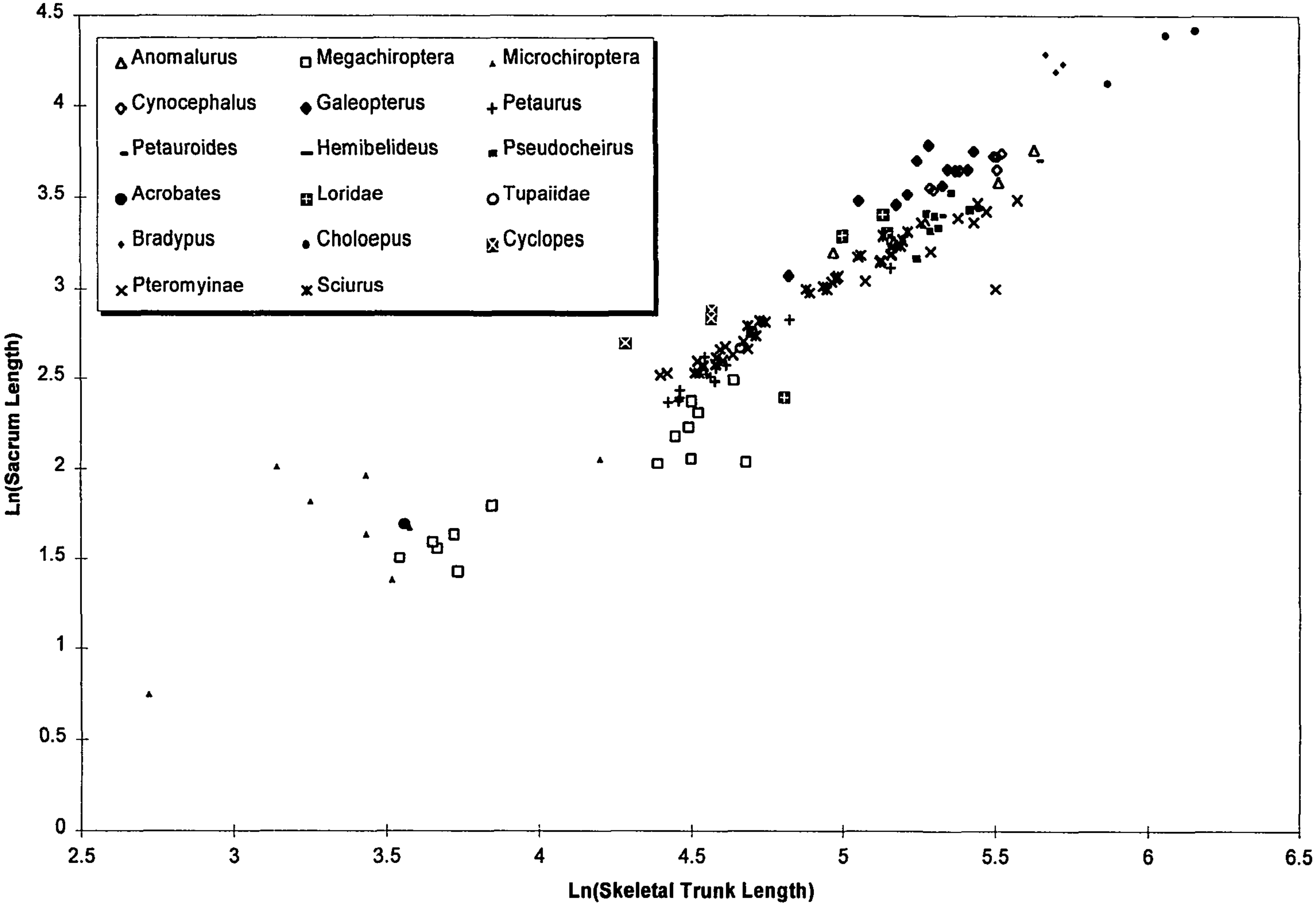

Figure 5.14a: Length of the sacrum in some mammals.

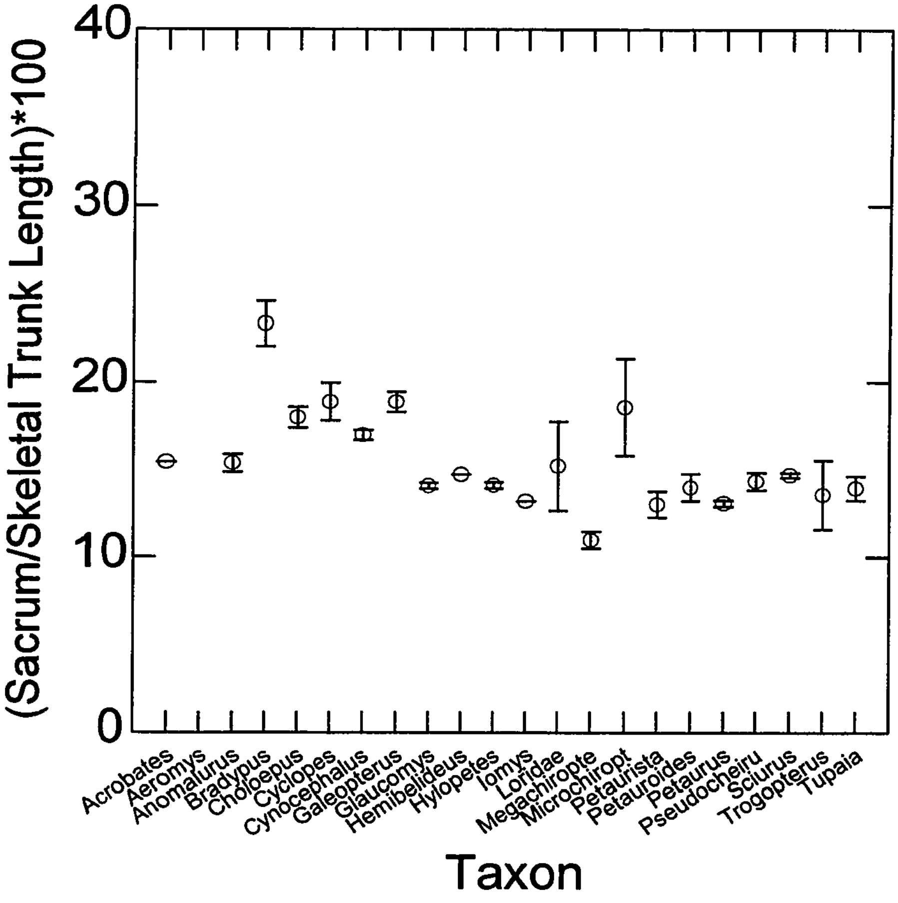

Figure 5.14b: Relative length of the sacrum in some mammals.

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load the spine heavily in other ways as well (i.e., terrestrial xenarthrans and bats). Lorids and dermopterans do have slightly shorter lumbar columns than the other mammals studied here, but not remarkably so. A long lumbar column may be important for dermopterans in the launching phase of their glide. This is the only phase of the glide where these animals can gain velocity without trading altitude for it. Some support for this position may be found among the sciurids. Here we see that the "flying" squirrels appear to have slightly longer lumbar columns than do Sciurus. These differences are very slight and require further study, but enhanced leaping ability in gliding mammals may be common (see below under hindlimbs).

THE SACRAL VERTEBRAE

The relative lengths of the sacral vertebrae among the mammals studied here seems to be more conservative than any of the other vertebral regions. Dermopterans, xenarthrans, and lorids appear to have slightly longer sacra, and bats appear to have slightly shorter sacra. However, there is some overlap in these values (Fig. 5.14a,b). Again this may be related to maintaining a rigid vertebral column during suspensory (specifically bridging) positional behaviors. This may be particularly important to the dermopterans, arboreal xenarthrans, and lorids because all of these taxa may extend the body horizontally from supports with only the hindlimbs, and sometimes the tail, supporting them. Bats use hindlimb suspension to a greater degree than any other mammal studied here, but this is almost entirely under branch suspension and produces an

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entirely different set of loadings on the pelvic girdle than do bridging or cantilevering behaviors.

TAILS

The taxa studied here show a wide degree of variability in the relative lengths of their tails. The data collected here do not show a significant difference in relative tail lengths between gliding and arboreal mammals. Of course such a coarse grained comparison is nearly useless given the variability in the data set. Within higher taxonomic categories, however, there are significant differences between arboreal and gliding taxa.

The two dermopteran genera do not differ significantly in relative tail lengths, but they do have short tails compared to most of the other taxa used in this study. The anomalurids also seem to have relatively short tails, but these are not significantly different than those of sciurines. However, anomalurids do have relatively shorter tails than pteromyines, as do sciurines (Thorington and Heaney, 1980, Fig 5.15, Table 5.7). In the marsupials there are no significant differences among the taxa studied here.

Thorington and Heaney (1980) offer a functional analysis explaining the relatively longer tails of pteromyines as compared to sciurines. These authors believe that the longer tails in the pteromyines aid in steering, and consider the distichous tails of the smaller flying squirrels and the uropatagia in the larger ones to serve analogous functions and roles. This also explains why the smaller flying squirrels do not seem to have relatively longer tails than non-gliding squirrels (Fig. 5.18). Under this hypothesis the larger flying squirrels have the

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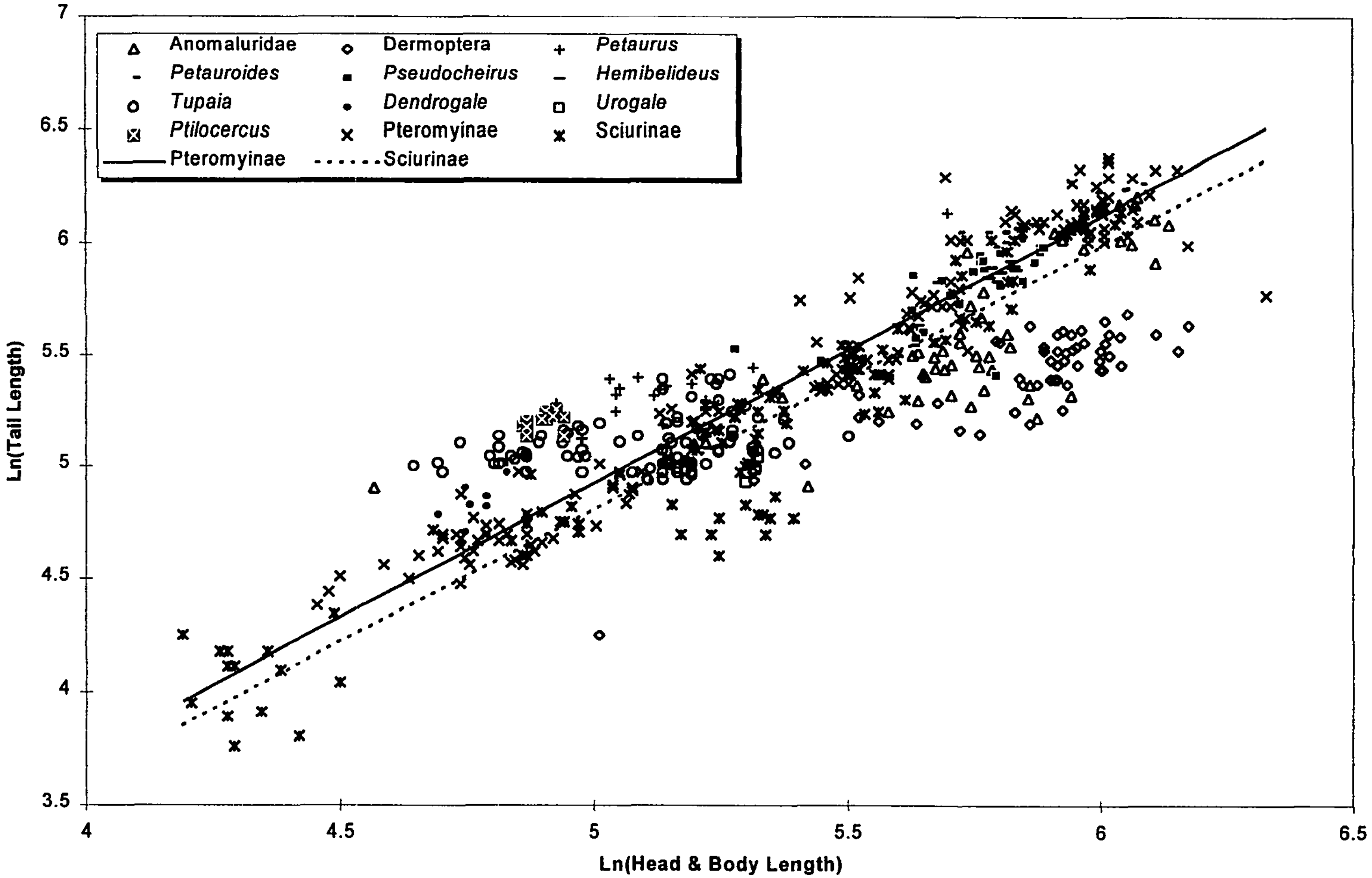

Figure 5.15: Tail Length in some mammals. Regression statistics are presented in table 5.7. Regression lines shown are for flying squirrels and tree squirrels.

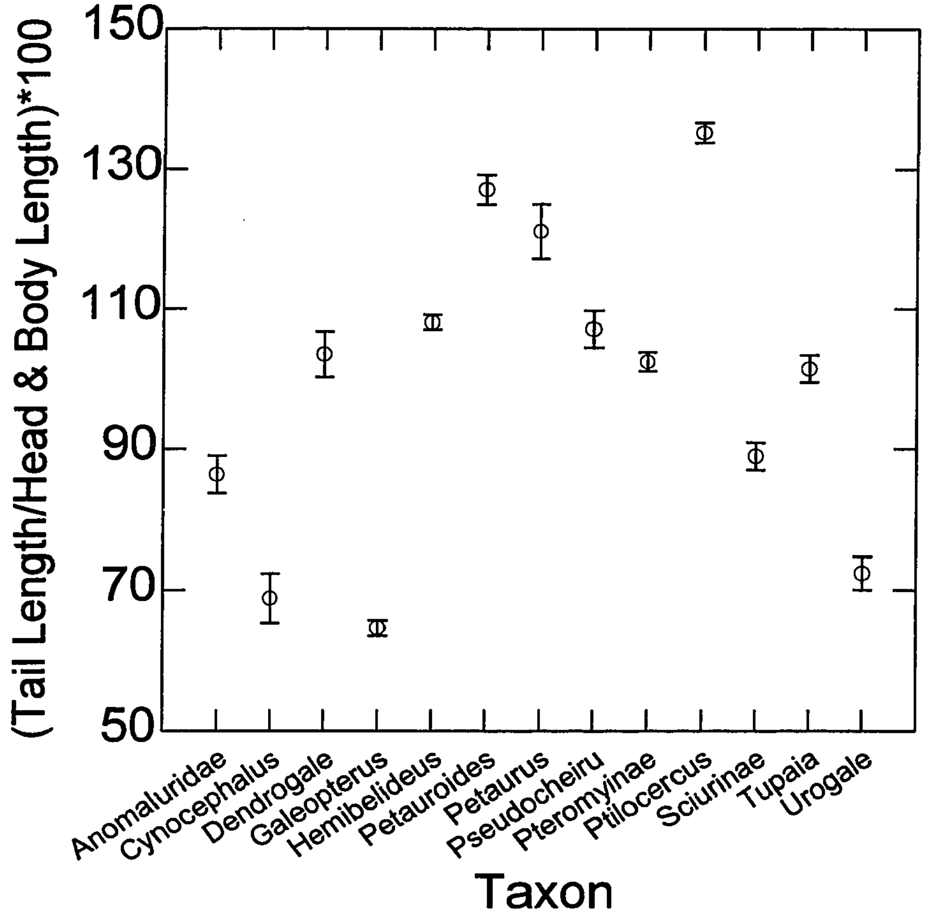

Figure 5.15b: Relative tail length in some mammals. Error bars are one standard error of the mean.

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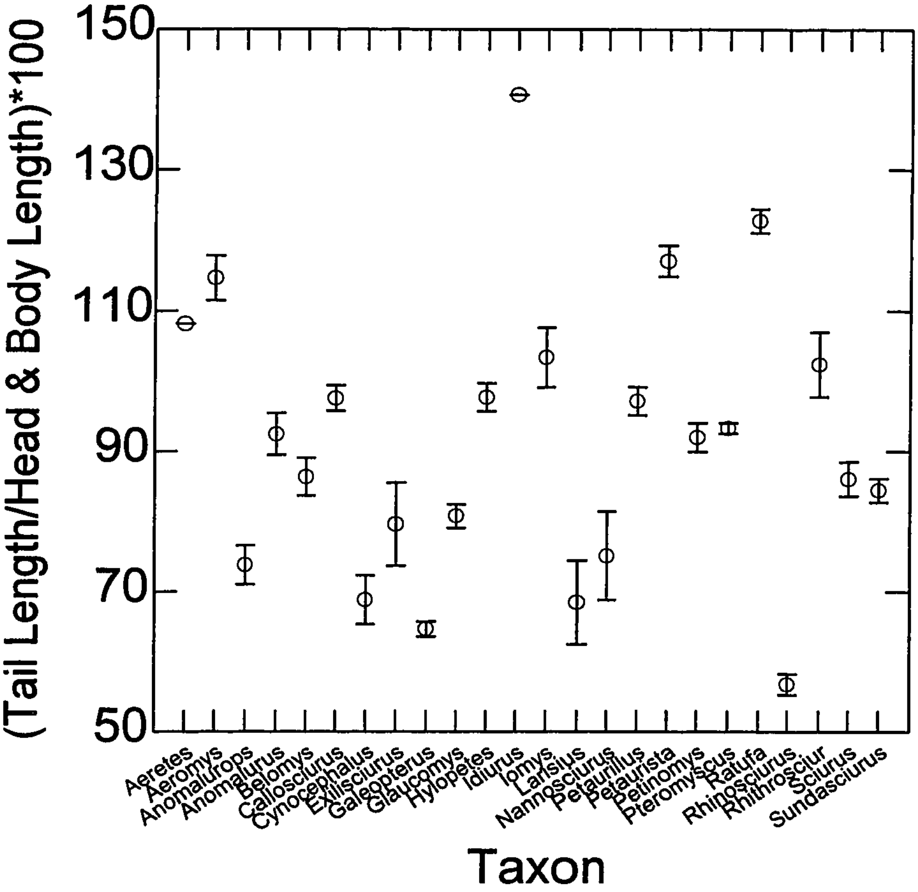

Figure 5.15c: Relative tail lengths in anomalurids, dermopterans, and sciurids. error bars equal one standard error of the mean.

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uropatagia performing at least some of the functions of the distichous tail in smaller flying squirrels. It is apparent however, that long tails are not associated with uropatagia because both Anomalurops and dermopterans have extensive uropatagia, but relatively short tails (Fig. 5.18, Table 5.7). Also, Idiurus has a uropatagium that is every bit as extensive as the larger anomalurids, but also has a relatively long tail..

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Table 5.7: Tail length statistics.

Least Squares Regression Statistics

		95% Confidence Intervals				
	Y Intercept	Lower	Upper	r-squared	T[1]	P
Pteromyinae	-1.045	-1.303	-0.787	0.94	-8.006	<0.0005
Sciurinae	-1.085	-1.537	-0.633	0.89	-4.769	<0.0006

		95% Confidence Intervals				
	Slope	Lower	Upper	Isometry	F[2]	P
Pteromyinae	1.194	1.147	1.242	1	66.393	<0.0005
Sciurinae	1.179	1.094	1.264	1	17.384	<0.0005

Bonferroni Test[3]

	1	2	3	4	5	6	7	8	9	10	11	12	13
1. Anomaluridae	1												
2. Cynocephalus		1											
3. Dendrogale		*	1										
4. Galeopterus	***		***	1									
5. Hemibelideus		**		***	1								
6. Petauroides	***	***		***		1							
7. Petaurus	***	***		***			1						
8. Pseudocheirus	***	***		***				1					
9. Pteromyinae	***	**		***		***	***		1				
10. Ptilocercus	***	***	***	***	*			***	***	1			
11. Sciurinae				***		***	***	***		***	1		
12. *Tupaia*	***	*		***		***	***			***	***	1	
13. Urogale						***	***			***			1

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	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1. <u>Aeretes</u>	1																							
2. <u>Aeromys</u>		1																						
3. <u>Anomalurops</u>		***	1																					
4. <u>Anomalurus</u>		***	***	1																				
5. <u>Belomys</u>		*			1																			
6. <u>Callosciurus</u>		**	***			1																		
7. <u>Cynocephalus</u>		***				**	1																	
8. <u>Exilsciurus</u>		***						1																
9. <u>Galeopterus</u>		***		***		***			1															
10. <u>Glaucomys</u>		***							*	1														
11. <u>Hylopetes</u>		***	***				***		***	*	1													
12. <u>Idiurus</u>			***				***	**	***	**		1												
13. <u>Iomys</u>			***				**		***				1											
14. <u>Lariscus</u>		***		***		***					***	***	***	1										
15. <u>Nannosciurus</u>		***									*	***			1									
16. <u>Petaurillus</u>									***							1								
17. <u>Petaurista</u>			***	***	***	***	***	***	***	***	***			***	***		1							
18. <u>Petinomys</u>		***	**						***					**			***	1						
19. <u>Pteromyscus</u>		***	*						***					*			***		1					
20. <u>Ratufa</u>				***	*	*	***	***	***	***				***	***			***	***	1				
21. <u>Rhinosciurus</u>		***		***		***							***			***	***	***	***	***	1			
22. <u>Rhithrosciurus</u>			**				*		***		***			***							***	1		
23. <u>Sciurus</u>		***							***			*					***			***	***		1	
24. <u>Sundasciurus</u>		***							***			*					***			***	*			1

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[1] T-test tests the hypothesis that y-intercepts are not significantly different from zero, at $p \leq 0.001$. Differences among y-intercepts are considered significantly different when the 95% confidence intervals of the intercept do not overlap.

[2] F-test tests the hypothesis that observed slopes of regression lines are not significantly different from isometry. Slopes were considered significantly different from isometry when $p \leq 0.001$. Differences among slopes are considered significantly different when the 95% confidence intervals.

[3] *, $p \leq 0.01$; **, $p \leq 0.001$; ***, $p \leq 0.0005$

CHAPTER 6: THE FORELIMB

It has long been noted that dermopterans and bats possess elongate and gracile postcranial skeletons (Schufelt, 1911; Pocock, 1926). Similar morphologies have also been noted for other gliding mammals (Thorington and Heaney, 1981; Runestad and Ruff, 1995) and suspensory climbers (Mendel, 1981a, 1981b, 1981c, 1985a, 1985b; Miller, 1935; Taylor, 1985; White, 1993) although these observations have only been quantified in the gliding mammals. In this chapter I examine the relative proportions of limb elements in an attempt to discriminate gliding mammals from nongliding mammals. Thorington and Heaney (1981) performed a similar analysis confined to flying squirrels as compared to tree squirrels. Their results showed that the flying squirrels do have generally longer limbs than their non-gliding relatives, although at low body sizes the regression lines for some comparisons crossed.

Runestad and Ruff (1995) examined a selection of gliding mammals and their close nongliding relatives but were more concerned with interpreting primate fossils, putatively gliders, and did not include in most of their analysis largely suspensory taxa, or chiropterans. Their analysis shows that gliding mammals do tend to have relatively longer and relatively more gracile limb bones than the nongliding taxa that they studied. There may however, be several problems with this study. First, the exclusion of chiropterans and other largely suspensory taxa circumscribes the conclusions of this work.

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Second, the body weights used by Runestad and Ruff (1995), at least for Cynocephalus, appear to be very inaccurate. They give the average weight of Galeopterus as 1,345 g., and that of Cynocephalus as 990 g. The weights taken just from USNM specimens average out to 1,408 g. for Galeopterus, but to 1,260 g. for Cynocephalus. Similarly their body weights for anomalurids appear to be too high (see Table 3.1).

RELATIVE LIMB LENGTHS IN RELATION TO SKELETAL TRUNK LENGTH (STL)

The forelimbs.—Bats, dermopteran and three toed sloths all have forelimb indices greater than 100 (Fig. 6.1). All of the other mammals studied here have forelimb indices between 42 and 80. However, gliding mammals do have longer forelimbs than their nongliding relatives (Thorington and Heaney, 1981), if these data are analyzed at lower taxonomic levels. For example, the flying squirrels do have slightly longer forelimbs than Sciurus (forelimb indices of 68 vs. 57), and these differences are significant ($t = 8.40$, $df = 38$, $p < 0.001$). However, ANOVA with Bonfferoni's correction indicate that this may not be universally true among all genera of sciurids. Similarly, Acrobates and Petaurus have relatively longer forelimbs than Pseudocheirus, Hemibelideus, and Petauroides ($p < 0.001$). In fact gliding mammals as a class have relatively longer forelimbs than arboreal taxa ($p < 0.001$). This holds true for rodents ($t = -8.74$, $df = 42$, $p < 0.0005$) and marsupials ($t = -7.40$, $df = 19$, $p < 0.0005$). Yet none of the relative forelimb indices of any nondermopteran gliding mammal comes close to the values seen in the bats or in dermopterans and Bradypus. Among dermopterans Galeopterus

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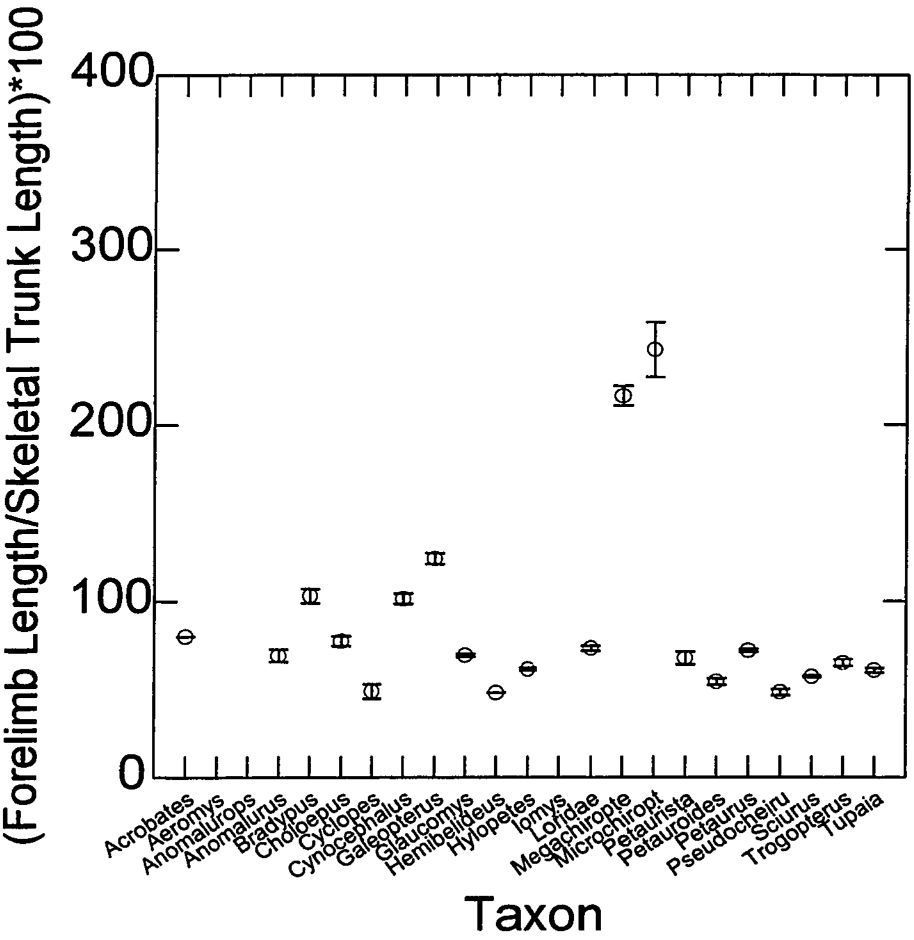

Figure 6.1: Relative forelimb length in some mammals. Error bars are one standard error of the mean.

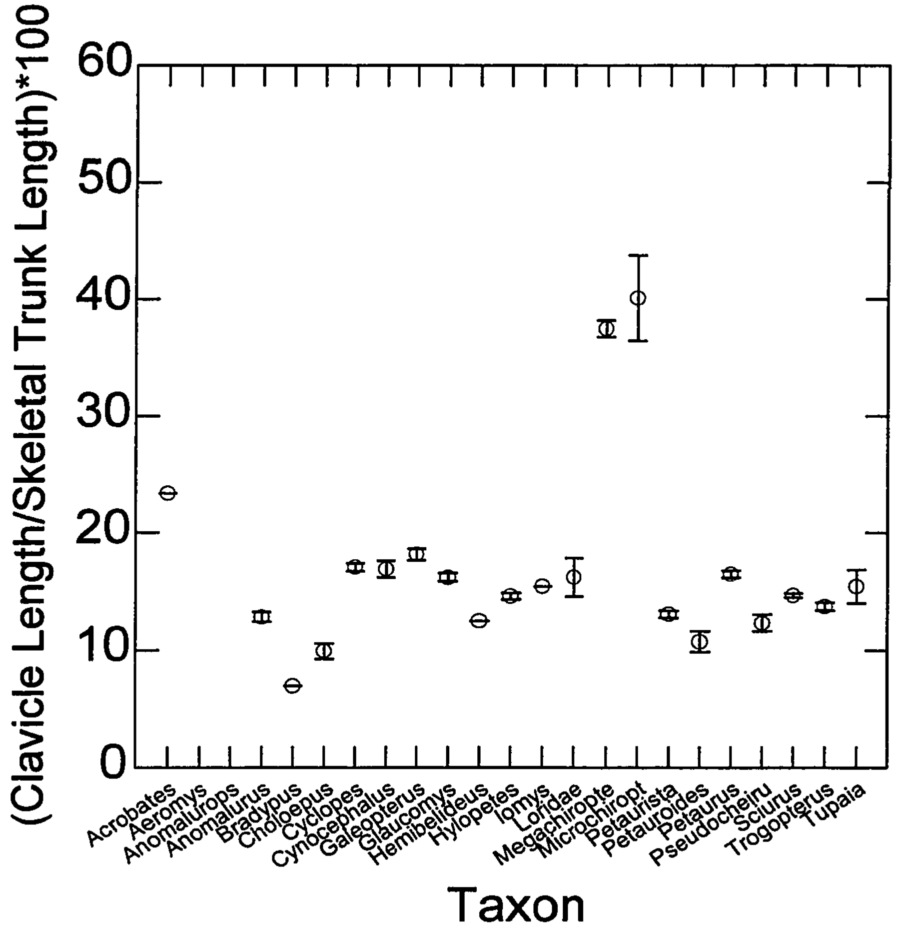

Figure 6.2: Relative clavicle length in some mammals. Error bars are one standard error of the mean.

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has a relatively longer forelimb than Cynocephalus ($t=5.52$, $df=14$, $p<0.001$).

Clavicle.—The clavicle also contributes to wing span and wing area because this structure largely determines the distance from midline of the body to the gleno-humeral joint. Bats have significantly longer clavicles than all other taxa studied here (Fig. 6.2; $p < 0.001$, megachiropterans vs. all other taxa; $p < 0.001$ microchiropterans vs. all other taxa). When the data are grouped by locomotor category again only the bats are different from all other taxa ($p < 0.001$). Among gliding taxa there are some differences among individual taxa but there are no systematic patterns of difference. In other words, the differences are not between pteromyines and anomalurids, or between anomalurids and dermopterans, etc. When differences among locomotor classes are examined in rodents and marsupials we also find no significant differences (rodents $t = 0.34$, $df = 47$, $p = 0.7373$; marsupials $t = -3.39$, $f = 21$, $p = 0.0028$). There are also no significant differences among dermopterans ($t = -1.61$, $df = 14$, $p = 0.1300$).

The humerus.—The relative length of the humerus is greatest in the bats (Fig. 6.3). The dermopterans and Bradypus also have significantly greater humeral indices than most of the other mammals studied here. The bats have significantly higher values than all other locomotor categories ($p < 0.001$), and the gliding mammals also have significantly higher values than the arboreal mammals (p , 0.001). However, gliding mammals do not have significantly longer humeri than either suspensory or climbing taxa. Among

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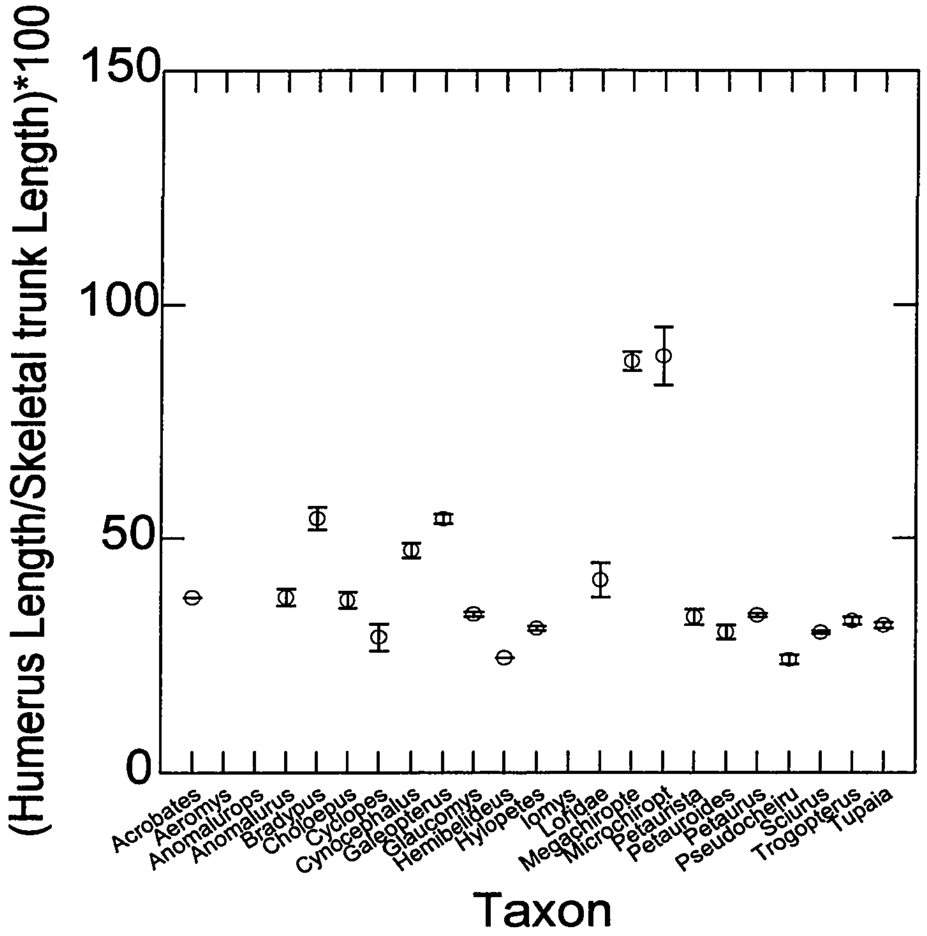

Figure 6.3: Relative humerus length in some mammals. Error bars are one standard error of the mean.

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gliding mammals dermopterans have relatively longer humeri than most other gliding mammals ($p < 0.001$), with the exception of Acrobates. Acrobates and Anomalurus have slightly longer humeri than the other nondermopteran gliders although these differences are not significant. Among the rodents the gliding taxa do have relatively longer humeri than Sciurus ($t = -4.92$, $df = 46$, $p < 0.0005$), and the same is true among the marsupials ($t = -9.14$, $df = 21$, $p < 0.0005$). This generally confirms the results of Thorington and Heaney (1981) and Runestad and Ruff (1994) although there are differences from the conclusions of the later authors (see below). Among the dermopterans there were no significant differences ($t = -4.06$, $df = 15$, $p = 0.0010$).

The radius.—The bats have relatively longer radii than all other mammals studied here (Fig. 6.4). Galeopterus has a relatively longer radius than all other mammals studied here except for Cynocephalus, Bradypus, and Cyclopes. When the data are partitioned into locomotor classes we see that bats still have relatively longer radii than all other mammals, but that gliding mammals also have relatively longer radii than arboreal taxa, even given the inclusion of anomalurids and Petauroides in the sample of gliding mammals (see Runestad and Ruff, 1994). Suspensory taxa however, do not have relatively longer radii than arboreal taxa. This lack of differentiation of suspensory taxa may in part result from including Cyclopes in the suspensory locomotor class. Cyclopes do not have relatively long radii. Among gliding

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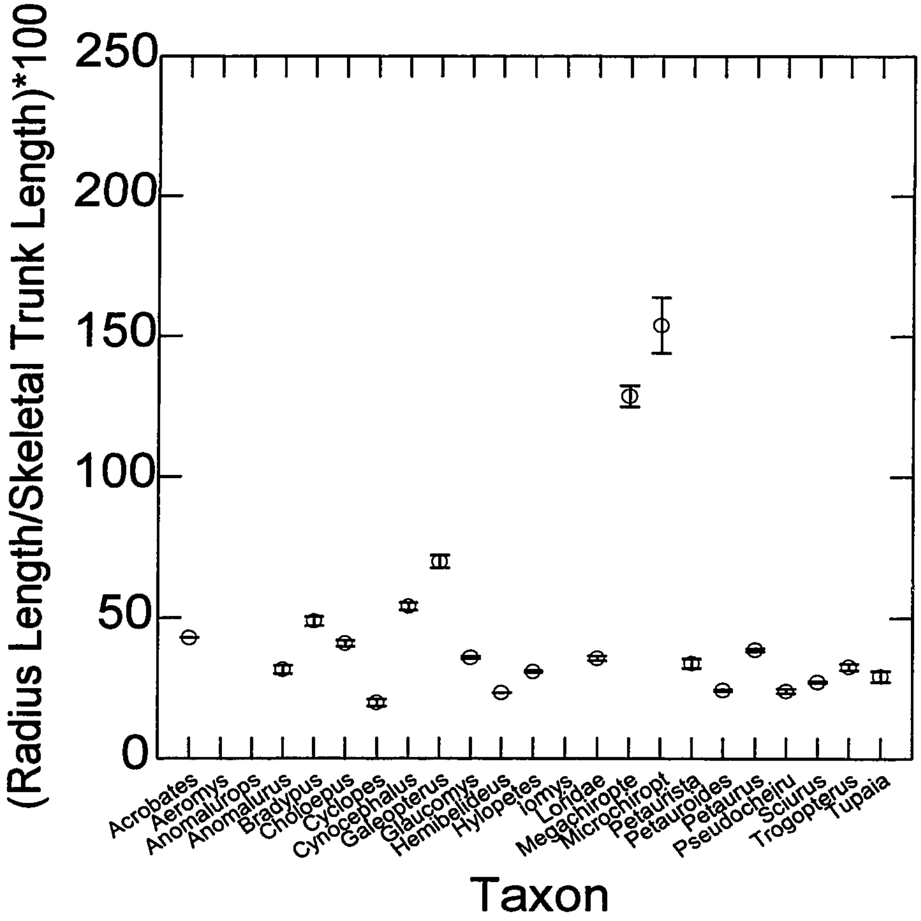

Figure 6.4: Relative radius length in some mammals. Error bars are one standard error of the mean.

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mammals the dermopterans have relatively longer radii than all other taxa except Acrobates. Gliding rodents have relatively longer radii than Sciurus ($t = -9.66$, $df = 43$, $p < 0.0005$) even though this sample includes the anomalurids which have relatively short radii for a rodent ($p < 0.001$). The same is true among the marsupials ($t = 0.38$, $df = 15$, $p = 0.7128$) where the gliding category includes Petauroides which have relatively short radii for a marsupial ($p < 0.001$). Among the dermopterans Galeopterus has a significantly longer radius than Cynocephalus ($t = -6.09$, $df = 14$, $p < 0.0005$).

CROSS SECTIONAL AREAS (**TCSA**), POLAR MOMENTS (**J**) AND SECOND MOMENTS OF AREA (**I**) IN RELATION TO BODY SIZE (**STL**)

The clavicle.—With respect to $\mathbf{TCSA}_{\mathrm{Clavicle(STL)}}$ (Fig 6.5) the bats are significantly different from all other taxa studied here, having relatively greater $\mathbf{TCSA}_{\mathrm{Clavicle(STL)}}$ ($p < 0.001$) The same holds when data are grouped into locomotor classes, only the bats are significantly different ($p < 0.001$). However, among gliding mammals the dermopterans have relatively greater $\mathbf{TCSA}_{\mathrm{Clavicle(STL)}}$ compared to most other taxa studied here. Interestingly, when rodents and marsupials are considered, we see that gliding rodents have relatively lower $\mathbf{TCSA}_{\mathrm{Clavicle(STL)}}$ ($t = 7.83$, $df = 47$, $p < 0.0005$) than Sciurus, while gliding marsupials are not statistically different from nongliding marsupials ($t = -1.57$, $df = 19$, $p = 0.1334$). There is no significant difference among dermopterans for $\mathbf{TCSA}_{\mathrm{Clavicle(STL)}}$ ($t = 0.23$, $df = 14$, $p = 0.8202$).

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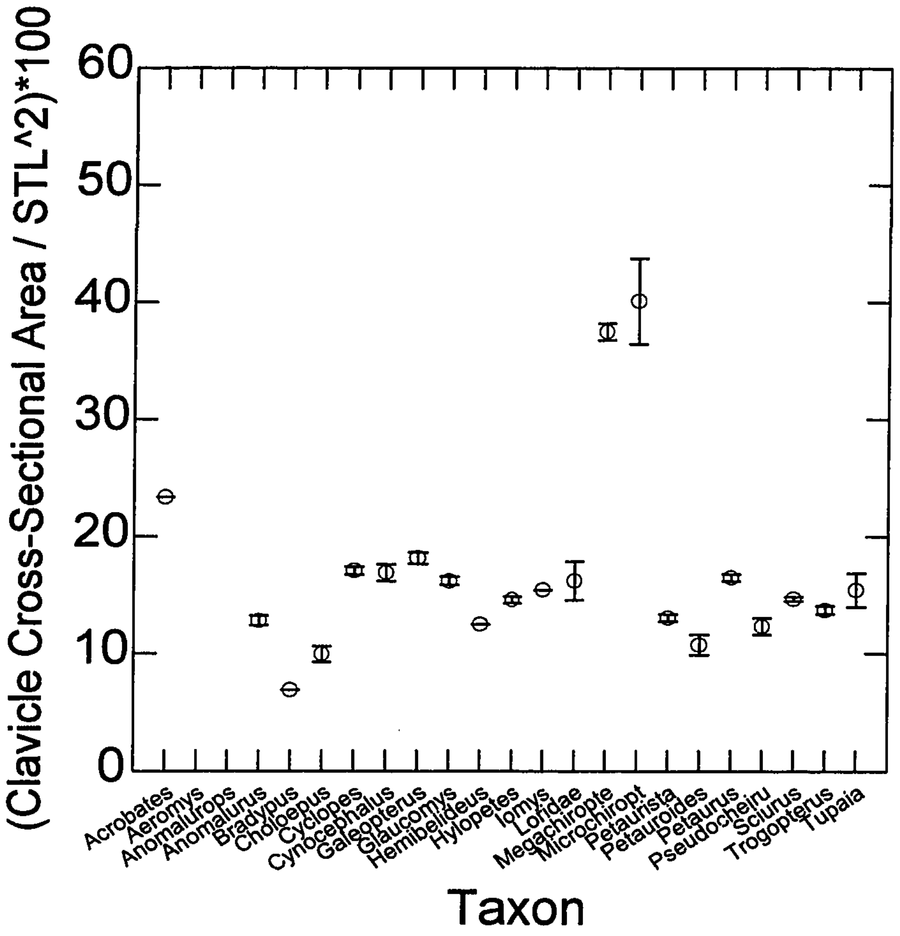

Figure 6.5: Relative cross-sectional area of the clavicle in some mammals. Error bars are one standard error of the mean.

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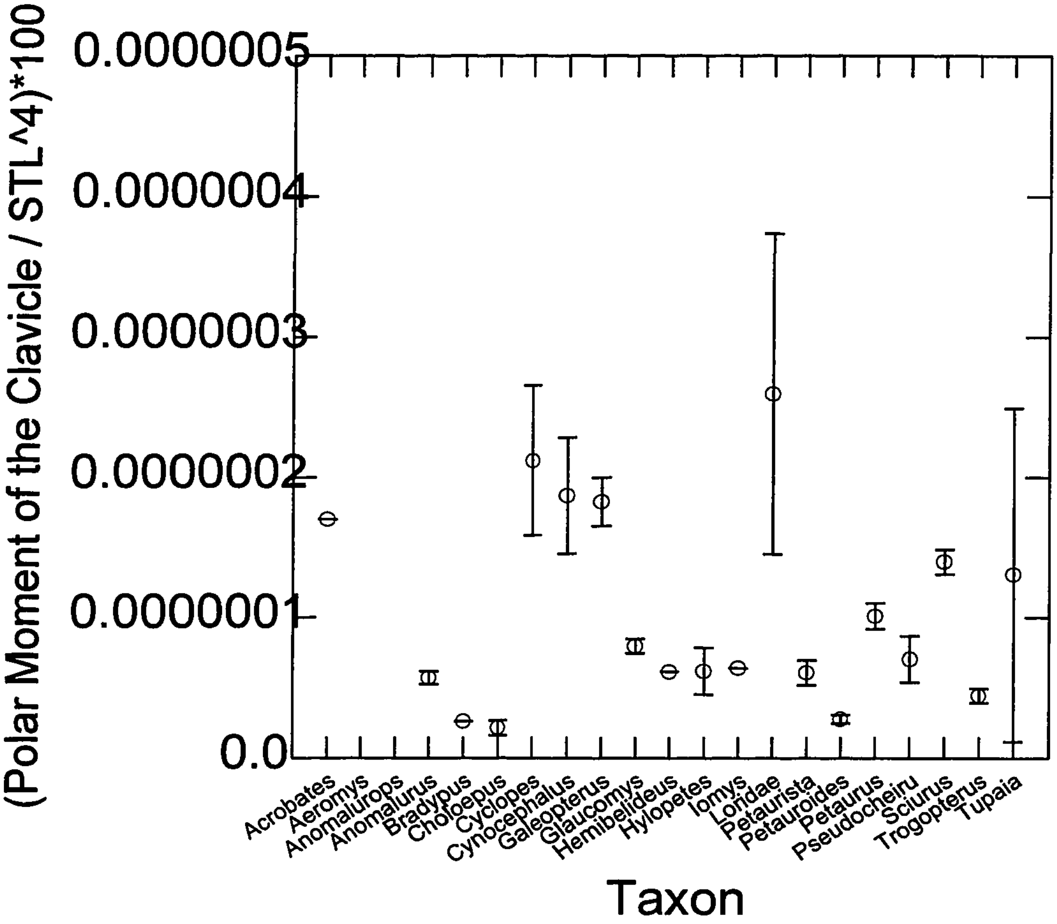

Figure 6.6: Relative polar moment of the clavicle in some mammals. Error bars are one standard error of the mean. Bats have been omitted for clarity. Megachiroptera, 6.58 * 10^{-6} ± 5.01 * 10^{-7}; Microchiroptera, 8.95 * 10^{-6} ± 1.65 * 10^{-6}.

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An examination of $J_{clavicle(STL)}$ shows a different picture. Once again bats have significantly greater values than all other mammals (Fig. 6.6). When data are grouped according to locomotor category bats are different from all other categories ($p < 0.001$ for megachiropterans; $p < 0.001$ for microchiropterans) but there are no significant differences among the other locomotor classes. However, lorids and Cyclopes actually have higher average $J_{clavicle(STL)}$ than do either of the dermopterans. Of the rodents, the gliding taxa actually have lower $J_{clavicle(STL)}$ than Sciurus ($t = 9.17$, $df = 47$, $p < 0.0005$), but among the marsupials there is no significant difference ($t = -1.41$, $df = 19$, $p = 0.744$). There are no significant differences among dermopterans ($t = 0.12$, $df = 14$, $p = 0.9025$).

$I_{ML,Clavicle(STL)}$ is higher in bats than in all other taxa studied here (Figure 6.7). It is also higher in megachiropterans than in microchiropterans. When data are grouped by locomotor category the only differences are still between bats and all other taxa. When considering only gliding mammals we see that dermopterans and Acrobates do have higher $I_{ML,Clavicle(STL)}$ as compared to other gliding taxa, but that these differences are not uniformly different among all taxa. In rodents, Sciurus have higher $I_{ML,Clavicle(STL)}$ than do the gliding taxa ($t = 10.71$, $df = 47$, $p < 0.0005$) while among the marsupials there are no significant differences ($t = 1.09$, $df = 19$, $p = 0.2890$). There are no significant differences among dermopterans ($t = -0.34$, $df = 14$, $p = 0.7625$).

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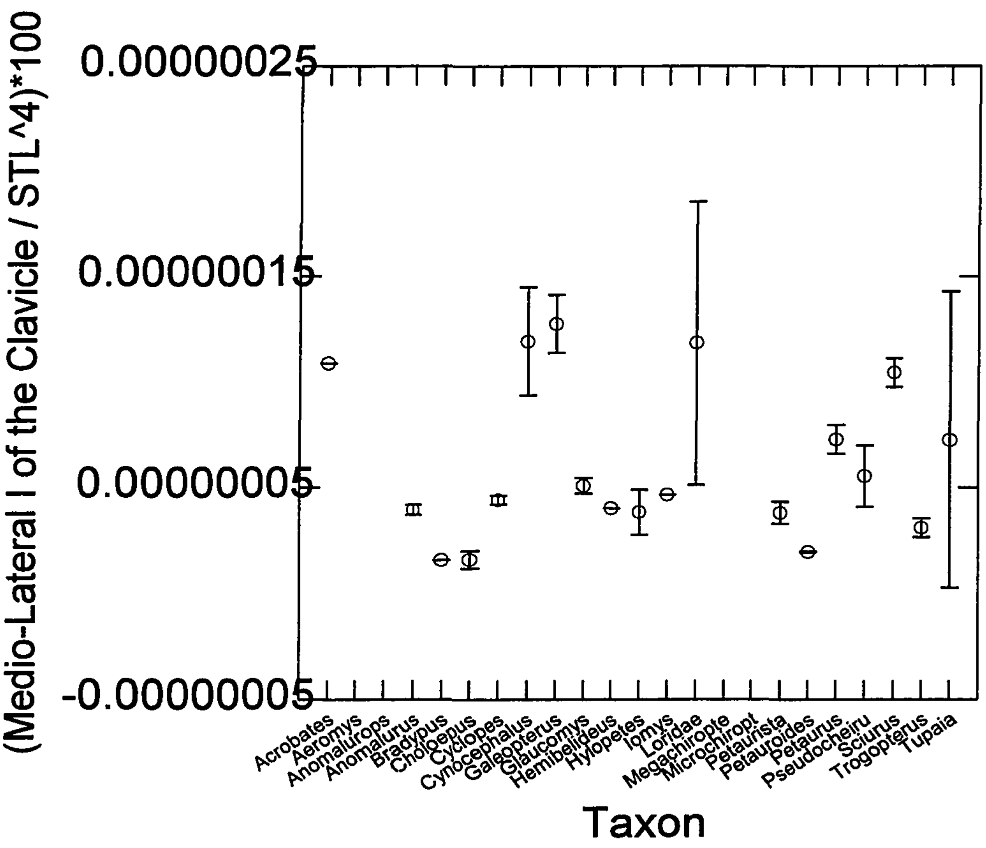

Figure 6.7: Relative medio-lateral bending moments of the clavicle in some mammals. Error bars are one standard error of the mean. Bats have been omitted for clarity. Megachiroptera, $5.26 * 10^{-6} \pm 4.17 * 10^{-7}$; Microchiroptera, $3.21 * 10^{-6} \pm 7.93 * 10^{-7}$.

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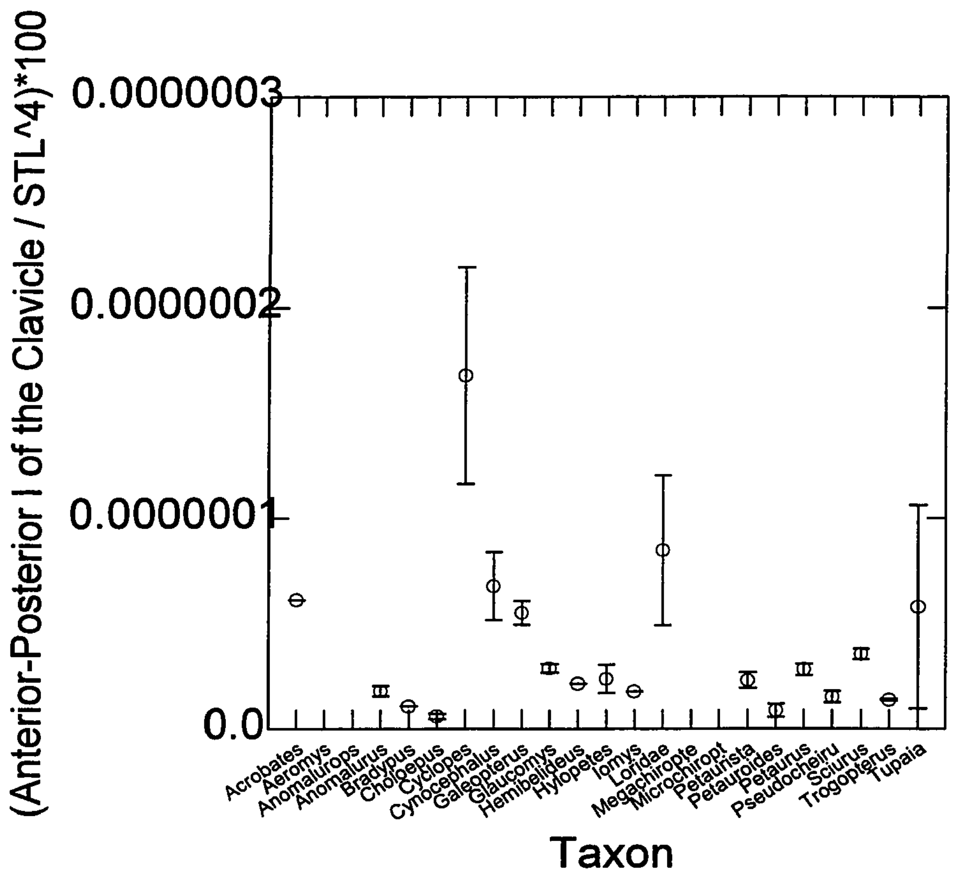

Figure 6.8: Relative anterior-posterior bending moments in the clavicle of some mammals. Error bars are one standard error of the mean. Bats have been omitted for clarity. Megachiroptera, 1.33 * 10^{-6} ± 1.08 * 10^{-7}; Microchiroptera, 5.74 * 10^{-6} ± 1.32 * 10^{-6}.

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A similar pattern is seen when looking at $\mathbf{I}_{\mathbf{AP,Clavicle(STL)}}$ (Fig. 6.8). Although the bats have higher values than all other taxa, only the microchiropterans are significantly different from all other taxa. Surprisingly, when data are grouped according to locomotor categories, bats are different from all other locomotor categories except the lorids. Again, it should be remembered that the suspensory locomotor category contains Cyclopes which appears very different from the sloths, and also clusters with this bat-lorid group. There are few significant differences among gliding mammals, but these differences do tend to be between Cynocephalus and other gliding taxa, Cynocephalus having higher values. Galeopterus and Acrobates also show higher values than other gliding mammals, but these tend not to be statistically significant. Among the rodents Sciurus has higher values for $\mathbf{I}_{\mathbf{AP,Clavicle(STL)}}$ than the gliding taxa ($t = 4.31$, $df = 47$, $p < 0.0005$), while among the marsupials there are no significant differences among gliding and arboreal taxa ($t=-1.95$, $df=19$, $p=0.0665$). Likewise there are no significant differences among dermopterans ($t = 0.98$, $df = 14$, $p = 0.3441$).

The humerus.—In terms of $\mathbf{TCSA}_{\mathbf{Humerus(STL)}}$ the bats again have higher values than the other taxa studied here, but Cyclopes is also relatively higher than most of the other taxa studied here (Fig. 6.9). When the data are grouped according to locomotor class the bats have relatively larger $\mathbf{TCSA}_{\mathbf{Humerus(STL)}}$ than all other taxa studied here. The only other significant difference is that gliders have significantly lower humeral cross sectional areas than do suspensory taxa. Within gliding mammals the dermopterans

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have relatively higher cross sectional areas of the humerus than do all other gliding mammals except Acrobates. Petauroides has the relatively lowest humeral cross sectional area, but is only significantly different from Petaurus, and that may well be the most significant comparison. However, the dermopterans do not have significantly different humeral cross sectional areas compared to either Bradypus or Choloepus when only dermopterans and xenarthrans are analyzed. Among rodents, gliding taxa do have relatively lower $\mathbf{TCSA}_{\mathbf{Humerus(STL)}}$ than arboreal taxa ($t = 10.99$, $df = 46$, $p < 0.001$), although again this is not the case among marsupials ($t = -0.99$, $df = 21$, $p < 0.001$). There were no significant differences among dermopterans ($t = -0.14$, $df = 15$, $p = 0.8914$).

Bats have larger relative $\mathbf{J}_{\mathbf{Humerus(STL)}}$ than do all other mammals studied here with the exception that megachiropterans and Tupaia are not statistically different (Fig. 6.10). Cyclopes also fall well above all nonchiropteran mammals, and when the bats are removed from the analysis Cyclopes has significantly larger $\mathbf{J}_{\mathbf{Humerus(STL)}}$ than all other nonchiropteran mammals. When taxa are grouped according to locomotion, only the flying animals (the bats) have relatively high $\mathbf{J}_{\mathbf{Humerus(STL)}}$. When only the gliding mammals are considered, the dermopterans have relatively higher $\mathbf{J}_{\mathbf{Humerus(STL)}}$ than other gliding mammals. However, when only the dermopterans and xenarthrans are considered, the dermopterans are not statistically different from either Bradypus or Choloepus. When the bats are added to this analysis we see that the dermopterans are also different from the bats, but that

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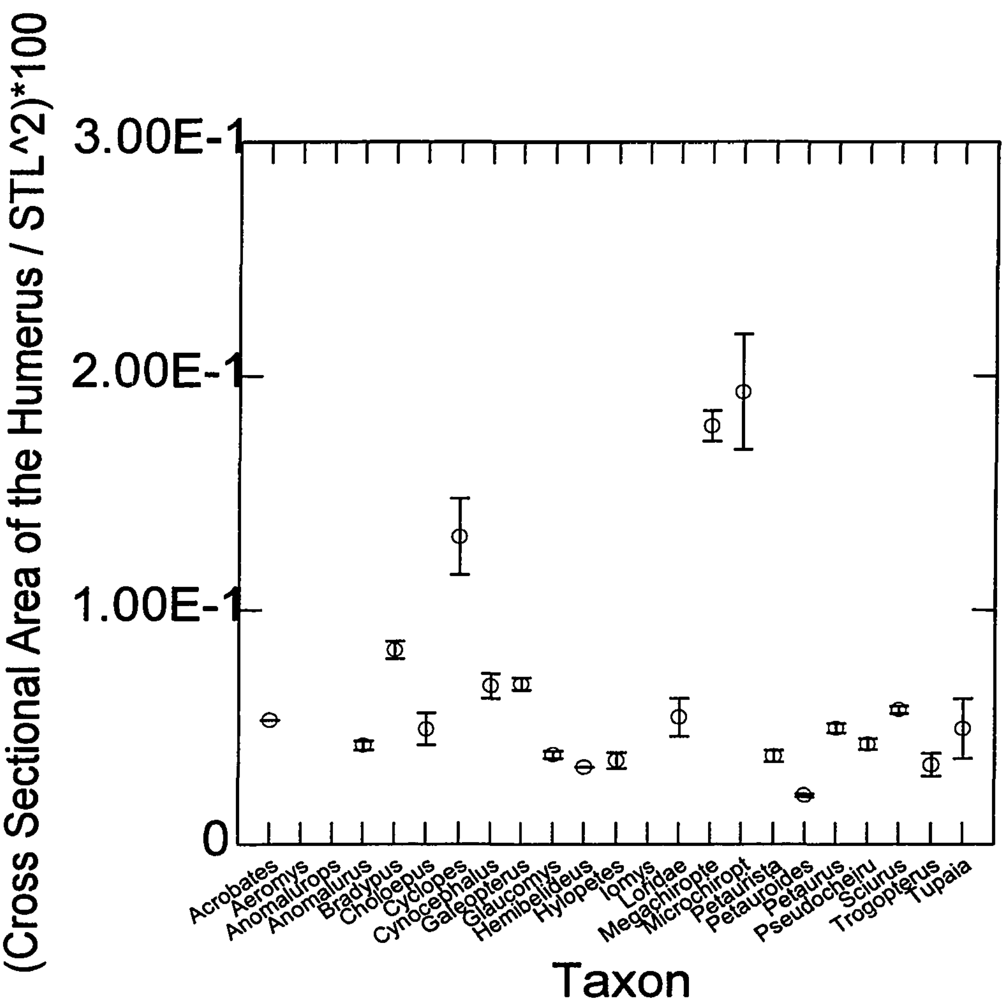

Figure 6.9: Relative cross sectional area of the humerus in some mammals. Error bars are one standard error of the mean.

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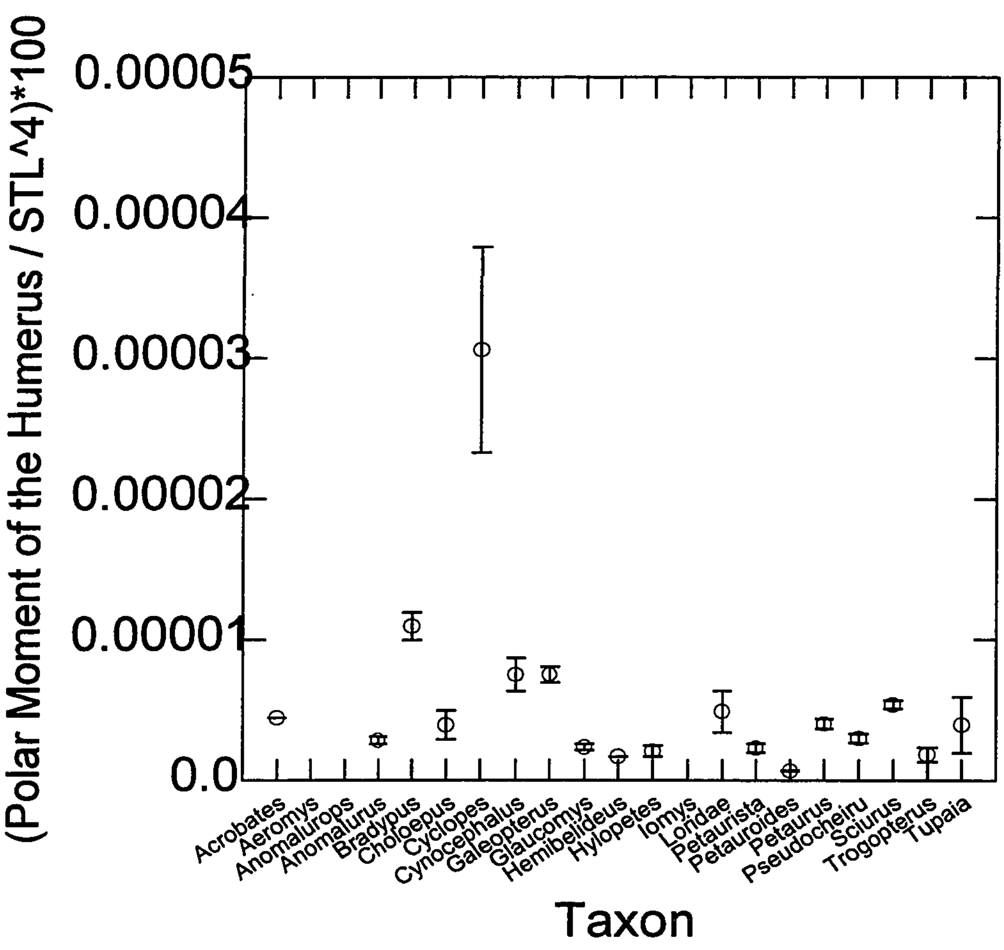

Figure 6.10: Relative polar moments of the humerus in some mammals. Error bars are one standard error of the mean. Bats have been omitted for clarity. Bats have been omitted for clarity. Megachiroptera, 5.17 * 10^{-5} $\pm$ 3.57 * 10^{-6}; Microchiroptera, 7.66 * 10^{-5} $\pm$ 1.74 * 10^{-5}.

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Cynocephalus is not different from the megabats. Among rodents we see that the gliders have low relative $J_{Humerus(STL)}$ compared to Sciurus ($t = 11.01$, $df = 46$, $p < 0.001$). However, among the marsupials there are no significant differences among locomotor classes ($t = -1.30$, $df = 21$, $p = 0.2086$). There are also no significant differences among dermopterans ($t = -0.003$, $df = 15$, $p = 0.9980$).

Relative I_{ML} and I_{AP} of the humerus show a similar picture (Fig. 6.11. 6.12). In general it is the megachiropterans and microchiropterans that are different from all other taxa. When taxa are grouped by locomotor category again only the bats are significantly different from the other locomotor categories for both $I_{ML,Humerus(STL)}$ and for $I_{AP,Humerus(STL)}$. Within gliding mammals dermopterans have higher $I_{ML,Humerus(STL)}$ than all other gliding mammals except Acrobates. In an analysis of bats, dermopterans and xenarthrans the only significant differences in $I_{ML,Humerus(STL)}$ are between dermopterans and the microchiropterans. The same picture is generally true for $I_{AP,Humerus(STL)}$ except that Cyclopes is also significantly different from microchiropterans, and that Galeopterus is now also significantly different from the megachiropterans. Among the rodents gliders have relatively low $I_{ML,Humerus(STL)}$ ($t = 9.95$, $df = 46$, $p < 0.001$) and relatively lower $I_{AP,Humerus(STL)}$ ($t = 11.78$, $df = 46$, $p < 0.001$) than Sciurus. There are no significant differences among locomotor classes of marsupial ($I_{ML,Humerus(STL)}$, $t = -1.68$, $df = 21$, $p = 0.1074$; $I_{AP,Humerus(STL)}$, $t = -0.96$, $df = 21$, $p = 0.3459$). There are no significant differences among dermopterans ($t = 0.38$, $df = 15$, $p = 0.7128$).

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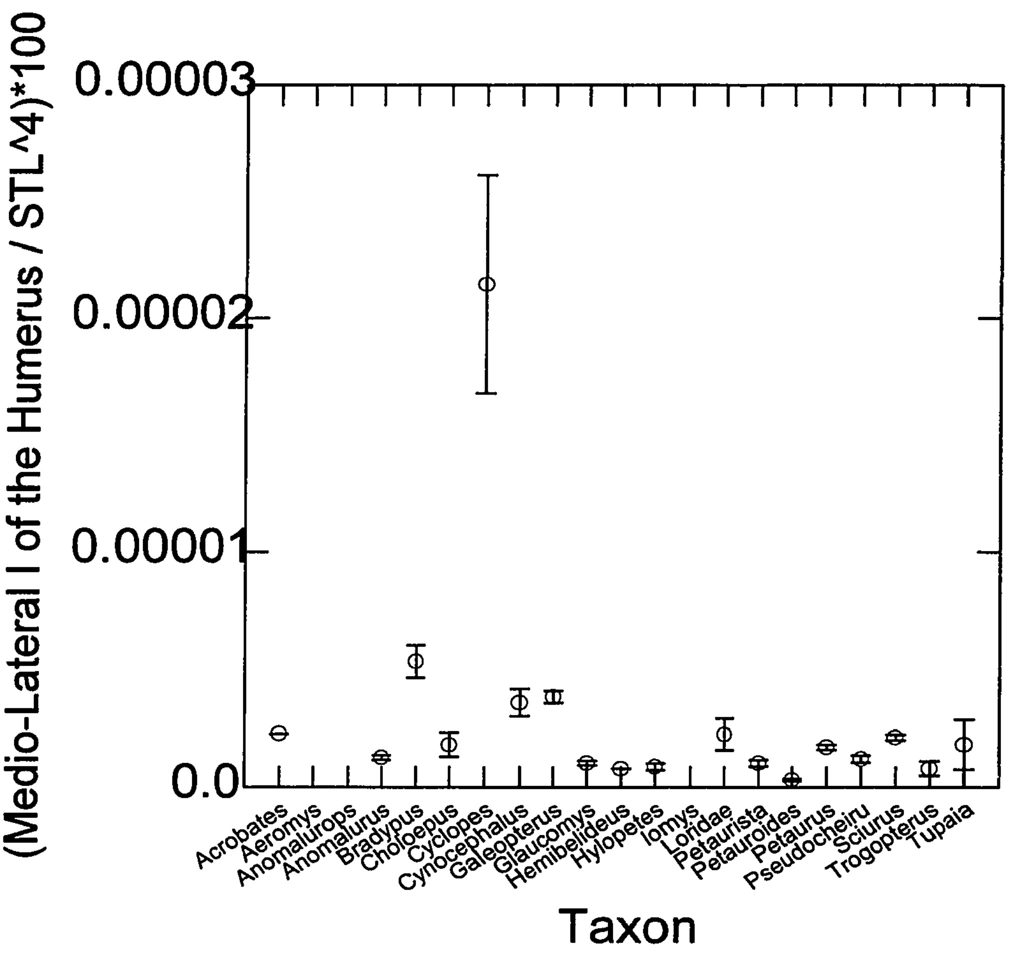

Figure 6.11: Relative medio-lateral bending moments of the humerus in some mammals. Error bars are one standard error of the mean. Bats have been omitted for clarity. Megachiroptera, $2.69 * 10^{-5} \pm 1.93 * 10^{-6}$; Microchiroptera, $4.14 * 10^{-5} \pm 9.68 * 10^{-6}$.

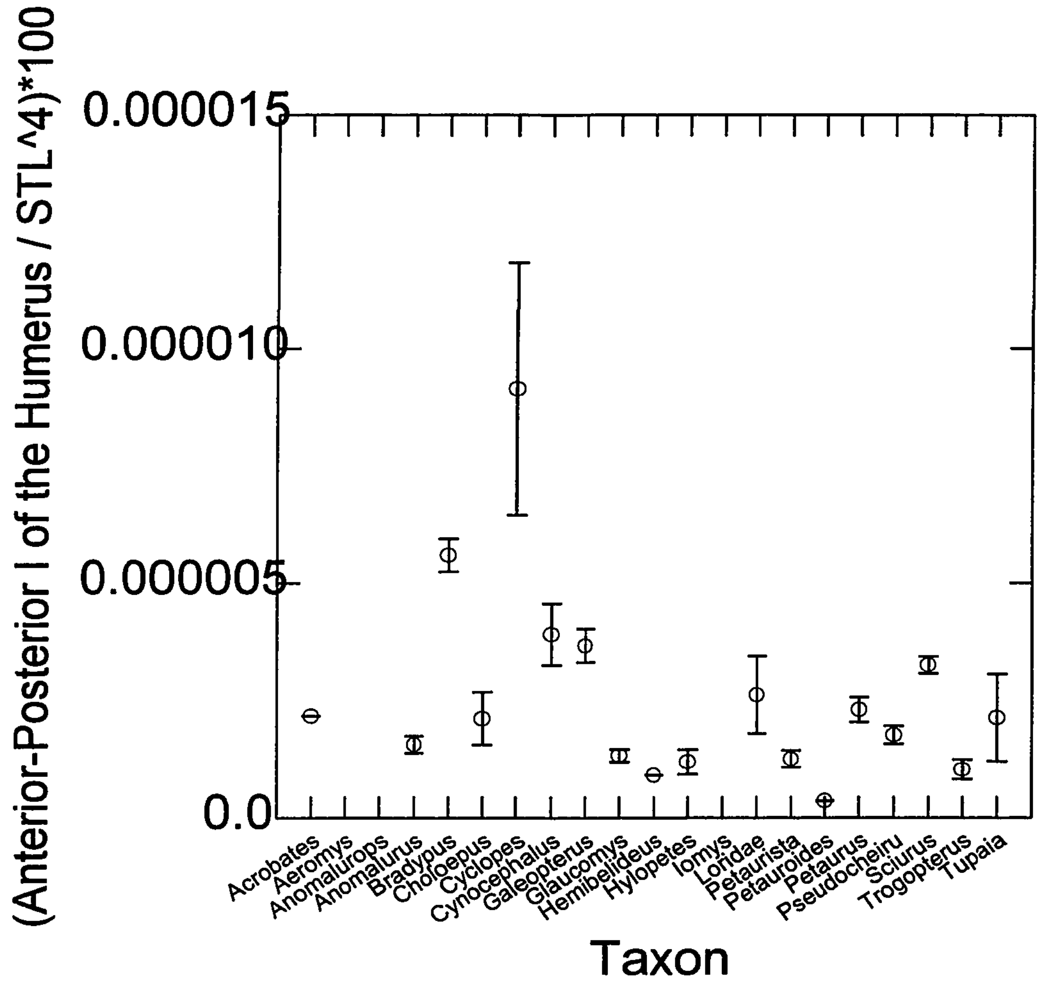

Figure 6.12: Relative anterior-posterior bending moments in the humeri of some mammals. Error bars are one standard error of the mean. Bats have been omitted for clarity. Megachiroptera, $2.48 * 10^{-5} \pm 1.66 * 10^{-6}$; Microchiroptera, $3.52 * 10^{-5} \pm 7.75 * 10^{-6}$.

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The radius.—$\mathbf{TCSA}_{\mathrm{Radius(STL)}}$ again tends to distinguish bats from all other taxa (Fig 6.13). Surprisingly, the bats have relatively large cross sectional areas of this bone. When data are partitioned by locomotor category the bats still have relatively high total cross sectional areas, but there are no significant differences among other locomotor classes. Among gliding mammals the dermopterans have relatively larger total cross sectional areas than most, but not all, of the other gliding mammals. Neither gliding rodents ($t = 3.10$, $df = 43$, $p = 0.0034$) or gliding marsupials ($t = -2.99$, $df = 19$, $p = 0.0075$) have significantly lower $\mathbf{TCSA}_{\mathrm{Radius(STL)}}$ than their nongliding relatives. There are no significant differences in $\mathbf{TCSA}_{\mathrm{Radius(STL)}}$ among dermopteran genera($t = 0.95$, $df = 14$, $p = 0.36$).

$\mathbf{J}_{\mathrm{radius(STL)}}$ also tends to separate the bats from all other taxa, although the picture is more complex here and megachiropterans are not significantly different from many of the other taxa studied here (Fig. 6.14). When the data are partitioned according to locomotion, again only the bats are different from all other locomotor categories. Among gliding mammals the dermopterans appear to be different from Anomalurus only ($p < 0.001$). In rodents ($t = 3.25$, $df = 43$, $p = 0.0020$) and marsupials ($t = -3.27$, $df = 19$, $p = 0.0040$) there are no significant differences among locomotor classes. Within the Dermoptera there are no differences among taxa ($t = 0.93$, $df = 14$, $p = 0.37$).

The story is similar with regard to second moments of area. $\mathbf{I}_{\mathrm{ML,Radius(STL)}}$ (Fig. 6.15) generally distinguishes microchiropterans from all other mammals.

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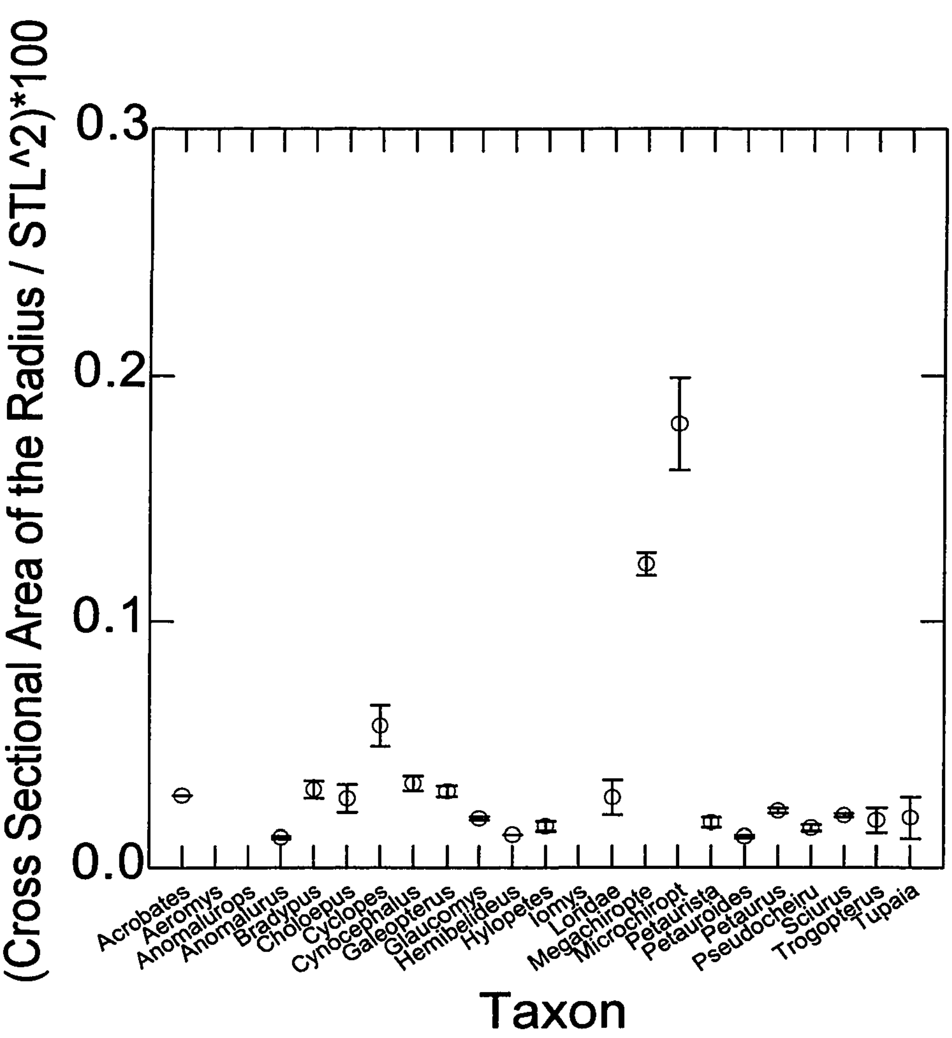

Figure 6.13: Relative cross sectional area of the radius in some mammals. Error bars are one standard error of the mean.

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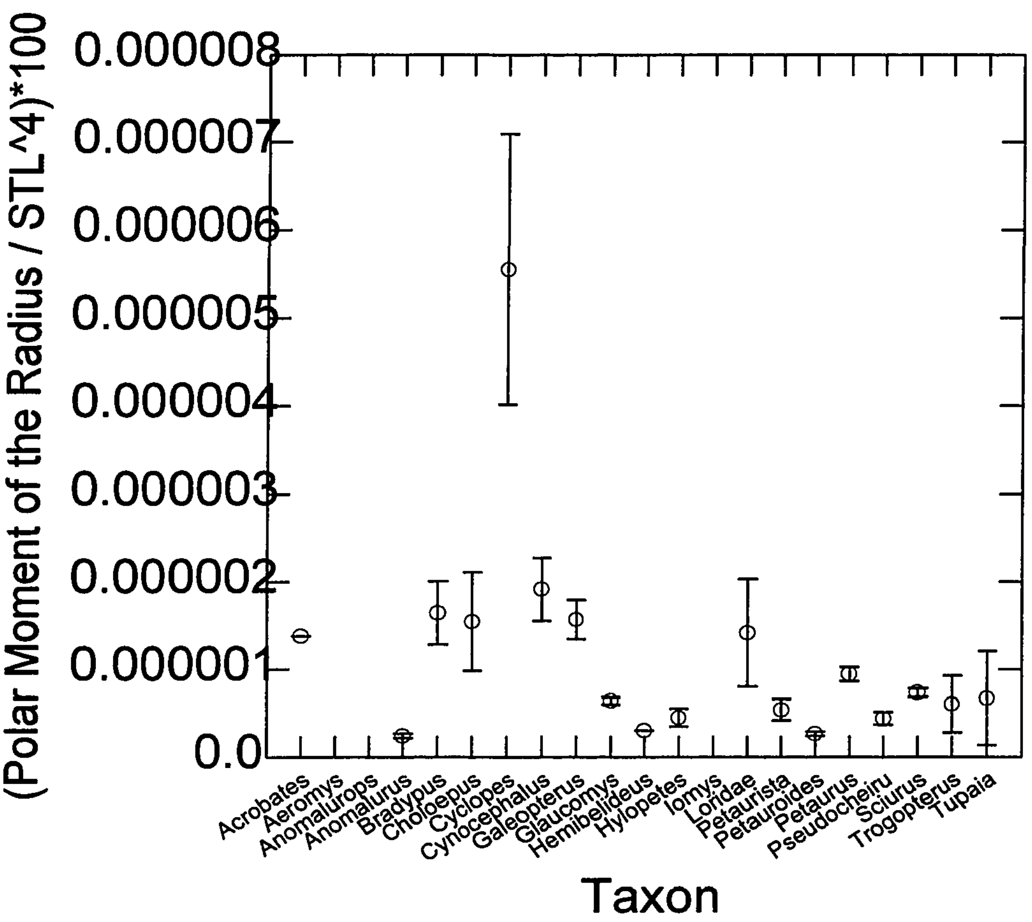

Figure 6.14: Relative polar moment of the radius in some mammals. Error bars are one standard error of the mean. Bats have been omitted for clarity. Megachiroptera, 2.46 * 10^{-5} $\pm$ 9.27 * 10^{-6}; Microchiroptera, 5.70 * 10^{-5} $\pm$ 9.88 * 10^{-6}.

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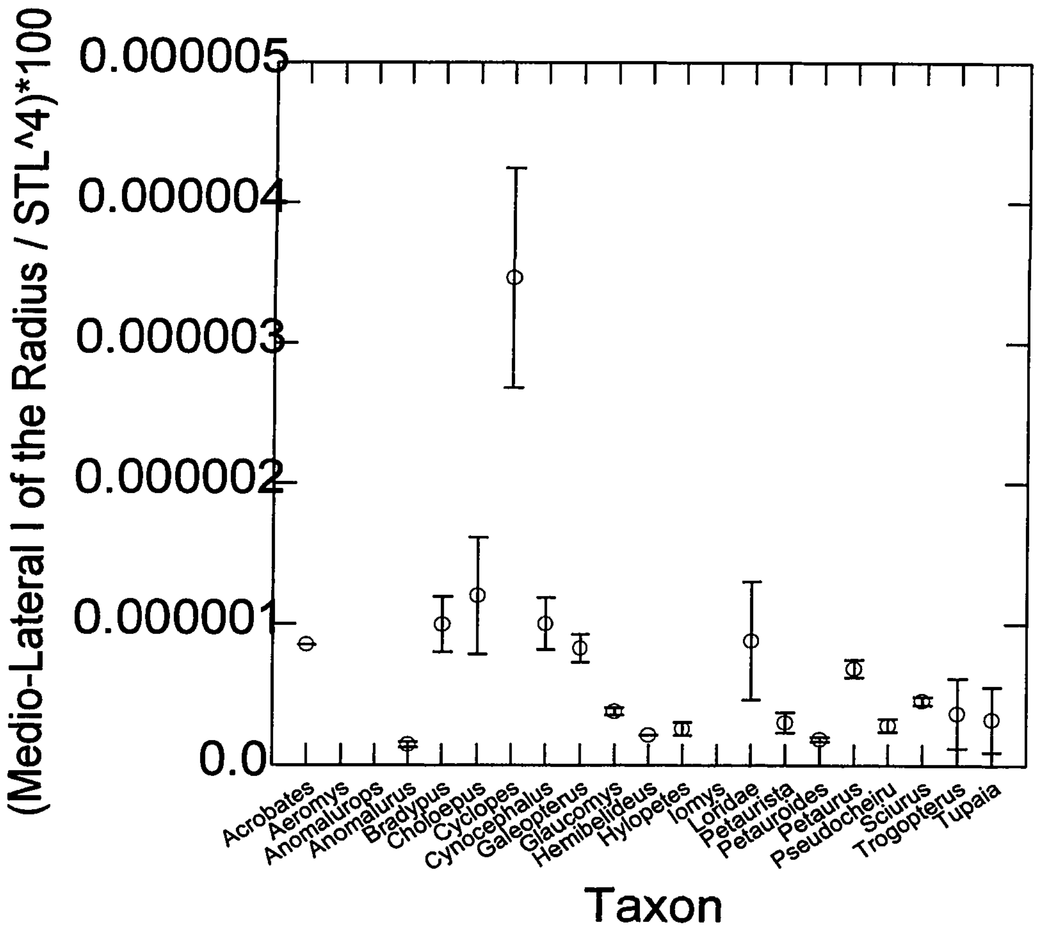

Figure 6.15: Relative medio-lateral bending moments of the radii of some mammals. Error bars are one standard error of the mean. Bats have been omitted for clarity. Megachiroptera, $1.21 * 10^{-5} \pm 8.97 * 10^{-7}$; Microchiroptera, $3.43 * 10^{-5} \pm 7.33 * 10^{-6}$.

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When the bats are removed from the analysis only Cyclopes turns out to be significantly different from all other nonchiopteran taxa ($p < 0.001$). When the data are partitioned according to locomotor categories the bats are different from all other locomotor classes except for the climbing lorids. Among gliding taxa the dermopterans have slightly higher $I_{ML,Radius}$ than some other gliding taxa, but not all of them. Analysis of only the dermopterans, xenarthrans, and lorids shows no significant differences among these taxa with the exception of Cyclopes. Gliding rodents do have lower $I_{ML,Radius}$ than Sciurus ($t = 3.80$, $df = 43$, $p < 0.001$), but there is no significant difference among gliding and arboreal marsupials ($t = -3.62$, $df = 16$, $p = 0.0018$). However, the lack of significance in the marsupials disappears when Petauroides is removed from the analysis. In this case, gliding marsupials have higher $I_{ML,Radius}$ than arboreal marsupials ($t = -5.88$, $df = 17$, $p < 0.001$). There were no significant differences among dermopterans ($t = 0.96$, $df = 14$, $p = 0.3893$). Again, the suggestion is that the dermopteran condition may reflect suspensory or slow climbing locomotion.

$I_{AP,Radius}$ distinguishes megachiropterans and microchiropterans from all other mammals (Fig. 6.16). Among locomotor categories there are significant differences only between the bats and all other locomotor categories. Within gliding mammals there are few significant differences in $I_{AP,Radius}$. However, an analysis of dermopterans, xenarthrans, and lorids shows that there are also no significant differences among these taxa. In rodents there is no significant difference among locomotor classes ($t = 2.20$,

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df = 43, p = 0.0334). The same is true for marsupials (t = -2.09, df = 19, p = 0.0504). There were also no significant differences among dermopterans (t = 0.86 df = 14, p = 0.4066).

Our discussion of limb properties has up to this point focused on aspects of the limbs in relation to the size of the animals. In such comparisons, it has become apparent that bats generally are different from all other mammals and that dermopterans, sloths, and sometimes the lorids often differ in similar ways although not to the same magnitude as the bats. In may cases it is also evident that the dermopterans are quite different from all other gliding mammals. In these cases though it is possible that body size estimators do not give us a clear functional picture of what is going on here. Since bats seem to have relatively long limbs, as well as relatively robust limbs it is possible that the changes in length or cross sectional properties are required to maintain functional equivalence. Specifically, the increase in cross sectional area of bat limb elements may be required to maintain the strength of a relatively long limb element. An analysis of cross sectional properties in relation to limb element length, instead of to a surrogate for body size, is required.

TCSA, J AND I IN RELATION TO LIMB ELEMENT LENGTH

The above results consider limb element lengths, cross sectional areas, polar moments, and second moments of area in relation to body size. In the following section **TCSA**, **J**, and **I** are reevaluated using the length of the component limb element as a scaling factor. Such a treatment is necessary

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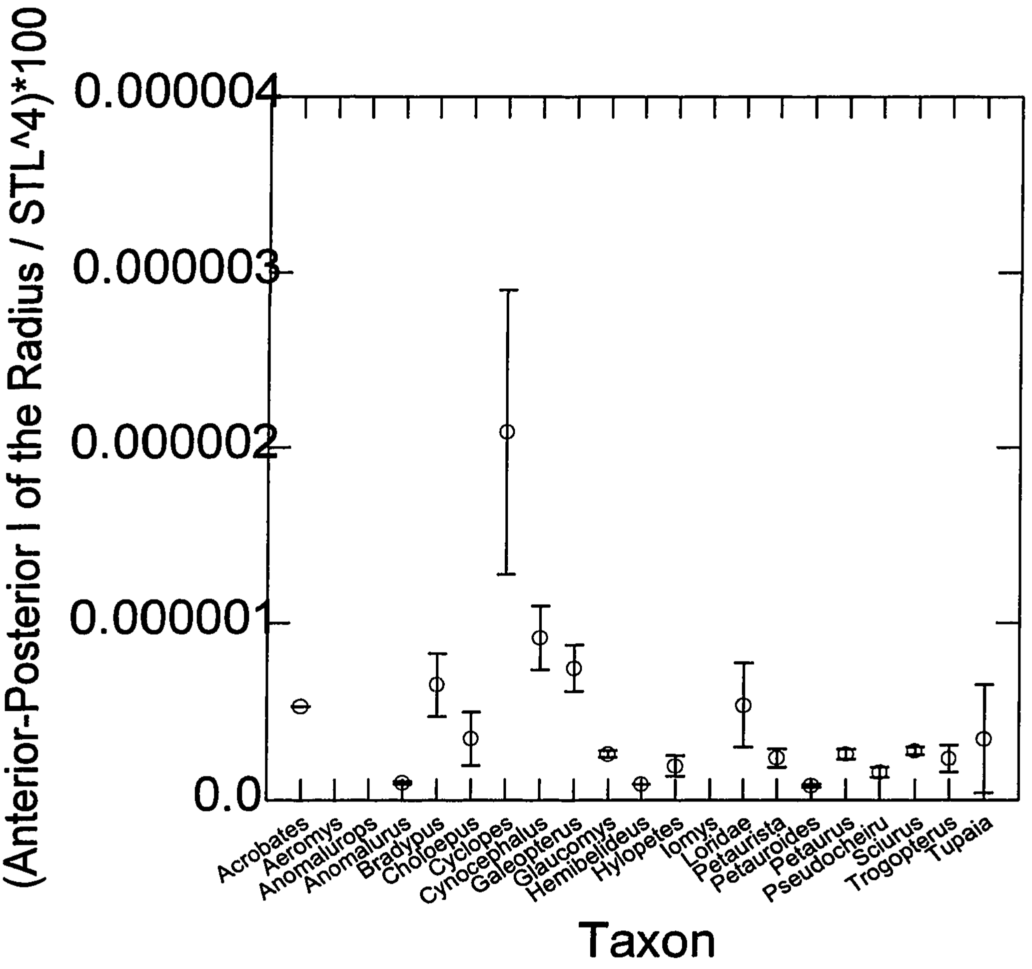

Figure 6.16: Relative anterior-posterior bending moments of the radii of some mammals. Error bars are one standard error of the mean. Bats have been omitted for clarity. Megachiroptera, 1.25 * 10^{-5} ± 9.27 * 10^{-7}; Microchiroptera, 2.27 * 10^{-5} ± 3.00 * 10^{-6}.

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to evaluate whether or not the differences in the above mentioned parameters are related to maintenance of functional equivalence.

The clavice.—There were no significant differences among taxa in terms of clavicular robusticity (Fig. 6.17). When grouped by locomotor category only the gliding mammals, with the lowest robusticity values, were different from the bats, with the highest robusticity values. However, within orders, gliding rodents have less robust clavicles than Sciurus ($t = 6.94$, $df = 50$, $p < 0.0005$) and gliding marsupials have less robust clavicles than arboreal marsupials ($t = 5.75$, $df = 19$, $p < 0.001$). There are no significant differences among dermopterans ($t = 2.37$, $df = 14$, $p = 0.0326$).

There are also no significant differences among the taxa studied here for $J_{Clavicle}$ corrected for clavicle length (Fig. 6.18). When the taxa are grouped according to locomotor category the only significant difference is between the bats and the gliding mammals ($p < 0.001$). The bats having the relatively highest polar moments of the clavicle and the gliding mammals having the lowest. Among gliding mammals there were no significant differences among taxa. In this analysis both rodent and marsupial gliders have lower $J_{Clavicle(Clav)}$ than their nongliding relatives (rodents, $t = 8.79$, $df = 50$, $p < 0.001$; marsupials, $t = 5.48$, $df = 19$, $p < 0.001$). Among dermopterans there was no significant difference ($t = 1.73$, $df = 14$, $p = 0.10$) in $J_{Clavicle(Clav)}$.

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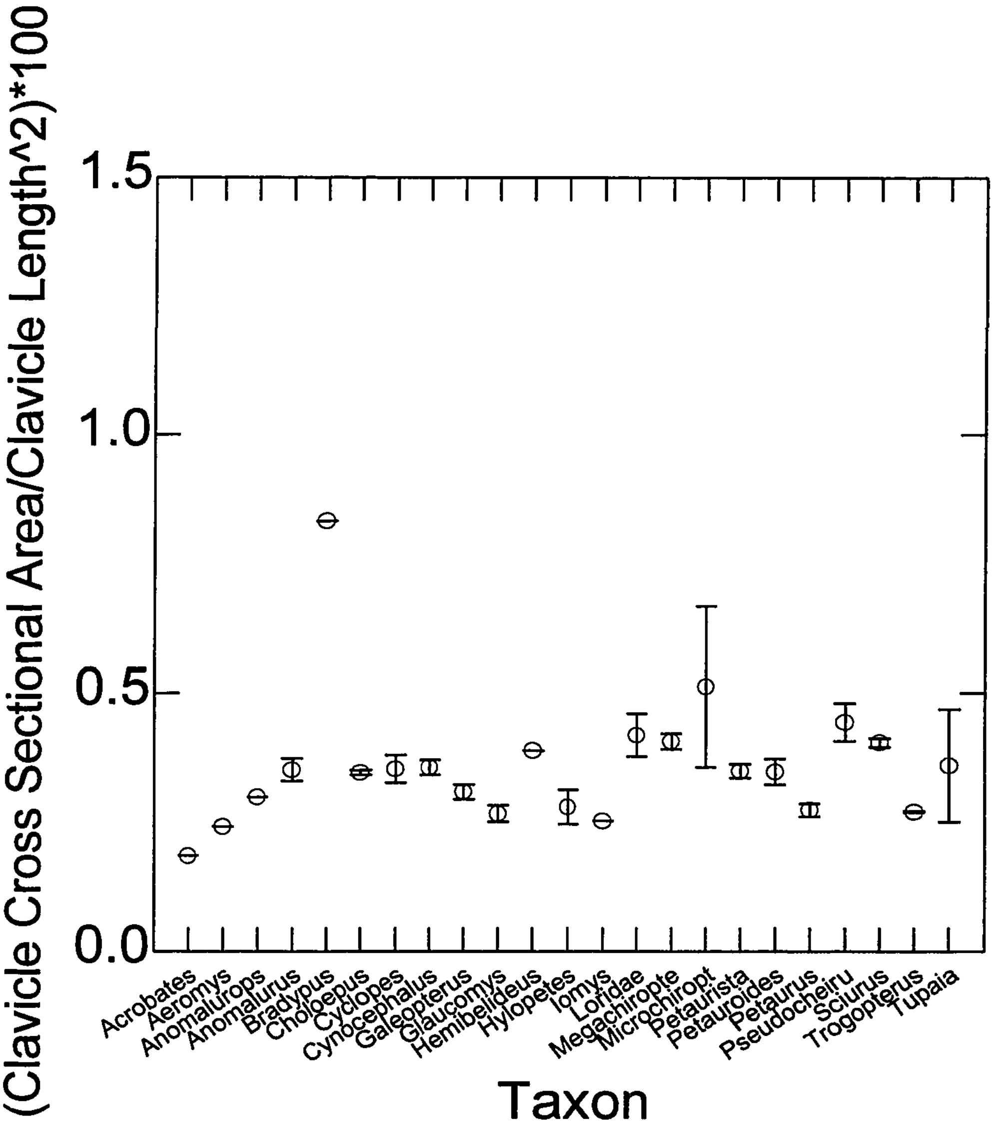

Figure 6.17: Clavicle robusticity in some mammals. Error bars are one standard error of the mean.

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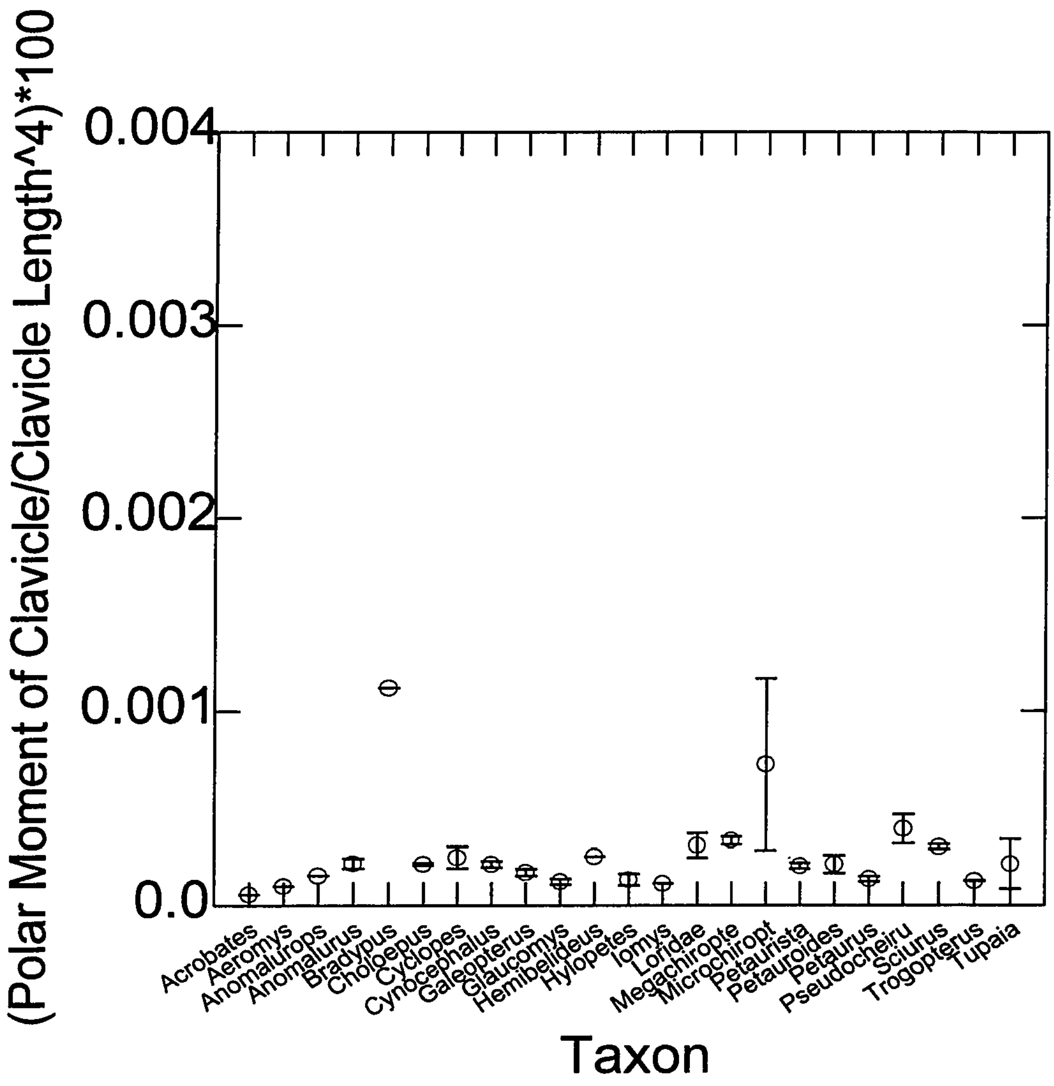

Figure 6.18: Polar moments of the clavicle in some mammals, corrected for clavicle length. Error bars are one standard error of the mean.

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When looking at $I_{ML,Clavicle(Clav)}$ and $I_{AP,Clavicle(Clav)}$ (i.e., bending moments corrected by clavicle length, Fig. 6.19, 6.20) we again see that there are far fewer differences than when these measures were corrected for body size. There are no differences among taxa for $I_{ML,Clavicle(Clav)}$, nor are there any significant differences for $I_{AP,Clavicle(Clav)}$. When grouped by locomotion the only difference in $I_{ML,Clavicle(Clav)}$ is between the gliders with the lowest values, and the bats with the highest values, and there are no significant differences among locomotor classes for $I_{AP,Clavicle(Clav)}$. Among rodents there are significant differences among gliders and Sciurus for $I_{ML,Clavicle(Clav)}$ ($t = 10.30$, $df = 50$, $p < 0.001$), and for $I_{AP,Clavicle(Clav)}$ ($t = 3.89$, $df = 50$, $p < 0.001$), with the gliding rodents having the lower values. Among the marsupials the situation is similar, with the gliding marsupials having significantly lower values for $I_{ML,Clavicle(Clav)}$ ($t = 5.08$, $df = 19$, $p < 0.001$),and for $I_{AP,Clavicle(Clav)}$ ($t = 5.05$, $df = 19$, $p < 0.001$). There were no significant differences among dermopterans ($I_{ML,Clavicle(Clav)}$, $t = 0.84$, $df = 14$, $p = 0.4155$; $I_{AP,Clavicle(Clav)}$, $t = 3.51$, $df = 14$, $p = 0.0035$).

The humerus.—In terms of humeral robusticity, Cyclopes is different from all other taxa studied here, and Pseudocheirus and Sciurus are different from many of the other taxa studied here (Fig. 6.21). Surprisingly, the arboreal taxa and the suspensory taxa have higher humeral robusticity values than the bats, gliding mammals, and lorids. However when only the dermopterans, lorids, and sloths are analyzed, there are no significant differences among these taxa. This suggests that the high robusticity values of suspensory taxa

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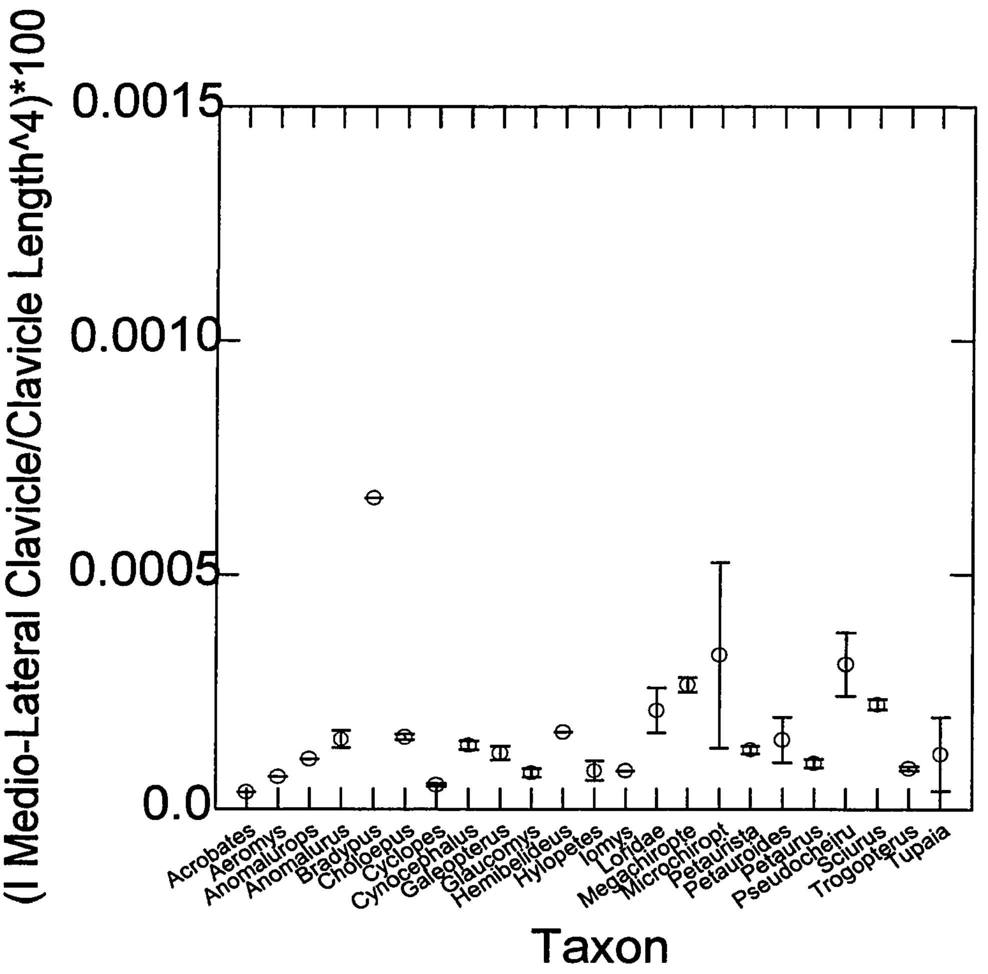

Figure 6.19: Medio-lateral bending moments of the clavicle in some mammals, corrected for clavicle length. Error bars are one standard error of the mean.

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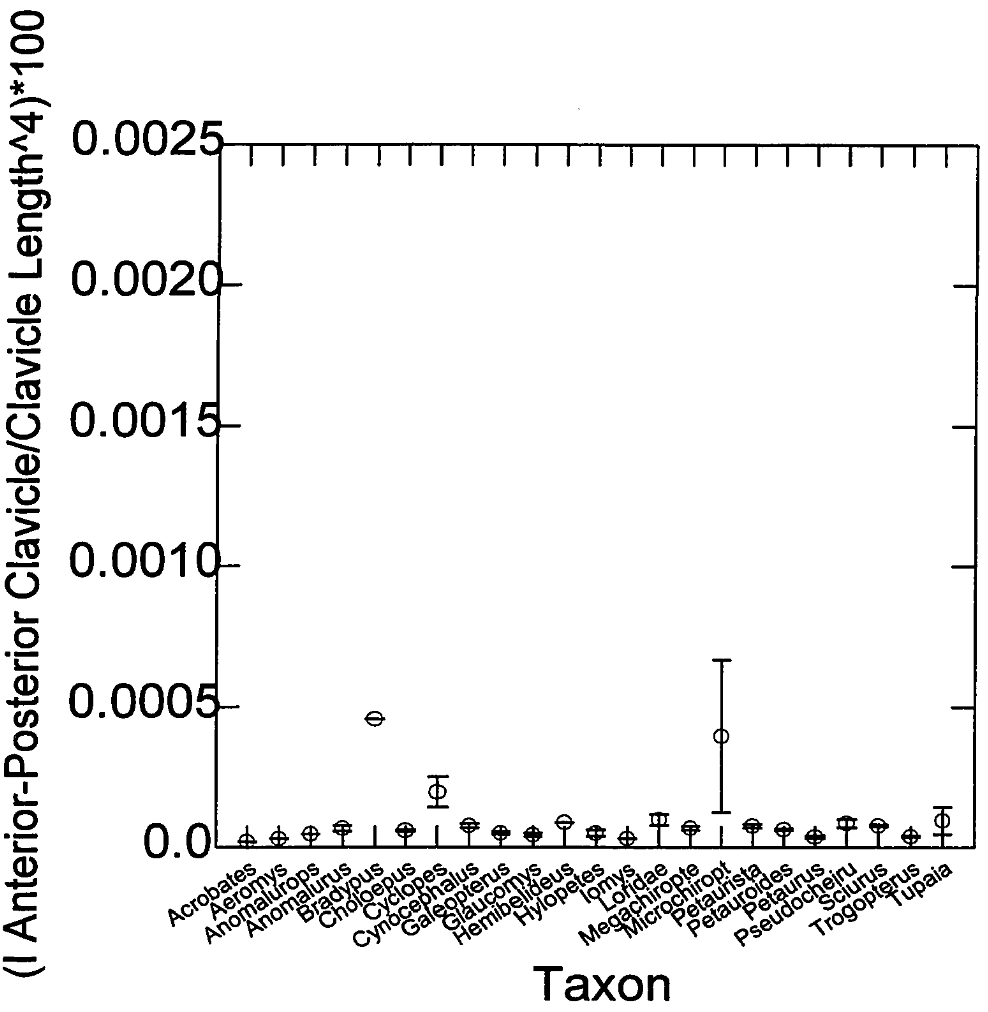

Figure 6.20: Anterior-posterior bending moments of the clavicle in some mammals, corrected for clavicle length. Error bars are one standard error of the mean.

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are due to the inclusion of Cyclopes in this category. Among gliding mammals, most of the differences are between Petaurus, with relatively high robusticity values, and other taxa. However, Galeopterus also has lower robusticity values than Glaucomys, Hylopetes, and Petaurus. In both rodents and marsupials, gliding taxa have lower values of humeral robusticity than their arboreal relatives (rodents, $t = 16.46$, $df = 52$, $p < 0.0005$; marsupials, $t = 6.77$, $df = 21$, $p < 0.0005$). Among dermopterans Galeopterus has a significantly less robust humerus than Cynocephalus ($t = 5.01$, $df = 17$, $p < 0.001$). Relatively gracile humeri then are characteristic of gliding mammals, bats, and sloths; but it is not possible to distinguish between these groupings.

For the polar moment of the humerus corrected for humerus length, only Cyclopes is significantly different from all other taxa studied here having higher polar moments (Fig. 6.22). Pseudocheirus and Sciurus are also different from many of the other taxa studied here. When the data are partitioned according to locomotor category we see that the Xenarthrans have higher values than arboreal taxa, gliders, and the bats, but not than the lorids. Among the gliding mammals only Petaurus has higher $J_{Humerus(Hum)}$ than any of the other gliding taxa. Among rodents ($t = 15.56$, $df = 52$, $p < 0.001$) and marsupials ($t = 6.55$, $df = 21$, $p < 0.001$) gliders have significantly lower values for $J_{Humerus(Hum)}$. Among dermopterans Cynocephalus has significantly higher $J_{Humerus(Hum)}$ than does Galeopterus ($t = 5.09$, $df = 17$, $p < 0.001$).

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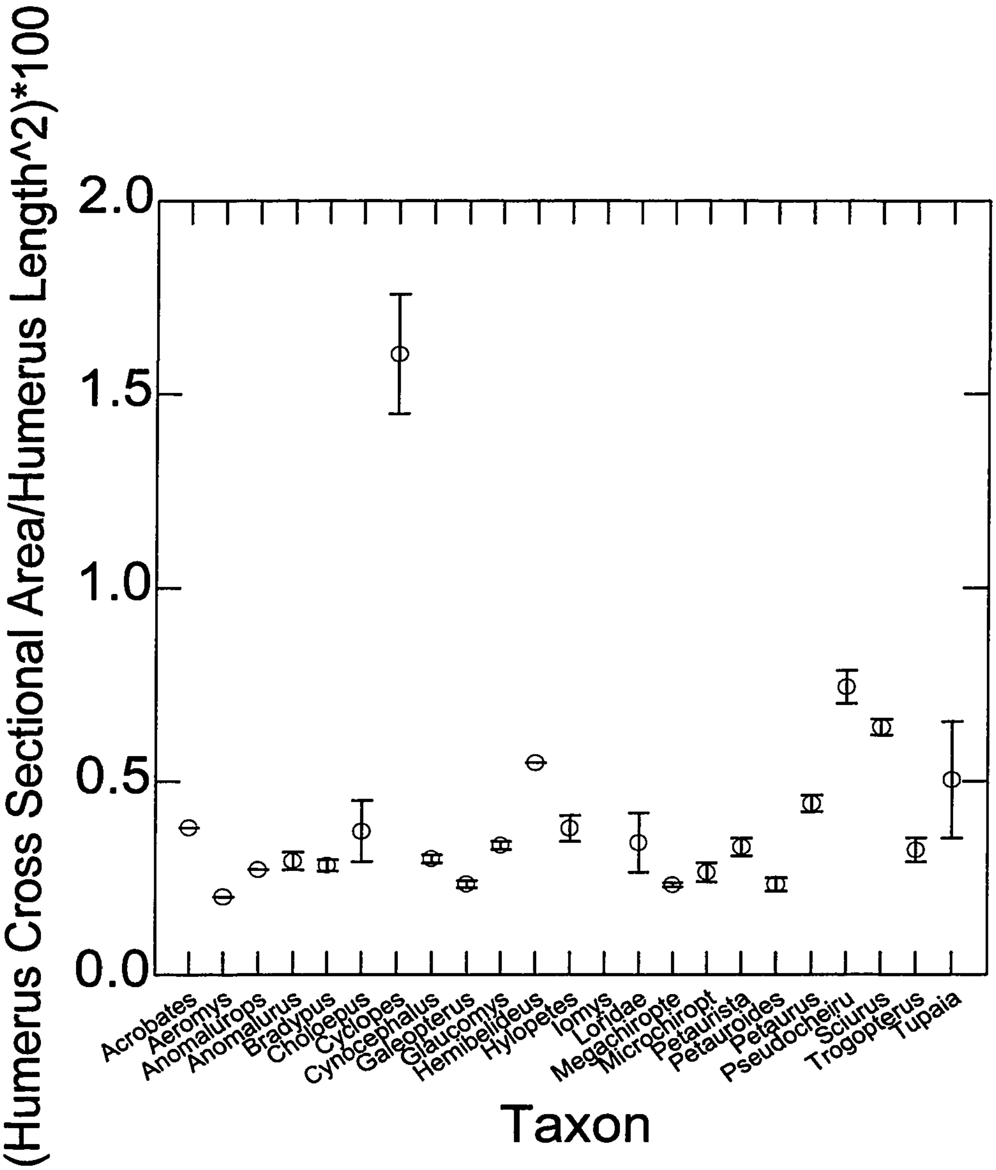

Figure 6.21: Humeral robusticity in some mammals. Error bars are one standard error of the mean.

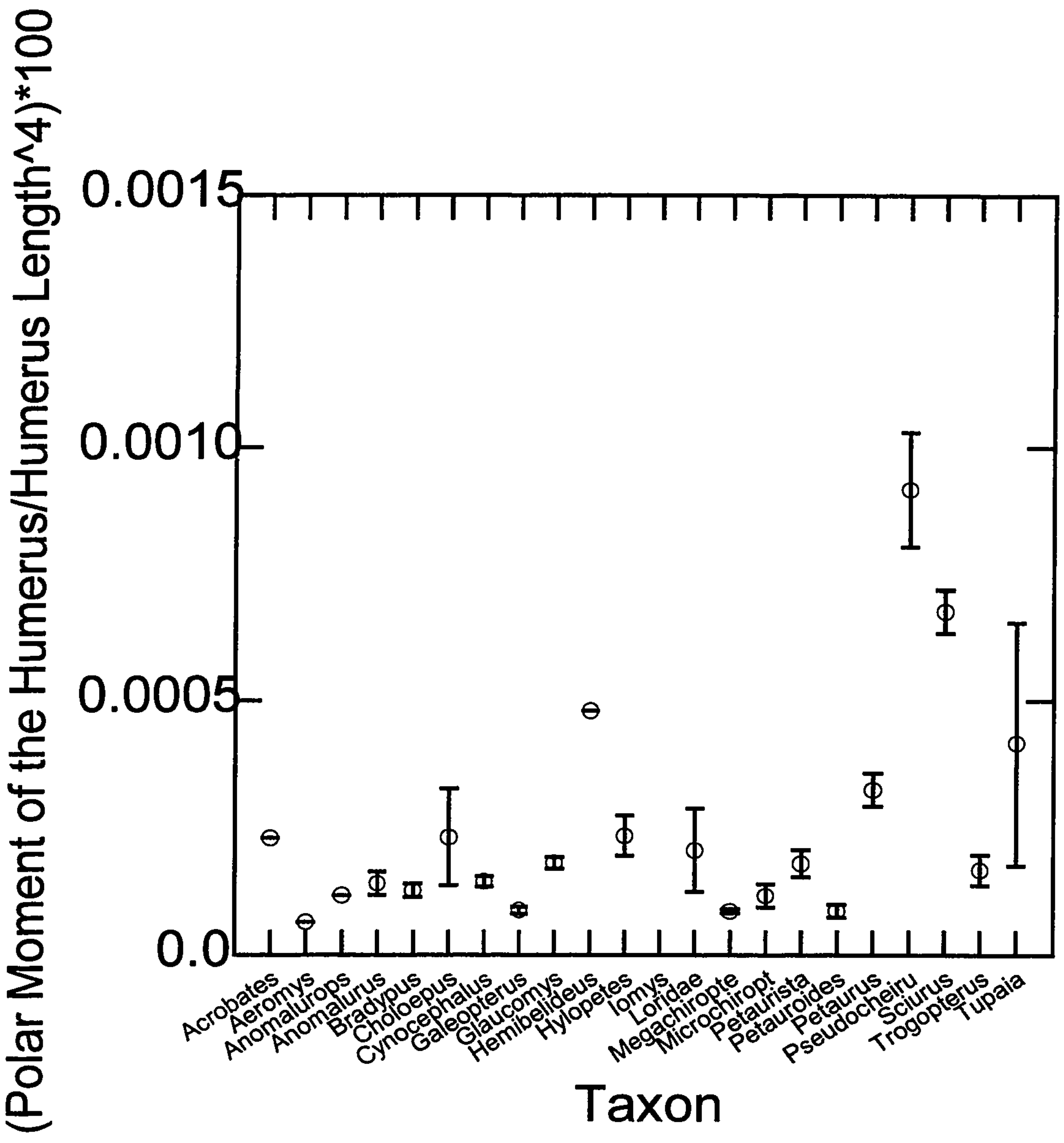

Figure 6.22: Polar moments of the humeri in some mammals, corrected for humerus length. Error bars are one standard error of the mean. Cyclopes omitted for clarity, 0.005 ± 0.001.

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For $I_{ML,Humerus(Hum)}$ and $I_{AP,Humerus(Hum)}$ Cyclopes is different from all other taxa studied here (Fig. 6.23, 6.24). In addition, Pseudocheirus and Sciurus are also different from most of the other taxa studied here for $I_{AP,Humerus(Hum)}$. When taxa are grouped according to locomotor category we find that suspensory taxa have relatively higher $I_{ML,Humerus(Hum)}$ than the other locomotor categories ($p < 0.001$) with the exception of the climbers. This may be largely due to the inclusion of Cyclopes in the suspensory locomotor category. Suspensory taxa are also higher in $I_{AP,Humerus(Hum)}$ than flying or gliding mammals, but so are the arboreal taxa. Among gliding mammals Petaurus has higher $I_{ML,Humerus(Hum)}$ and higher $I_{AP,Humerus(Hum)}$ of the humerus than most of the other taxa studied here. Among rodents the gliders have lower $I_{ML,Humerus(Hum)}$ ($t = 14.91$, $df = 52$, $p < 0.001$) and lower $I_{AP,Humerus(Hum)}$ ($t = 15.46$, $df = 52$, $p < 0.001$) than do Sciurus. Among marsupials, the gliders have lower $I_{ML,Humerus(Hum)}$ ($t = 8.24$, $df = 21$, $p < 0.001$) and lower $I_{AP,Humerus(Hum)}$ ($t = 5.65$, $df = 21$, $p < 0.001$) than the arboreal marsupials. Among dermopterans $I_{ML,Humerus(Hum)}$ is not significantly different among taxa ($t = 3.68$, $df = 17$, $p = 0.0018$), but $I_{AP,Humerus(Hum)}$ is ($t = 5.15$, $df = 17$, $p < 0.001$). In this analysis we again see that dermopterans seem to cluster well with other gliding mammals. We also see that bats no longer stand out so starkly from other mammals.

The radius.—Radial robusticity is higher in Cyclopes than in all other mammals, and is also higher in Sciurus than most of the other mammals

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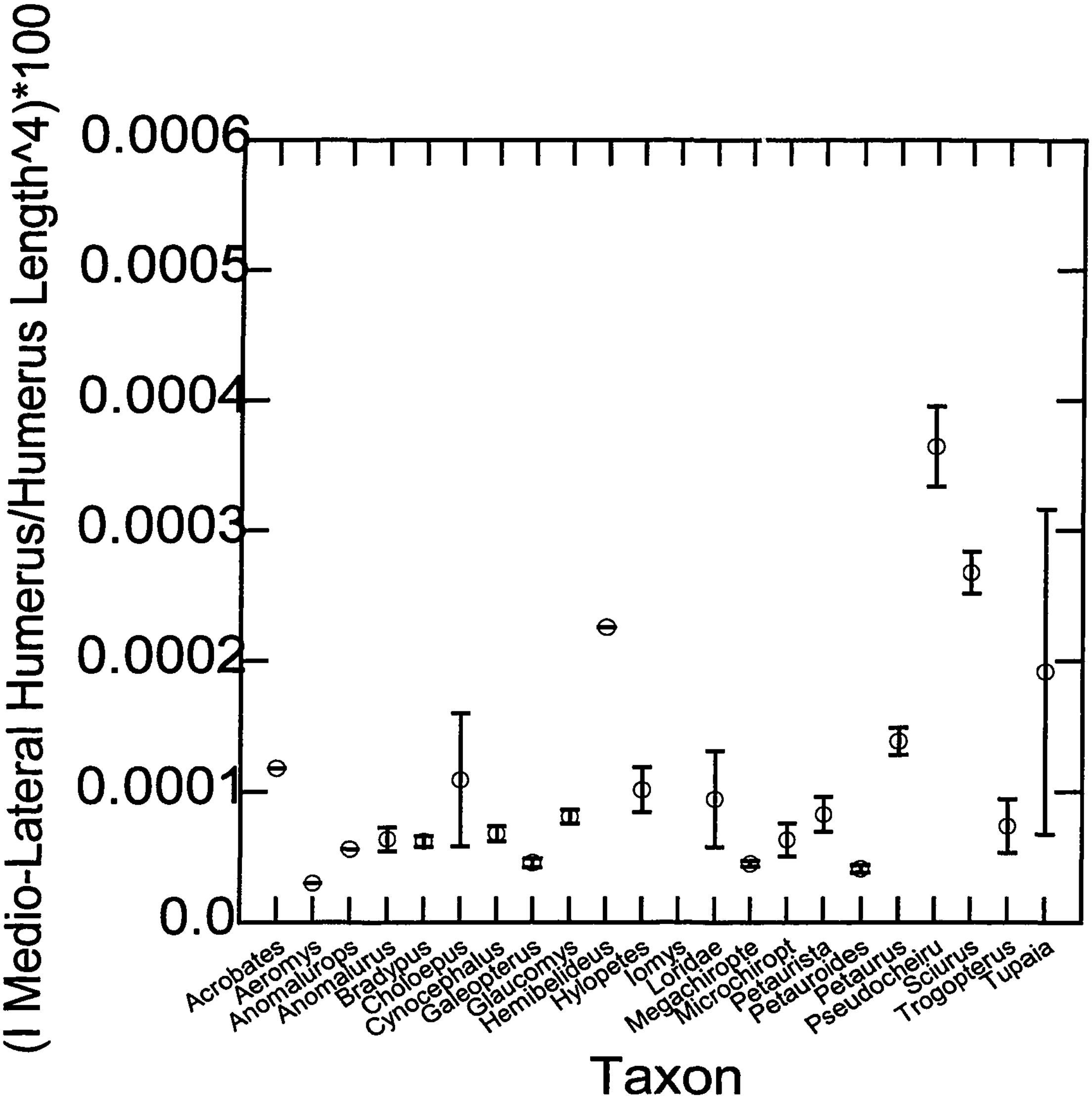

Figure 6.23: Medio-lateral bending moments of the humerus in some mammals, corrected for humerus length. Error bars are one standard error of the mean. Cyclopes omitted for clarity, 0.003 ± 4.49 * 10^{-4}.

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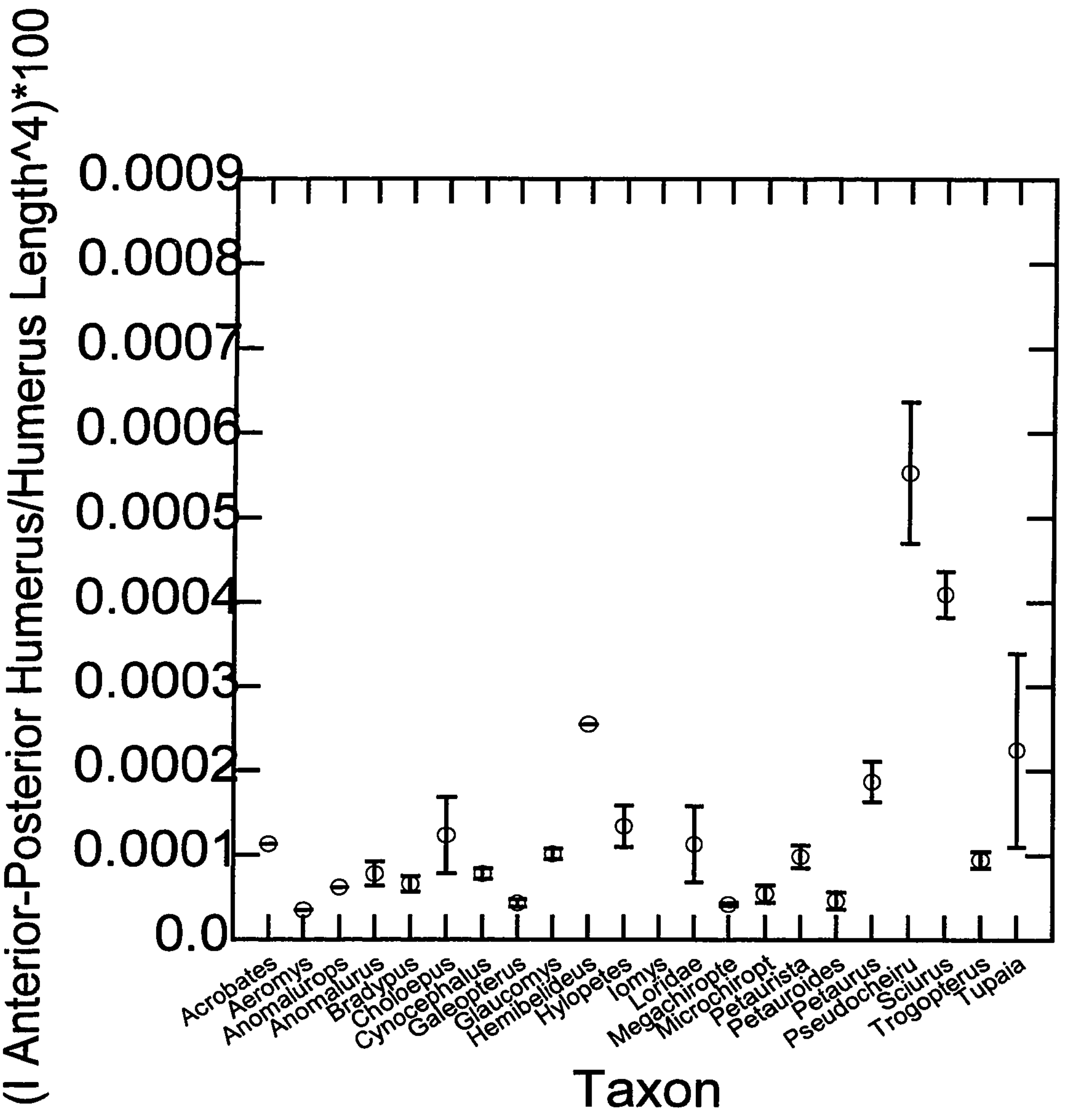

Figure 6.24: Anterior-posterior bending moments of the humerus in some mammals, corrected for humerus length. Error bars are one standard error of the mean. *Cyclopes* omitted for clarity, $0.001 \pm 2.24 * 10^{-4}$.

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studied here (Fig. 6.25). Among locomotor categories, bats and gliding mammals have lower robusticity values than arboreal and suspensory taxa, but again Cyclopes distorts the position of the sloths. When only dermopterans, lorids, and sloths are analyzed there are no significant differences among these taxa in terms of radial robusticity. In both the rodents and marsupials, the gliders have lower robusticity values than the arboreal taxa (rodents, $t = 16.46$, $df = 52$, $p < 0.001$; marsupials, $t = 6.77$, $df = 21$, $p < 0.001$). There are also significant differences among dermopterans with Galeopterus having less robust radii ($t = 5.02$, $df = 17$, $p < 0.001$).

For the polar moments of the radius again Cyclopes is significantly different from all other taxa (Fig. 6.26), and dermopterans and bats are no longer different from other mammals. When partitioned by locomotor category the Xenarthrans are again higher than arboreal, gliding and flying taxa, although again, the inclusion of Cyclopes in this category is largely responsible for this difference. Among gliding mammals Galeopterus and Petauroides are both different from many of the other gliding mammals, but Galeopterus has the lowest values of all the gliding mammals, and Petauroides has the highest values. It is interesting that Aeromys, the anomalurids, and the dermopterans cluster around the lower end of the distribution for gliding mammals, but these differences are not

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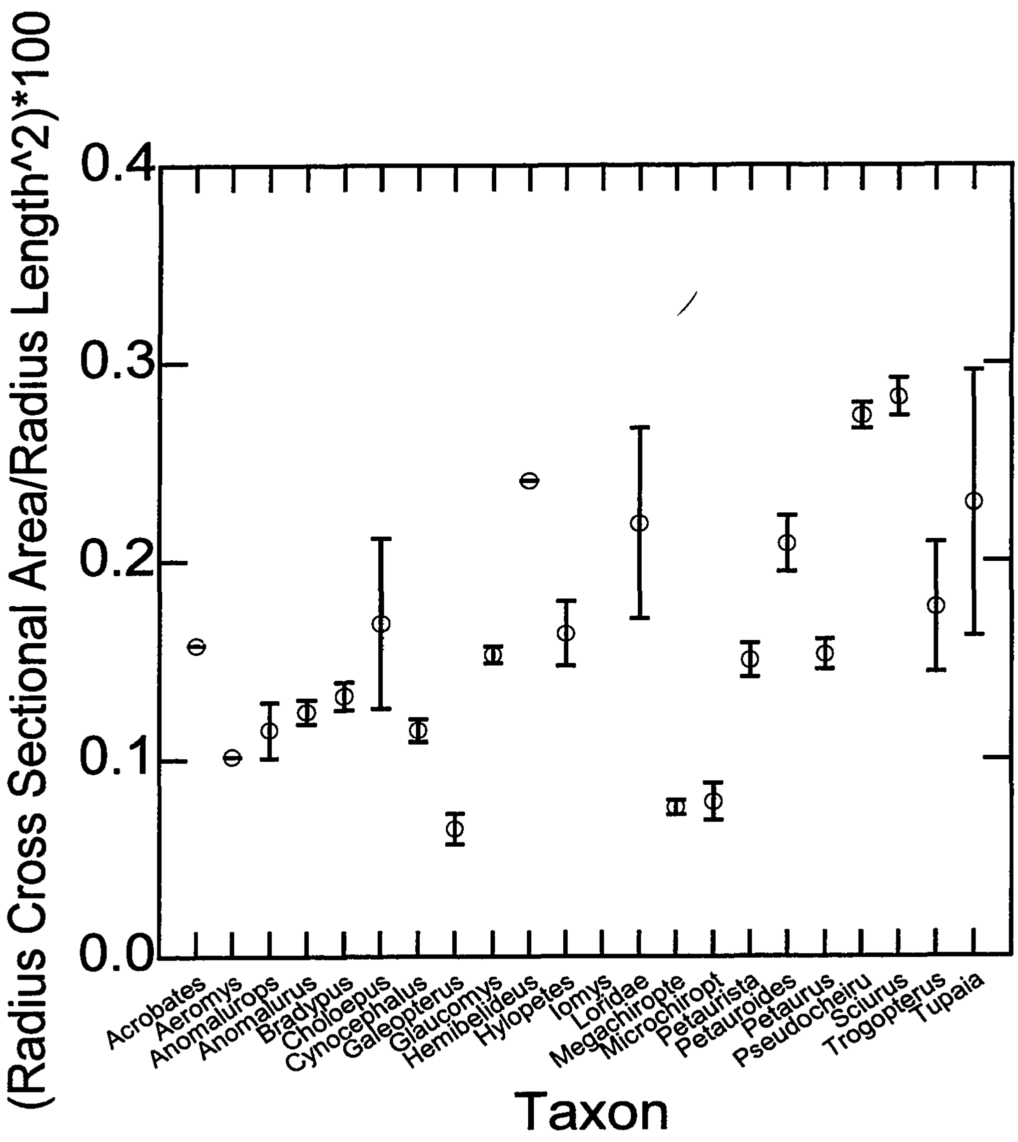

Figure 6.25: Radius robusticity in some mammals. Error bars are one standard error of the mean. Cyclopes omitted for clarity, 1.43 ± 0.09.

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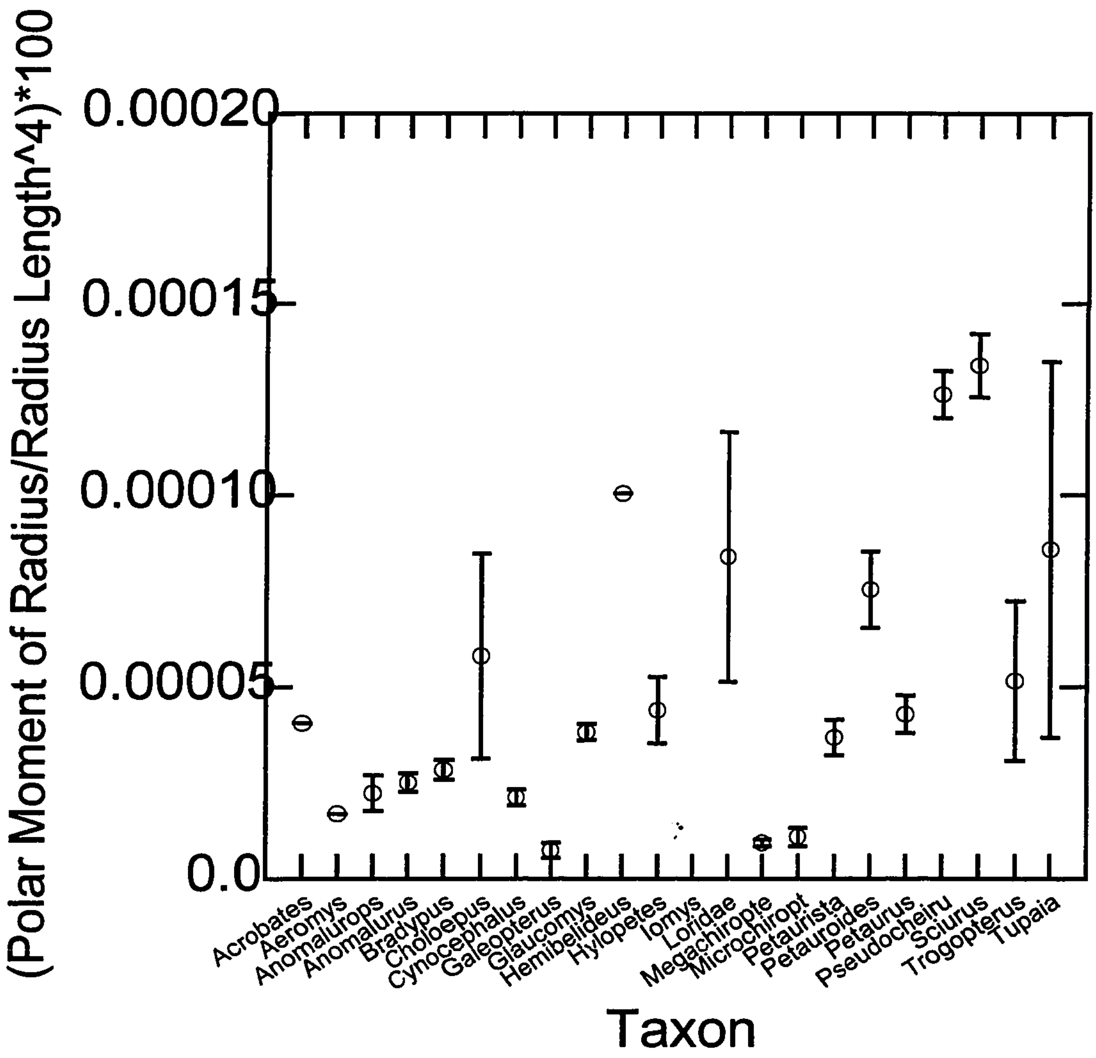

Figure 6.26: Polar moments of the radius in some mammals, corrected for radius length. Error bars are one standard error of the mean. <u>Cyclopes</u> omitted for clarity, 0.003 ± 4.96 * 10^{-4}.

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significant in this sample. Even more interesting is the fact that the bats also cluster very low in this distribution, very close to the value for Galeopterus. In both rodents and marsupials the gliders have lower relative $J_{radius(Rad)}$ (rodents, $t = 15.77$, $df = 53$, $p < 0.001$; marsupials, $t = 9.69$, $df = 19$, $p < 0.001$). Among the dermopterans Cynocephalus has relatively higher $J_{radius(Rad)}$ ($t = 5.20$, $df = 16$, $p < 0.001$). Again, dermopterans, especially Galeopterus, seem different from other gliding mammals in the same way as bats. The pattern of this clustering is certainly different from what one would predict for the bats. Given the high forces that one would expect to be acting on the bat wing during flight, and the necessary extremes of pronation and supination occurring in the wing beat cycle (Swartz, 1998) one would predict relatively high resistance to torsion in the radius of bats.

For both relative $I_{ML,Radius(Rad)}$ and $I_{AP,Radius(Rad)}$ Cyclopes has higher values than all other taxa (Fig. 6.27, 6.28). When taxa are grouped according to locomotor categories suspensory taxa have higher values for I_{ML} and I_{AP} than all other locomotor categories except the climbing taxa. Among gliding mammals Galeopterus has lower values than many of the other gliding mammals, and Petauroides has higher values for $I_{ML,Radius(Rad)}$ than many other taxa. Again we see that the bats tend to cluster near the lower end of this distribution along with Galeopterus. In both rodents and marsupials bending moments are lower in the gliding taxa ($I_{ML,Radius(Rad)}$: rodents, $t = 17.07$, $df = 53$, $p < 0.001$; marsupials, $t = 7.17$, $df = 19$, $p < 0.001$. $I_{AP,Radius(Rad)}$:

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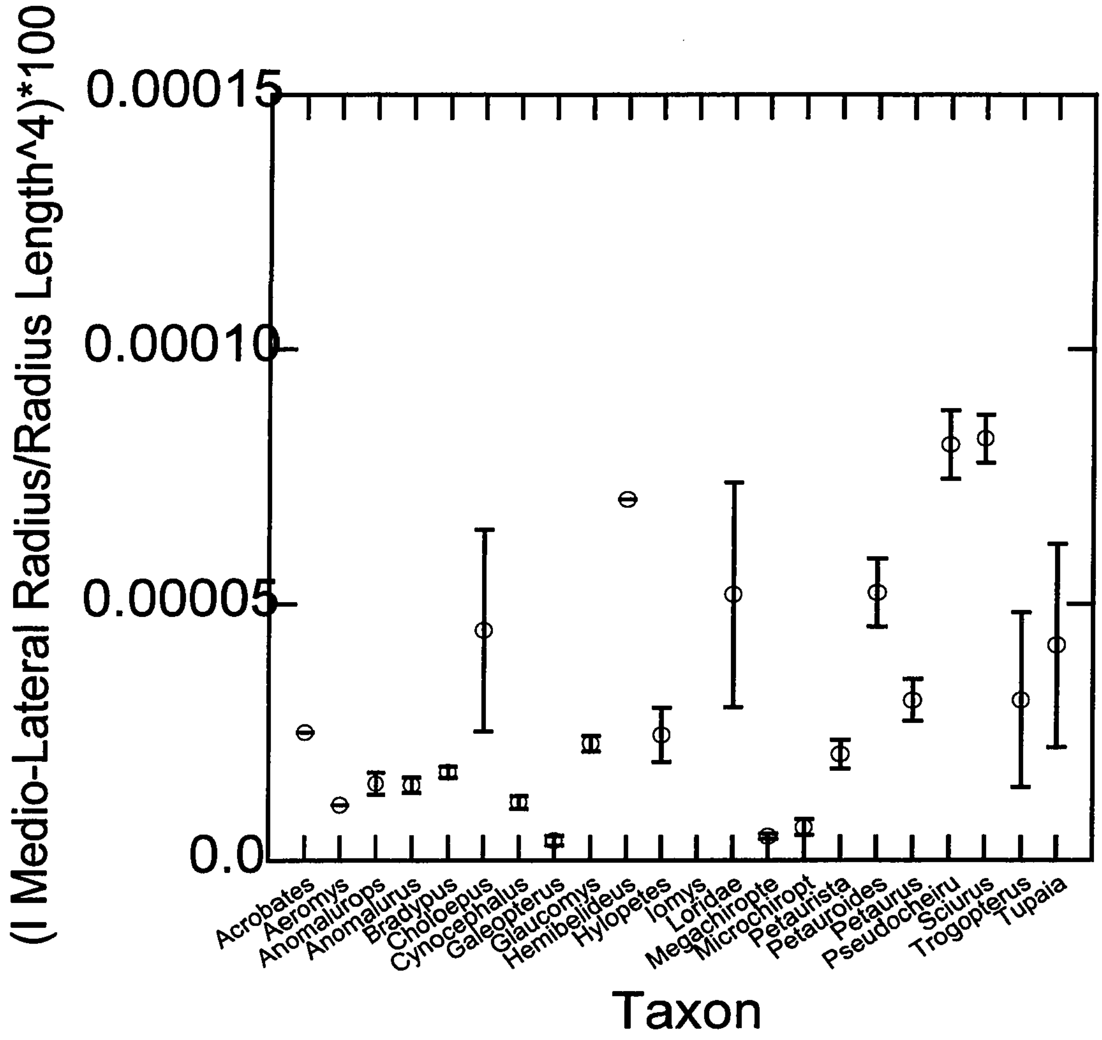

Figure 6. 27: Medio-lateral bending moments of the radius in some mammals, corrected for radius length. Error bars are one standard error of the mean. *Cyclopes* omitted for clarity, $0.002 \pm 4.20 * 10^{-4}$.

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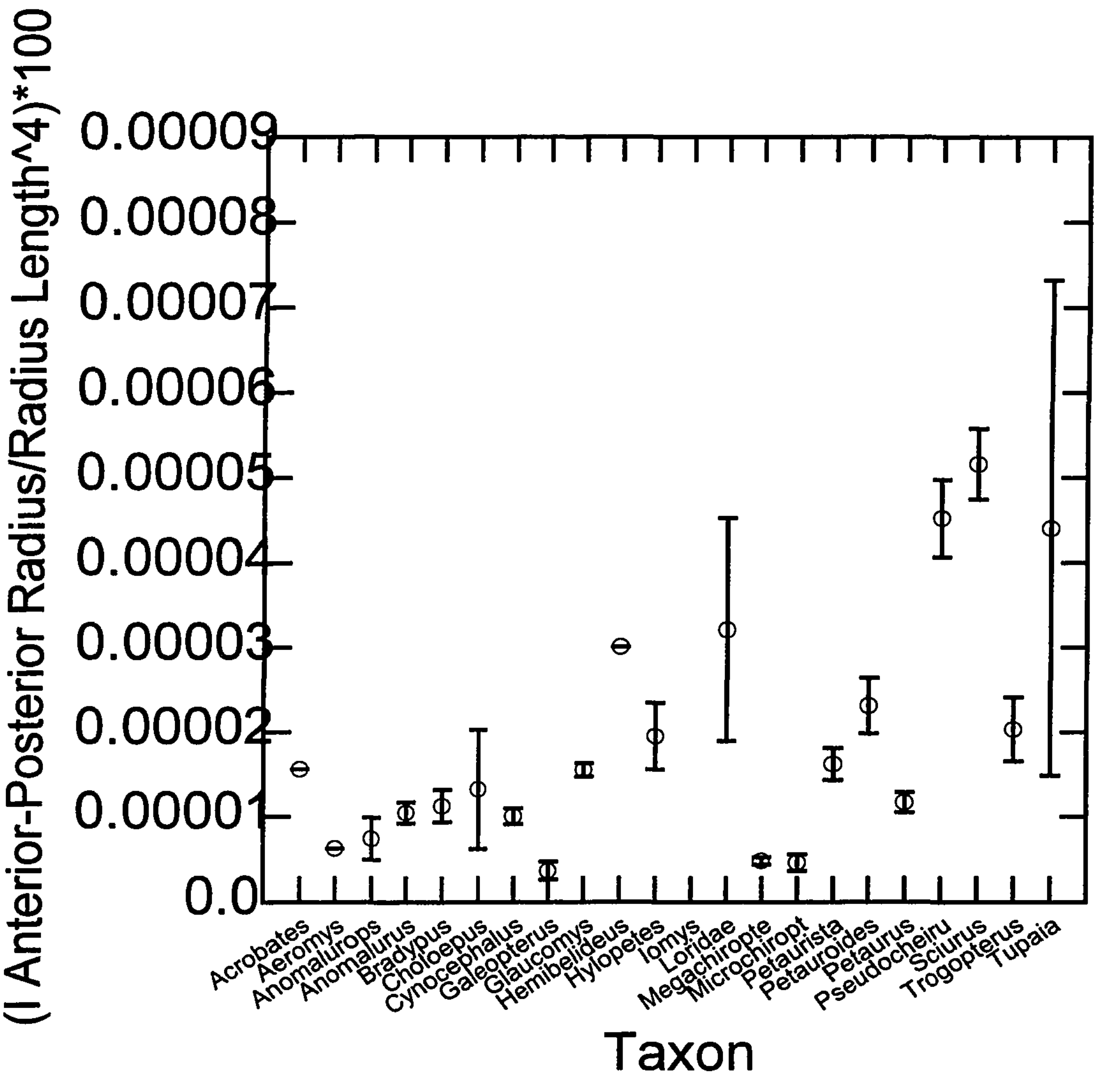

Figure 6.28: Anterior-posterior bending moments of the radius in some mammals, corrected for radius length. Error bars are one standard error of the mean. <u>Cyclopes</u> omitted for clarity, 0.001 ± 1.55 * 10^{-4}.

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rodents, t = 12.07, df = 53, p < 0.001; marsupials, t = 8.07, df = 19, p < 0.001). Within the Dermoptera Cynocephalus has higher values for both $I_{ML,Radius(Rad)}$ and $I_{AP,Radius(Rad)}$ than Galeopterus ($I_{ML,Radius(Rad)}$ t=5.16, df=16, p<0.001; $I_{AP,Radius(Rad)}$ t=4.89, df=16, p<0.001).

THE SCAPULA

Length of the scapular spine.—Megachiropterans, microchiropterans, Acrobates, Cyclopes, Tupaia, and Sciurus all have relatively longer scapular spines than the other taxa studied here. The bats are statistically different from all other taxa (p < 0.001) except Acrobates, Cyclopes, Hemibelideus, Iomys, and Tupaia. However, Acrobates, Cyclopes, Hemibelideus, Iomys, and Tupaia are not statistically different from any other taxa studied here. An analysis of all taxa exclusive of the bats was not performed because the bats are not drastically different from the other taxa in the sample in this measure. When the data are grouped according to locomotor category, bats show significantly higher values for the relative length of the scapular spine than any other locomotor category (p < 0.001). When only gliding mammals are analyzed, Acrobates has significantly higher values than all other gliding mammals (p < 0.001). When only sciurids are analyzed, Sciurus has a significantly longer dorsal scapular spine than do the pteromyines (t = 8.099, df = 46, p < 0.001). However, there was no significant difference between gliding and arboreal marsupials (t = -1.726, df = 20, p = 0.101), or between dermopterans (t = -0.172, df = 14, p = 0.860).

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Length of the vertebral border of the scapula.—Bats have significantly longer vertebral borders of the scapula ($p < 0.001$) than the other mammals studied here. However, dermopterans, *Bradypus* and *Cyclopes* also all have high values for this measure. When the bats are removed from the analysis, dermopterans, *Bradypus* and *Cyclopes* are still different from some of the other taxa, but they are not now different from one half of the taxa studied, and the differences that are seen do not break down along phylogenetic lines. When taxa are grouped by locomotor category, bats have significantly higher values than all other locomotor categories ($p < 0.001$), but there are no significant differences among any other locomotor categories. Among gliding mammals, dermopterans have significantly higher values that all other taxa ($p < 0.001$) except *Acrobates*, *Anomalurus*, and *Iomys*. Among rodents, gliding taxa have relatively shorter vertebral borders of the scapula than *Sciurus* ($t = 6.573$, df = 46, $p < 0.001$). Among diprotodontians there were no significant differences among locomotor categories ($t = -0.031$, df = 20, $p = 0.976$). There was no difference between the dermopteran genera ($t = 0.208$, df = 14, $p = 0.866$).

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CHAPTER 7: THE PHALANGES

Dermopterans have unique hands. Characters from the hands and the wrist have been used in numerous studies concerned with the interordinal relationships of the dermopterans (Beard, 1989, 1990, 1993; Grasse, 1955; Pocock, 1926; Shufelt, 1911; Stafford and Thorington, 1998). However, but with one exception (Simmons and Quinn, 1994) there has yet to be any careful consideration of the function and role of the dermopteran fingers.

In pursuing this work several avenues were investigated. First, the relative lengths of the digits (proximal phalanx length + intermediate phalanx length); second, the relative lengths of the metacarpals; and third, the relative lengths of the intermediate phalanges with respect to the proximal phalanges [(intermediate phalanx length / proximal phalanx length)*100]. Four questions were of specific interest. First, do bats and dermopterans have relatively longer fingers than all of the other taxa studied here? Second, do bats and dermopterans have relatively longer metacarpals than the other taxa studied here? Third, do bats and dermopterans have relatively longer intermediate phalanges with respect to the proximal phalanges than the other taxa studied here (Beard, 1989, 1990, 1993)? Fourth, does Petaurus have an elongated the fifth digit, or parts of it, reflecting the expansion of the patagium onto this digit?

Relative digit length.—Relative length of the first digit is actually the relative length of the first proximal phalanx. In bats and flying lemurs the propatagium extends al least out onto the first proximal phalanx and this measure reflects to

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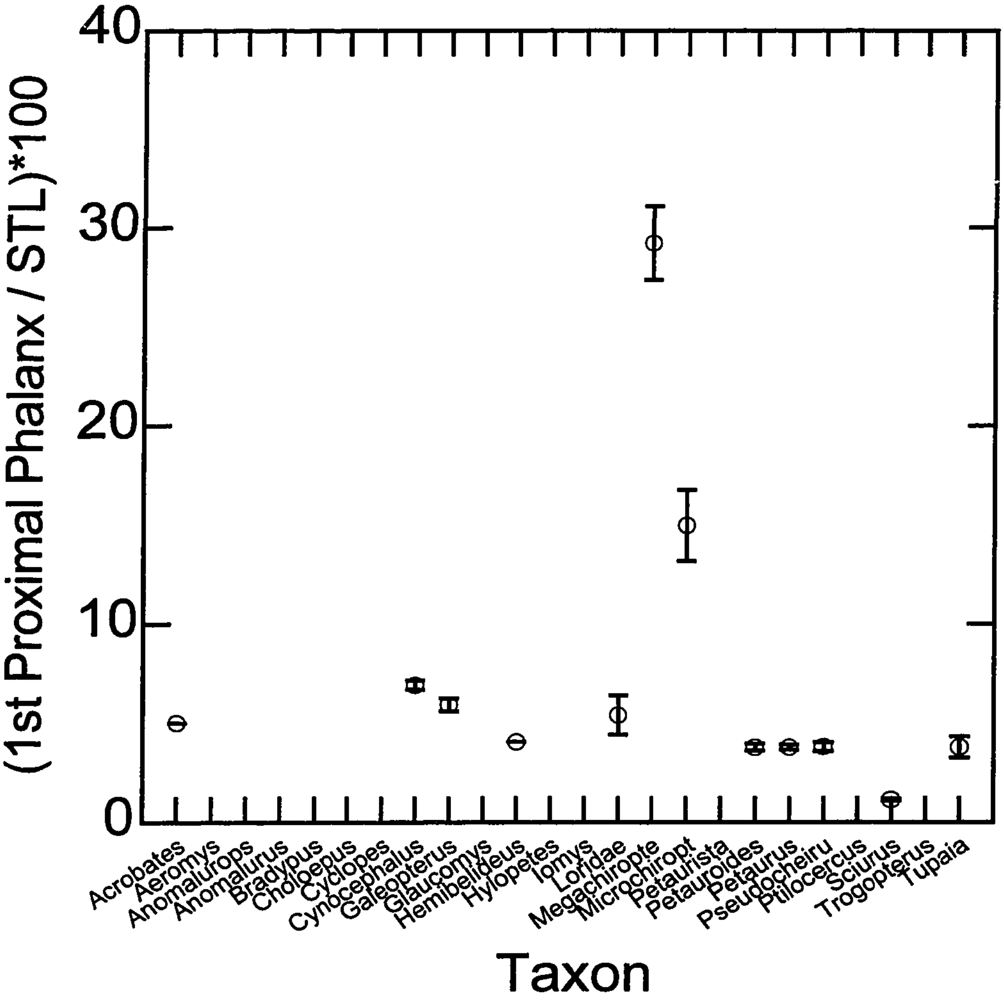

Figure 7.1: Relative length of the first digit in some mammals. Error bars equal one standard error of the mean.

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some degree the extent of the propatagium (Fig. 7.1). In a comparison among all taxa we see that the megachiropterans have longer first digits that all other taxa ($p < 0.001$), and that microchiropterans have longer first digits than Petaurus, Pseudocheirus, and Sciurus ($p < 0.001$). When the bats are excluded from the analysis dermopterans have significantly longer first digits than most, but not all, other mammals. Also, Sciurus has relatively short first digits ($p < 0.001$), and lorids generally have relatively long first digits. Among locomotor categories, flying mammals (bats) have longer first digits than animals in other locomotor categories ($p < 0.001$). Among gliding mammals, dermopterans have relatively longer first digits than other gliding mammals except Petauroides ($p < 0.001$). There are no significant differences among diprotodontians ($F = 2.509$, $df = 4$, $p = 0.102$), or among dermopterans ($t = 3.276$, $df = 5$, $p = 0.029$) for relative first digit length.

A comparison among all of the taxa studied here shows that megachiropterans ($p < 0.001$) and microchiropterans ($p < 0.001$) have relatively longer second digits than any other taxon studied here. However, sloths and dermopterans also cluster well above all other mammals for this character (Fig. 7.2). When bats are excluded from the analysis, dermopterans do have relatively longer second digits than other mammals ($p < 0.001$), with the exception of the sloths. A comparison among locomotor categories shows bats being distinct from all other locomotor categories with the exception of the climbing category ($p < 0.001$). This category contains only the lorids, and is represented by only one specimen in this particular analysis. Analysis of

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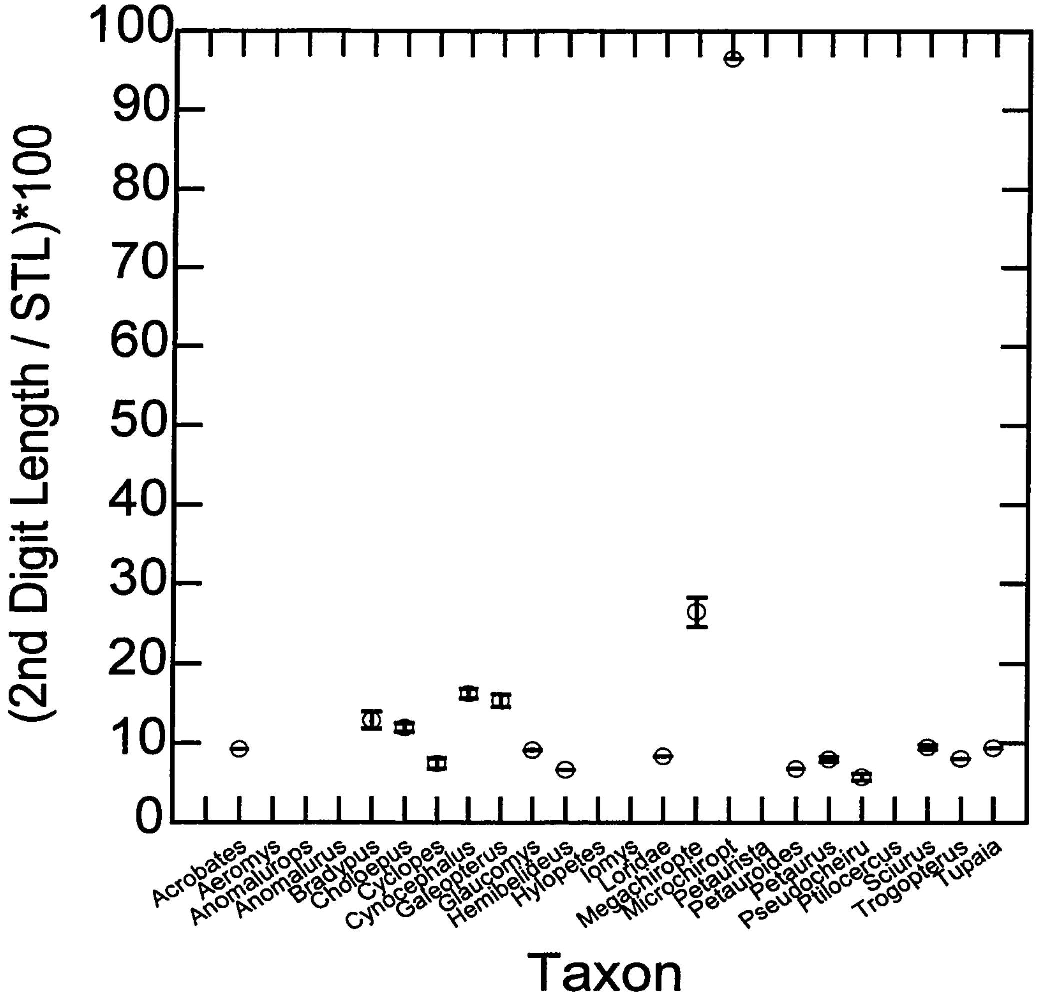

Figure 7.2: Relative length of the second digit in some mammals. Error bars equal one standard error of the mean.

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gliding mammals only, reveals dermopterans to have significantly longer second digits than all other gliding mammals ($p < 0.001$). Comparisons among diprotodontians ($F = 8.845$, $df = 4$, $P = 0.005$) and among dermopterans ($t = 1.173$, $df = 4$, $P = 0.306$) reveal no significant differences among taxa for relative second digit length.

For the relative length of the third digit (Fig. 7.3), again only the bats are significantly different from all other taxa studied here ($p < 0.001$). When bats are removed from the analysis dermopterans are significantly longer than most other taxa ($p < 0.001$). However, Cynocephalus is not significantly different from either Acrobates or Bradypus, and neither of the dermopterans is significantly different from the lorids. Among locomotor categories the distinction between bats and all other categories holds ($p < 0.001$). Among gliding mammals dermopterans again have relatively longer third digits than all other taxa ($p < 0.001$) with the exception of Acrobates. Among diprotodontians, the only significant difference is between Petaurus and Petauroides, with Petaurus having the longer third digit ($p < 0.001$)._The dermopterans were not significantly different from each other ($t = -0.805$, $df = 4$, $P = 0.466$) in this measure.

Relative fourth digit length shows a similar pattern as the third digit (Fig. 7.4). The bats have relatively longer fourth digits than any other taxa studied here ($p < 0.001$). When bats are removed from the analysis the dermopterans are different from most of the other taxa studied here ($p < 0.001$). The exceptions to this are Acrobates, Bradypus, the lorids, Iomys, and Trogopterus. However,

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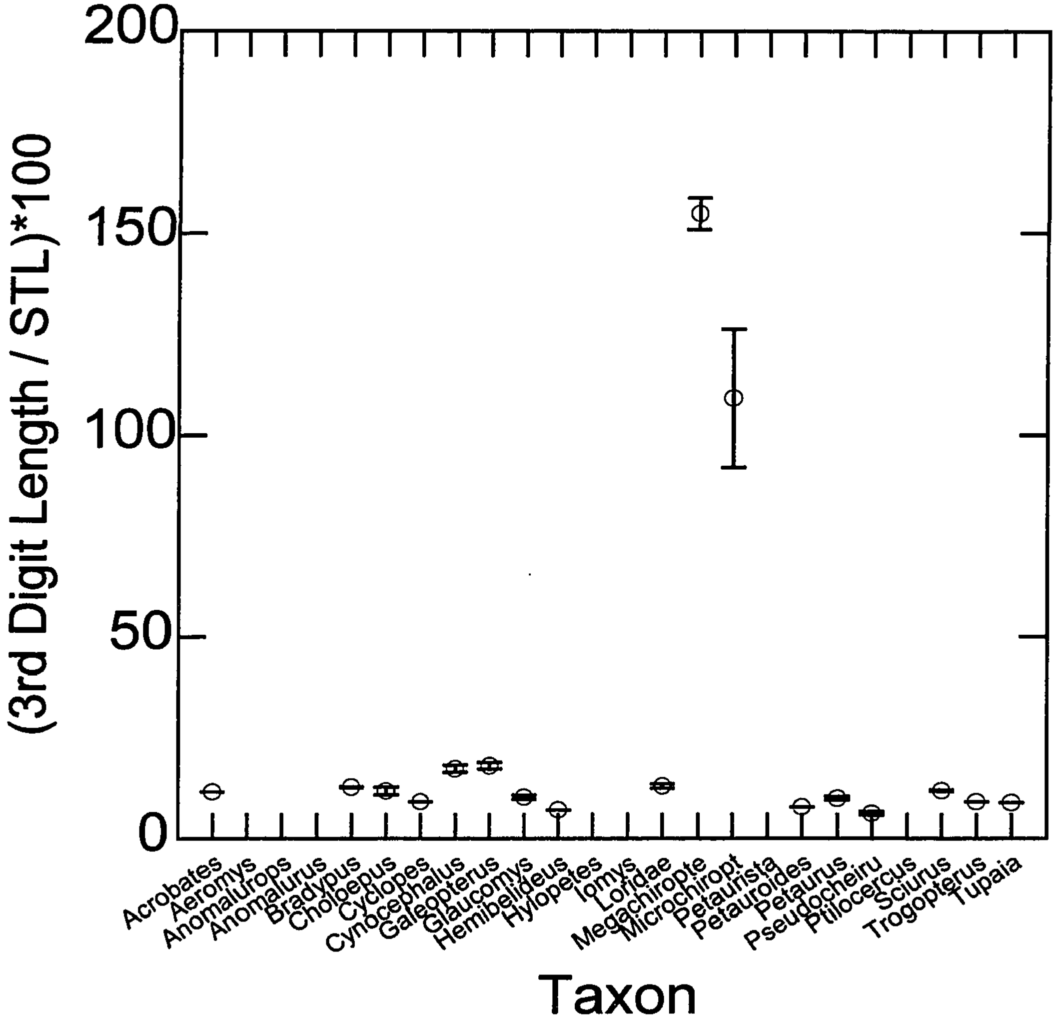

Figure 7.3: Relative length of the third digit in some mammals. Error bars equal one standard error of the mean.

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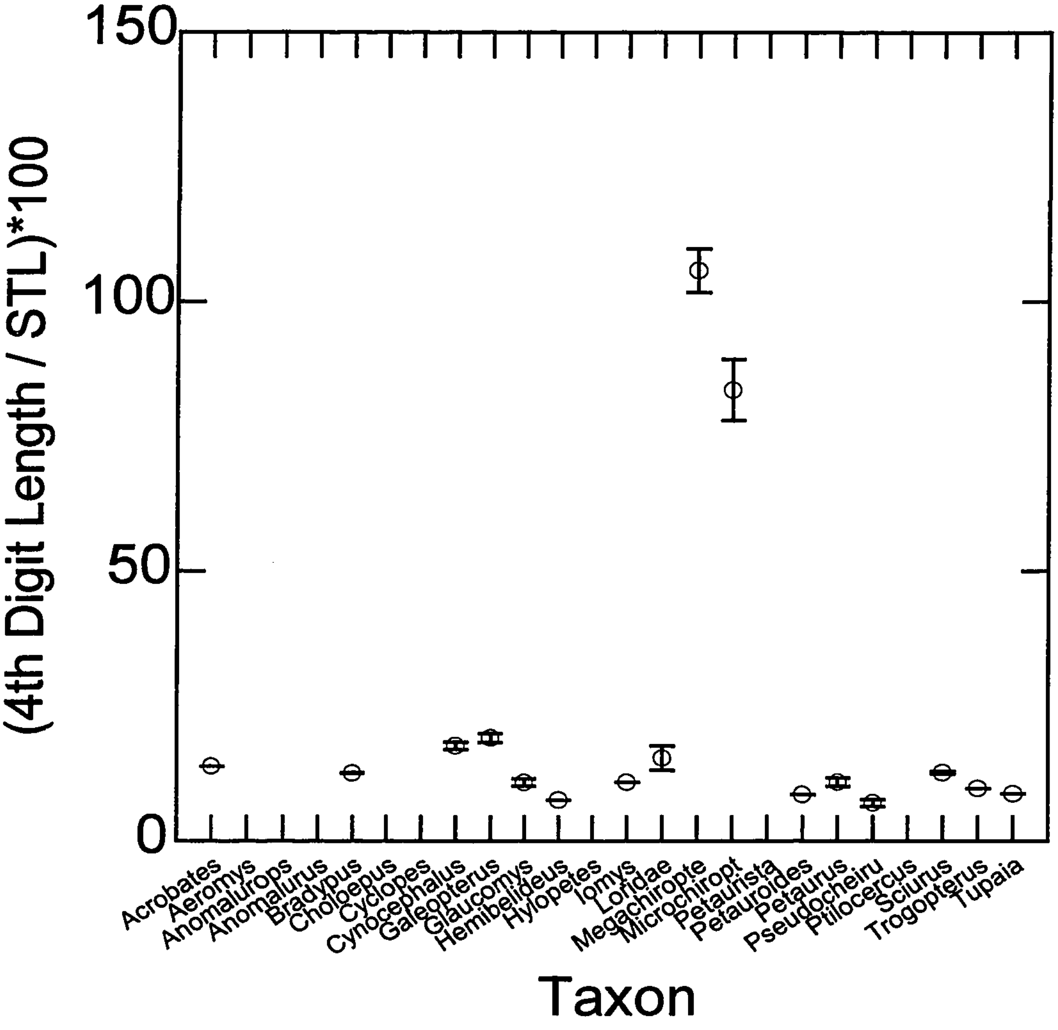

Figure 7.4: Relative length of the fourth digit in some mammals. Error bars equal one standard error of the mean.

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Iomys and Trogopterus are only represented by one individual each and have relatively shorter fourth digits ($p < 0.001$) than the other rodents studied here. These other rodents, Sciurus and Glaucomys, do have significantly shorter fourth digits than the dermopterans ($p < 0.001$). Therefore it is reasonable to state that only Acrobates, Bradypus, and the lorids have similar relative fourth digit lengths to the dermopterans. Among locomotor categories, again only the bats are distinct from the other locomotor categories ($p < 0.001$). Among gliding mammals the dermopterans have the relatively longest fourth digits ($p < 0.001$) with three exceptions, Acrobates, Trogopterus, and Iomys. Each of these taxa are only represented by single individuals, and again Trogopterus and Iomys do not really have very long fingers. Surprisingly, among diprotodontians there were no significant differences among taxa ($F = 11.524$, $df = 4$, $P = 0.010$). There were also no significant differences among the dermopterans ($t = -1.676$, $df = 5$, $P = 0.155$) for relative fourth digit length.

Regarding the relative length of the fifth digit (Fig. 7.5) the situation is again similar. In a comparison among all taxa the bats are significantly different from all other taxa ($p < 0.001$). When bats are excluded from the analysis dermopterans have relatively longer fifth digits ($p < 0.001$) than all the other taxa. In a comparison among locomotor categories only the bats are different from any of the other locomotor categories ($p < 0.001$). Among gliding mammals, the dermopterans again have relatively longer fifth digits than all other gliding mammals ($p < 0.001$) except for Acrobates. Among diprotodontians, Petaurus ($p < 0.001$) has relatively longer fifth digit than

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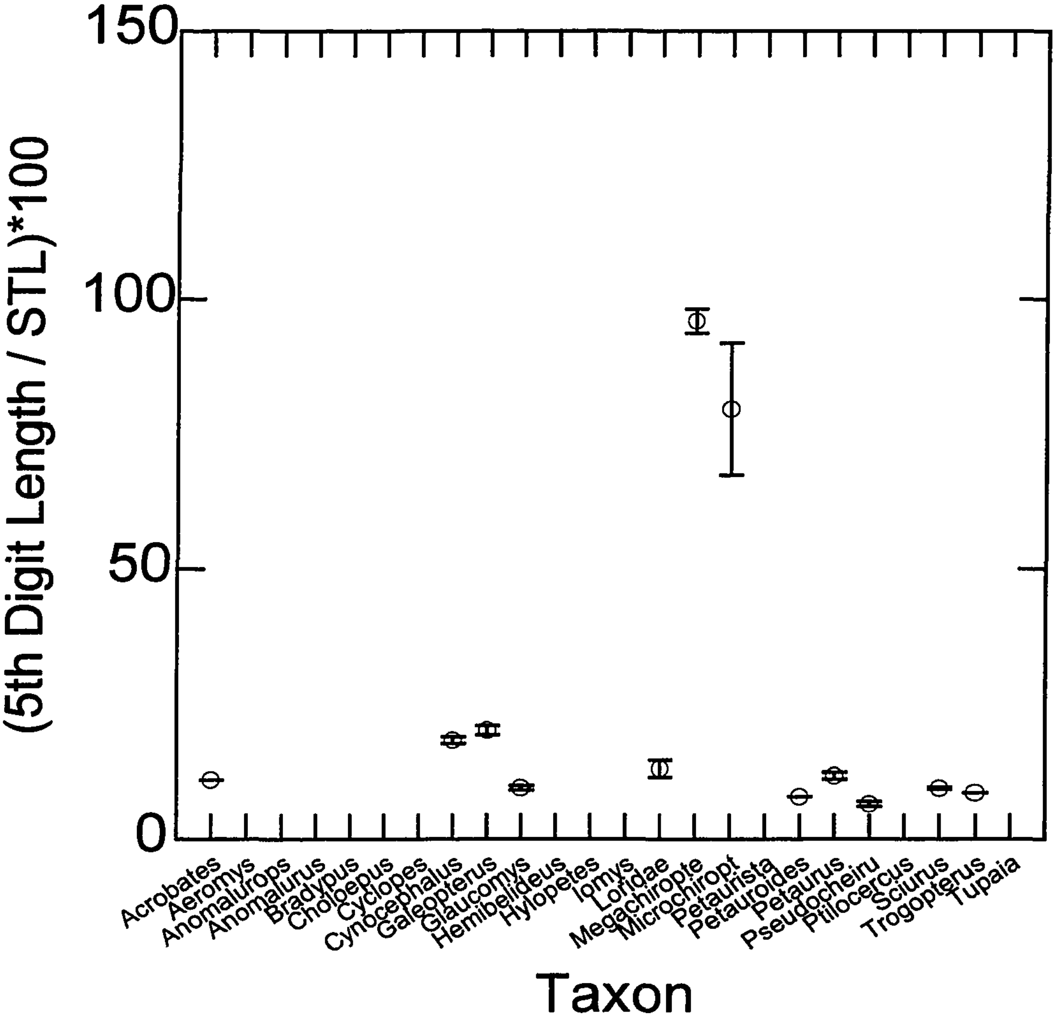

Figure 7.5: Relative length of the fifth digit in some mammals. Error bars equal one standard error of the mean.

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Petauroides, but this is the only significant difference. There are no significant differences among the two dermopteran taxa (t = -2.184, df = 5, P = 0.078).

Relative metacarpal length.—Bats have significantly ($p < 0.001$) longer first metacarpals than any of the other taxa studied here (Fig. 7.6). Acrobates, Choloepus, dermopterans, lorids, and Tupaia also have relatively long first metacarpals, and Sciurus and Glaucomys have relatively short metacarpals. However, many of these later differences are not significant in this data set. When bats are removed from the analysis we see that dermopterans ($p < 0.001$) have significantly longer first metacarpals than most other taxa, with the exceptions of Acrobates, Choloepus, lorids, and Tupaia. It is also shown that the sciurids have relatively short first metacarpals ($p < 0.001$). Bats also remain the only significantly different taxa when the data are analyzed by locomotor category ($p < 0.001$). Among gliding mammals the dermopterans have longer first metacarpals than all other gliding mammals except Acrobates. The flying squirrels appear to have relatively short first metacarpals, but so do Sciurus. There are no significant differences among diprotodontians in this measure (F = 6.990, df = 4, P = 0.003), nor are there significant differences among dermopterans (t = -0.881, df = 7, P = 0.408).

The situation regarding second metacarpal length is very similar to that of first metacarpal length. Bats are significantly different ($p < 0.001$) from all other taxa when all taxa are analyzed together. When bats are removed from the analysis (Fig. 7.7) the dermopterans show significantly longer second metacarpals ($p < 0.001$) than all other taxa except Bradypus, and Galeopterus is

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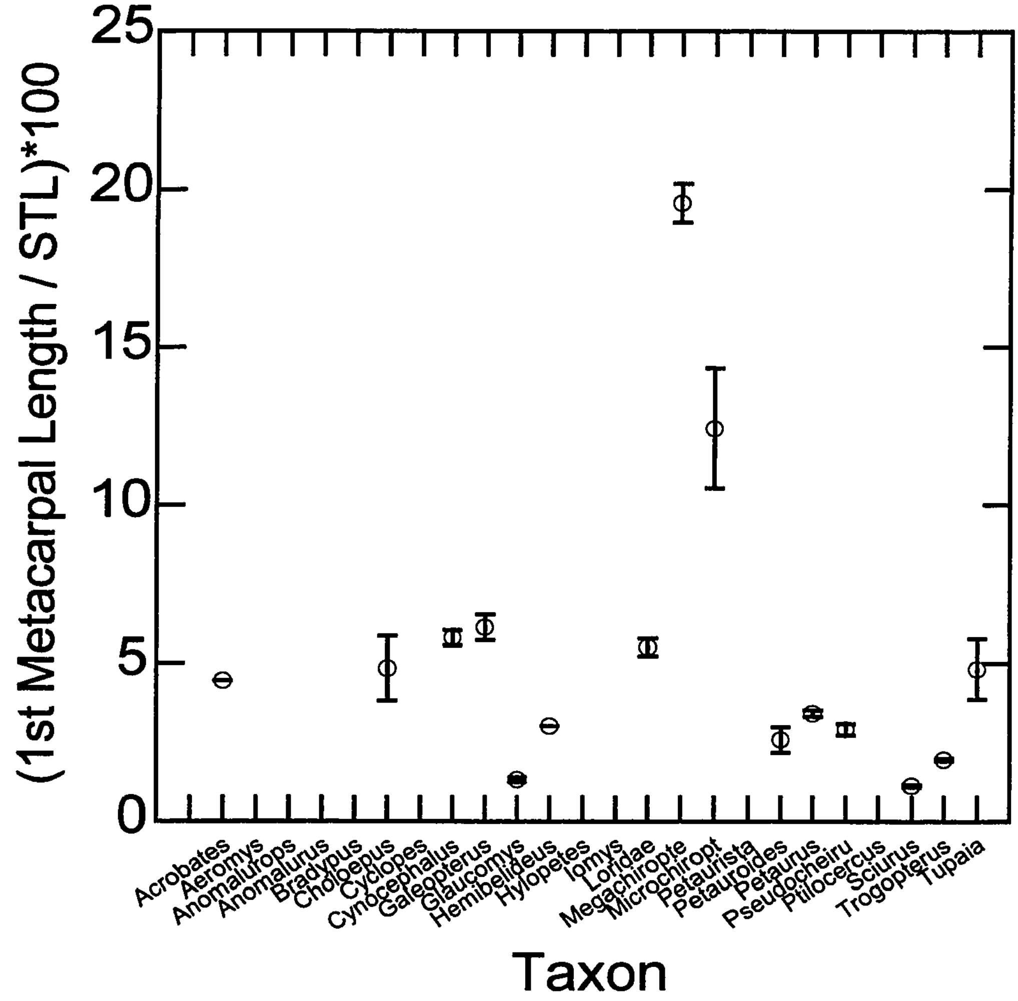

Figure 7.6: Relative first metacarpal length in some mammals. Error bars equal one standard error of the mean.

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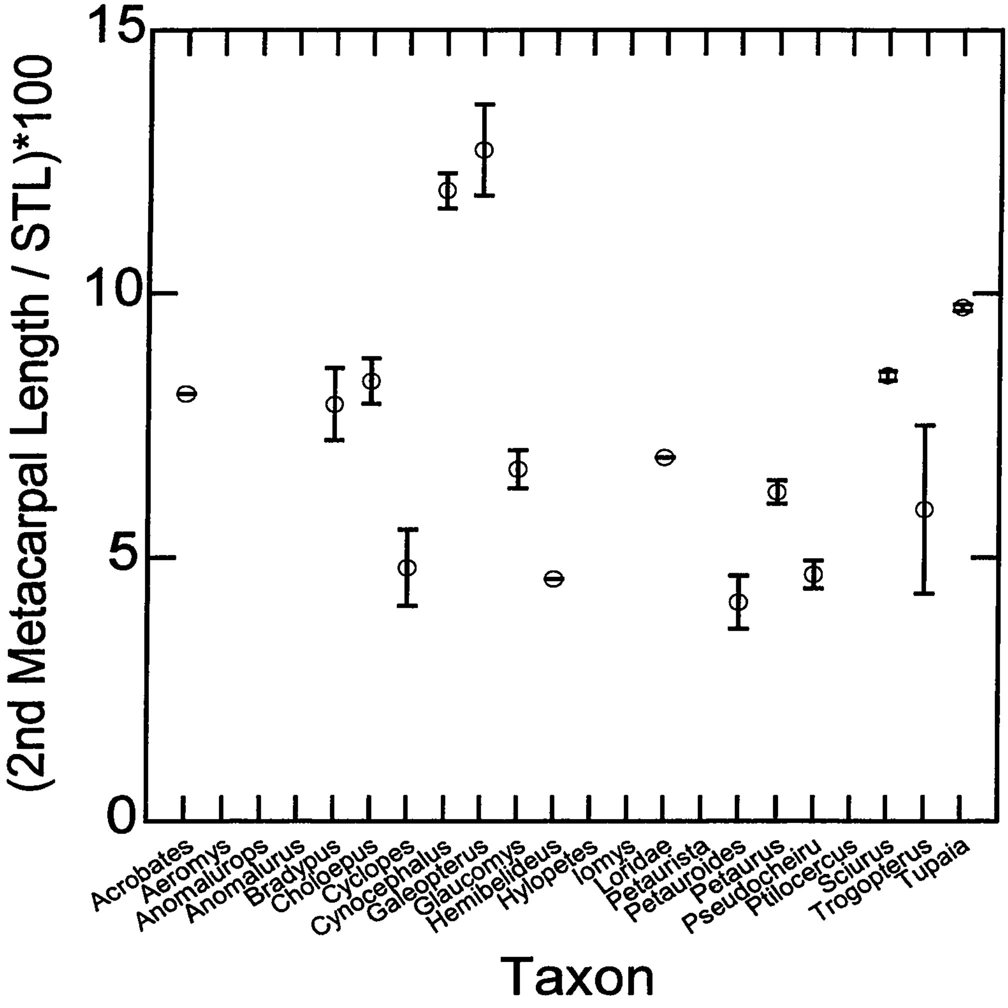

Figure 7.7: Relative second metacarpal length in some mammals. Error bars equal one standard error of the mean. Bats have been omitted for clarity. Megachiroptera, 70.27 ± 2.33; Microchiroptera, 136.66 ± 6.71.

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not significantly different from Choloepus. The sloths are also different, with longer second metacarpals, from many other taxa in this analysis. When taxa are partitioned according to locomotor category, again only the bats are different from all other locomotor categories ($p < 0.001$). Among gliding mammals, the dermopterans have significantly longer second metacarpals than any other taxa studied here ($p < 0.001$). Among diprotodontians Acrobates has relatively longer second metacarpals than does Petauroides ($p < 0.001$), but there are no significant differences among any other taxa. There is no significant difference between the two dermopteran genera ($t = -0.064$, $df = 7$, $P = 0.951$).

Bats have relatively longer third metacarpals ($p < 0.001$) than all other taxa studied here (Fig. 7.8). When bats are removed from the analysis the dermopterans have relatively longer third metacarpals than all other taxa ($p < 0.001$). Surprisingly, Tupaia and Sciurus also show relatively higher values than most of the other taxa studied here ($p < 0.001$). It is also apparent here that the nongliding marsupials tend to have relatively short third metacarpals. An analysis among diprotodontians reveals significant differences between Acrobates and Petauroides ($p < 0.001$) only, but there is little doubt that a larger sample size would show the gliding marsupials to have relatively longer third metacarpals than their nongliding relatives ($t = -2.959$, $df = 17$, $p = 0.009$). An analysis among locomotor categories again shows only bats to be different from all other categories ($p < 0.001$). A comparison among gliding mammals shows dermopterans to have higher values for relative third metacarpal length than all

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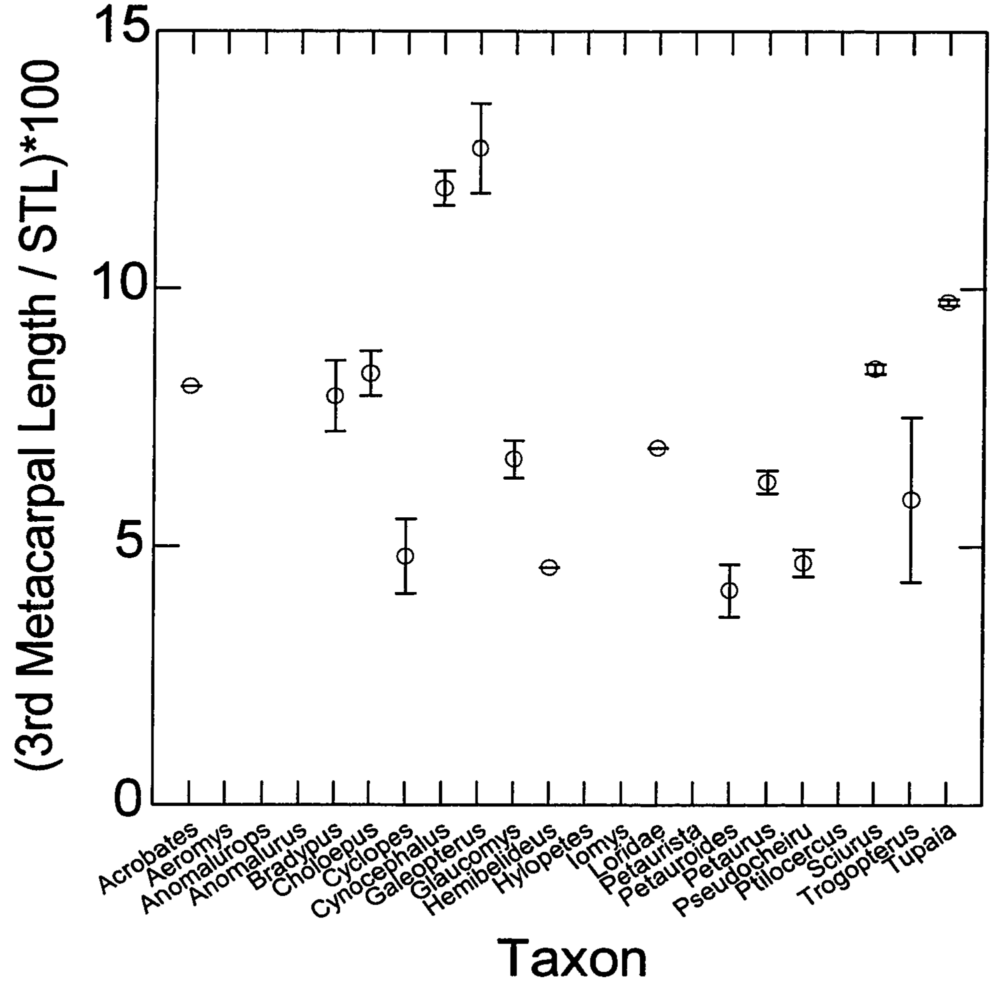

Figure 7.8: Relative third metacarpal length in some mammals. Error bars equal one standard error of the mean. Bats have been omitted for clarity. Megachiroptera, 96.44 ± 2.23; Microchiroptera, 142.05 ± 11.53.

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other taxa except Acrobates ($p < 0.001$). There are no significant differences among dermopterans ($t = -1.079$, $df = 7$, $p = 0.316$).

For relative fourth metacarpal length, again, the bats have higher values than all other non-chiropteran taxa (Fig. 7.9) ($p < 0.001$). When bats are removed from the analysis dermopterans have relatively longer fourth metacarpals than all other mammals ($p < 0.001$). Nongliding marsupials seem to have relatively shorter fourth metacarpals, and Sciurus and Tupaia also seem to have relatively long fourth metacarpals. Among locomotor categories, again only the bats have relatively long fourth metacarpals ($p < 0.001$). Among gliding mammals the dermopterans have the relatively longest fourth metacarpals ($p < 0.001$), although Cynocephalus is not significantly different from Acrobates. Among diprotodontians only Petaurus and Petauroides are significantly different for this measure. Again, a larger sample size of marsupials may show significant differences in relative fourth metacarpal length between gliding taxa and non gliding taxa ($t = -3.55$, $df = 16$, $P = 0.003$). There were no significant differences among dermopterans ($t = -1.740$, $df = 7$, $P = 0.125$).

Bats have significantly longer relative fifth metacarpals than all other mammals in this study (Fig. 7.10) ($p < 0.001$). when bats are removed from the analysis the dermopterans are shown to have relatively longer fifth metacarpals ($p < 0.001$) than all other taxa. Tupaia and Sciurus are no longer remarkably different from the other taxa studied, nor is Acrobates.

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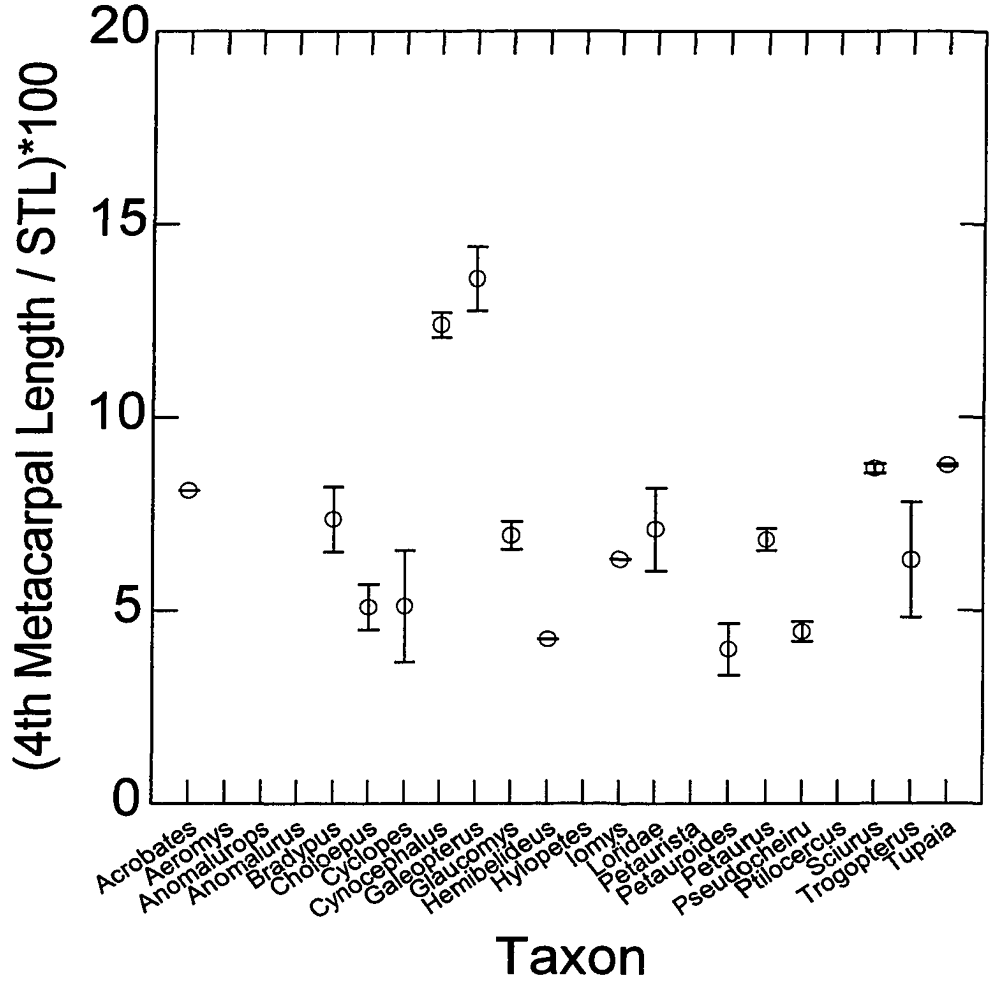

Figure 7.9: Relative fourth metacarpal length in some mammals. Error bars equal one standard error of the mean. Bats have been omitted for clarity. Megachiroptera, 92.87 ± 1.99; Microchiroptera 144.69 ± 7.12.

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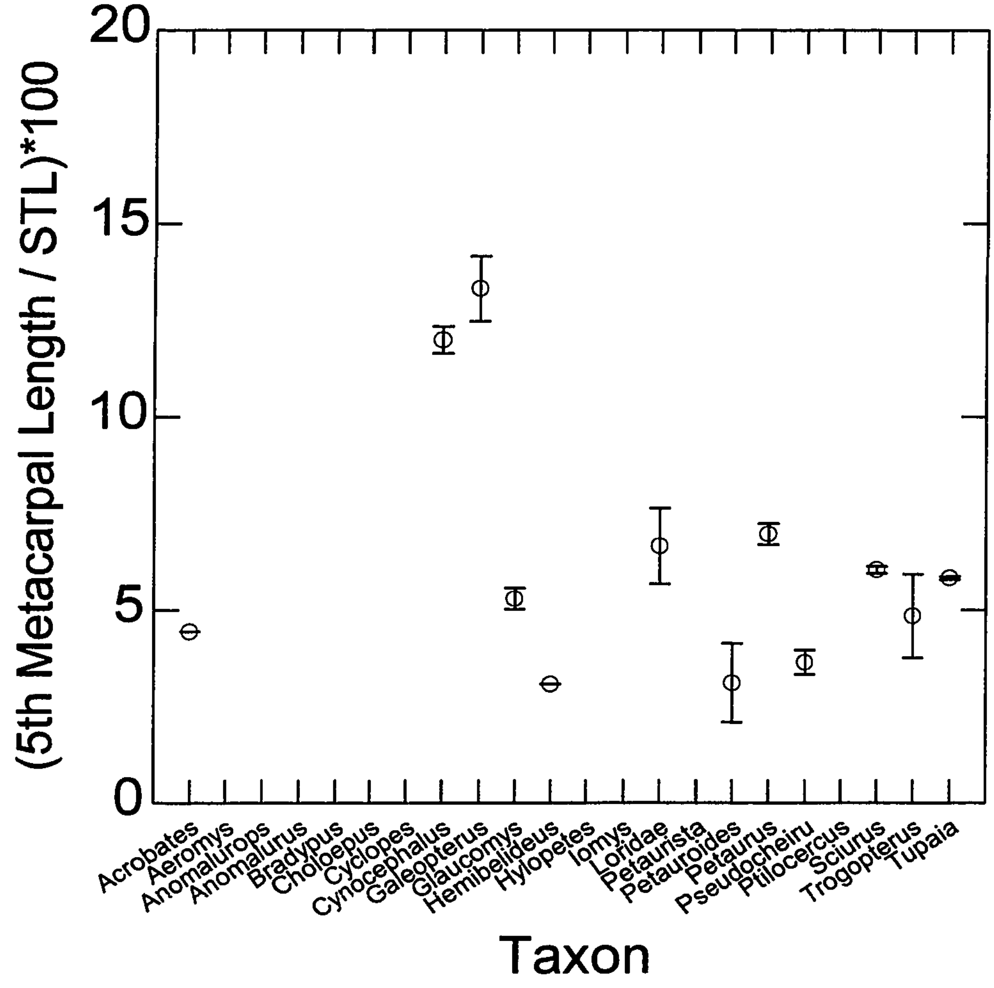

Figure 7.10: Relative fifth metacarpal length in some mammals. Error bars equal one standard error of the mean. Bats have been omitted for clarity. Megachiroptera, 92.32 ± 1.93; Microchiroptera, 142.19 ± 6.93.

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Now however, Petaurus and the lorids seems at the upper end of the nondermopteran range of values. Again an analysis among locomotor categories shows the bats to be different from all other categories ($p < 0.001$). Among gliding mammals, dermopterans have relatively longer fifth metacarpals than all other taxa ($p < 0.001$), and Petaurus has relatively longer fifth metacarpals than Petauroides ($p < 0.001$). When only diprotodontians are considered, Petaurus has relatively longer fifth metacarpals than Petauroides and Pseudocheirus ($p < 0.001$). Larger sample sizes for Acrobates and Hemibelideus would probably yield significant differences as well. There were no differences between dermopterans ($t = -1.870$, $df = 7$, $P = 0.104$)

Interphalangeal proportions.—The sloths have the highest intermediate phalanx indices for the second digit (Fig. 7.11) ($p < 0.001$). The dermopterans and Glaucomys have lower indices than the sloths, but higher indices than the megachiropterans, Petaurus, Petauroides, Sciurus, and Tupaia. When the xenarthrans are removed from the analysis the dermopterans have higher second digit intermediate phalanx indices than all other taxa ($p < 0.001$) except the microchiropterans. The microchiropterans have higher indices than all other taxa except the dermopterans, Glaucomys, and Trogopterus. When the data are grouped by locomotor category, only the suspensory taxa are significantly different from all other taxa ($p < 0.001$). Among gliding mammals, dermopterans have the highest index values, and are significantly different ($p < 0.001$) from all other gliders

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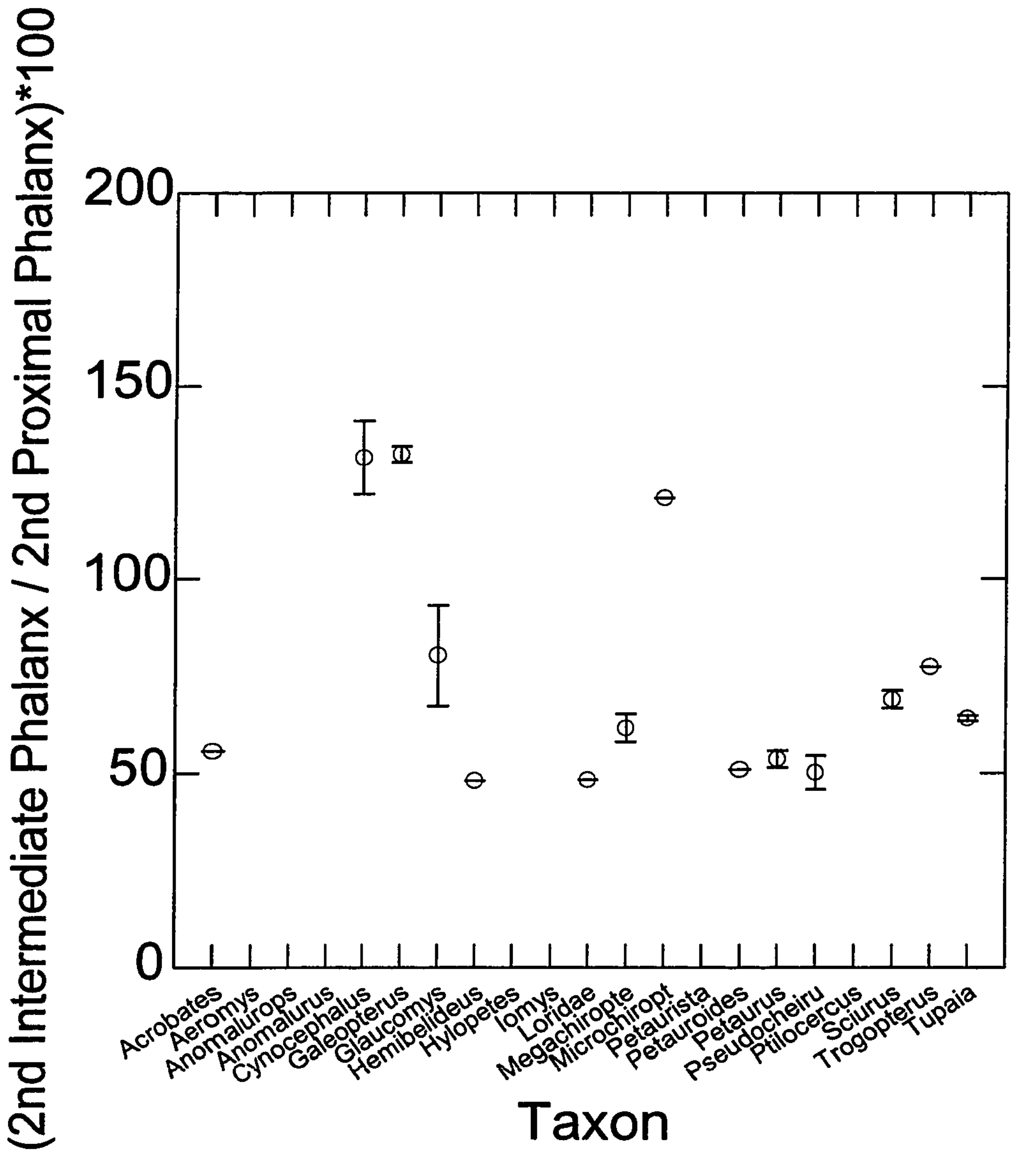

Figure 7.11: Second intermediate phalanx index in some mammals. Error bars equal one standard error of the mean. Xenarthrans have been omitted for clarity. Bradypus, 562.19 ± 28.12; Choloepus, 494.58 ± 41.45; Cyclopes, 140.63 ± 15.63.

except for Glaucomys and Trogopterus. There were no significant differences among diprotodontians (F = 0.337, df = 4, P = 0.846), or between dermopterans (t = -0.087, df = 5, p = 0.934). The xenarthrans have the highest values for the third intermediate phalanx index (Fig. 7.12), and are significantly different from all other taxa ($p < 0.001$) with the exception that Galeopterus and Cyclopes are not significantly different. When xenarthrans are removed from the analysis there are no significant differences among the remaining taxa. Still, only the volitantians have indices over 100. When the data are grouped by locomotor category, suspensory taxa (xenarthrans) have significantly higher values than all other taxa, and flying taxa (bats) have significantly higher values than arboreal taxa ($p < 0.001$). An analysis of gliding mammals shows dermopterans to have higher values than all other gliding mammals ($p < 0.001$) except Trogopterus. However, Trogopterus is represented by only one individual here. There were no differences among diprotodontians (F = 1.842, df = 4, P = 0.214) or dermopterans (t = -1.951, df = 6, P = 0.167).

For the intermediate phalanx index of the fourth digit (Fig. 7.13), Bradypus has significantly larger values than all other taxa ($p < 0.001$), and the dermopterans are significantly higher than many other taxa ($P < 0.001$). When Bradypus is removed from the analysis the dermopterans have significantly higher values than all taxa ($p < 0.001$) except Iomys, chiropterans, Ptilocercus, and Trogopterus. With the exception of the chiropterans, all of these taxa are represented by single individuals. Again,

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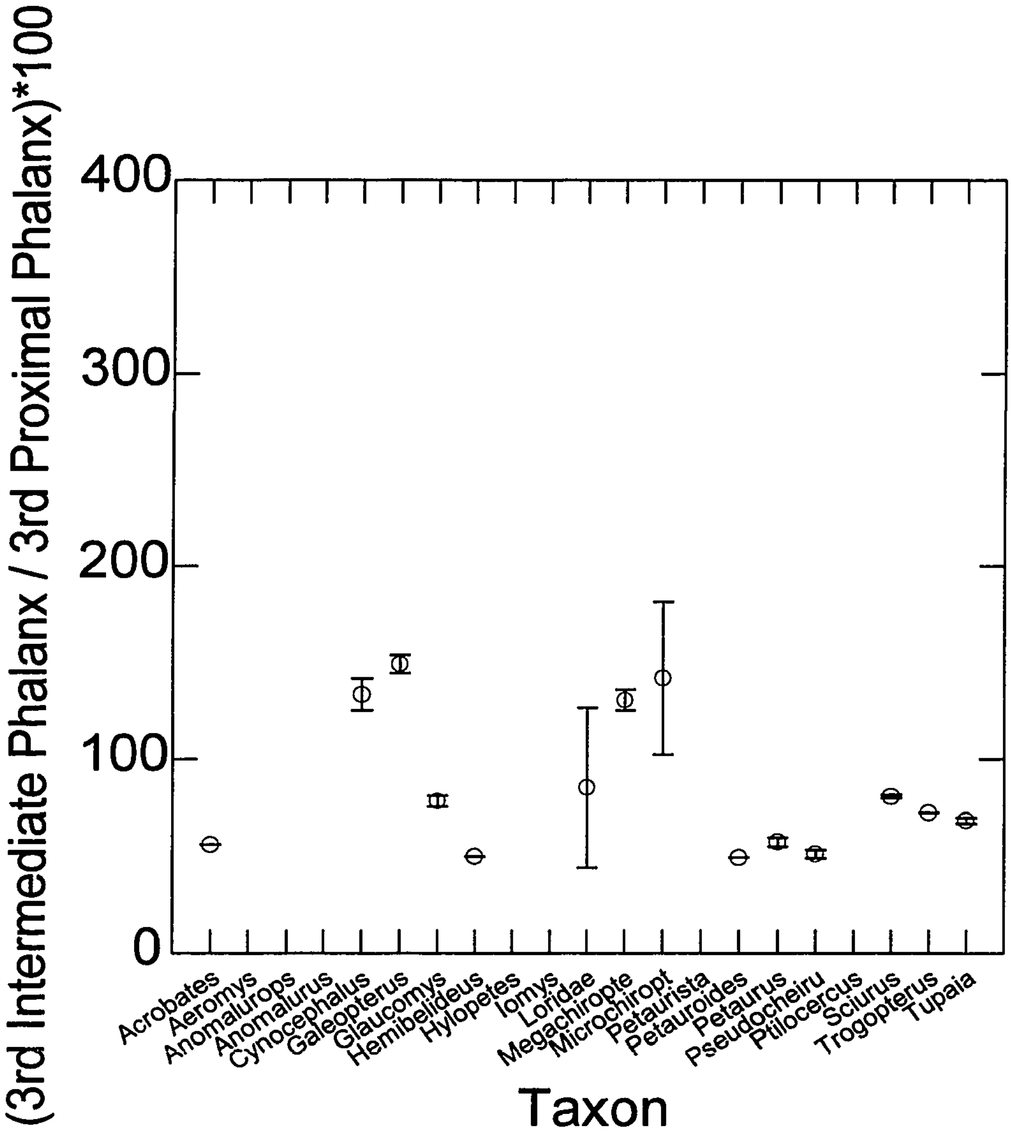

Figure 7.12: Third intermediate phalanx index in some mammals. Xenarthrans not shown (Bradypus, 602.03 ± 29.55; Choloepus, 514.17 ± 54.54; Cyclopes, 381). Error bars equal one standard error of the mean.

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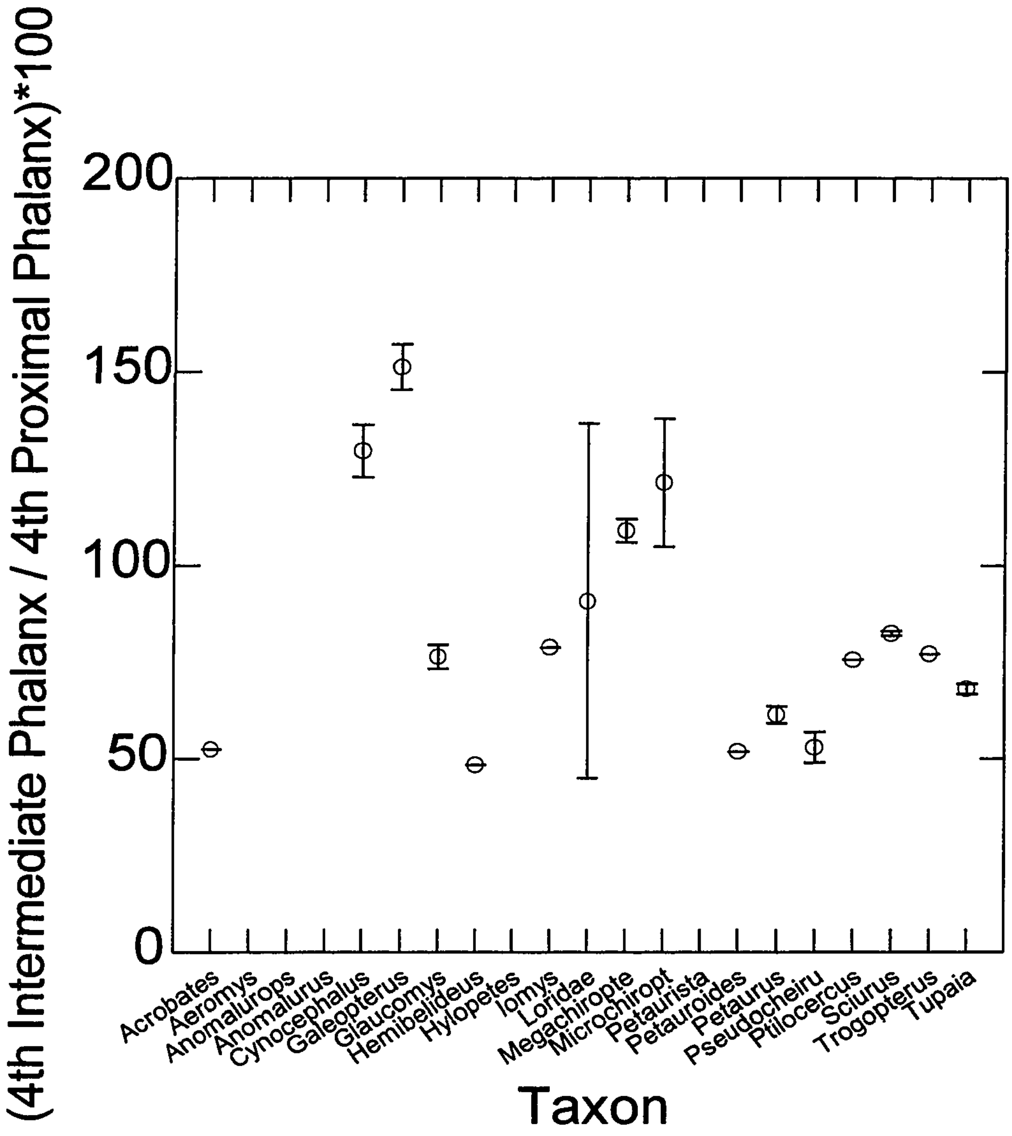

Figure 7.13: Fourth intermediate phalanx index in some mammals. Xenarthrans not shown (<u>Bradypus</u>, 553.98 ± 6.13). Error bars equal one standard error of the mean.

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however, only volitantians have values over 100. When the data are grouped according to locomotor category, the suspensory taxa have significantly higher values than all other taxa ($p < 0.001$), and the flying taxa have significantly higher values than the arboreal taxa ($P < 0.001$). When only gliding mammals are considered, the dermopterans have higher values than all other gliders ($p < 0.001$) except Iomys and Trogopterus. There were no significant differences among diprotodontians ($F = 1.693$, $df = 4$, $P = 0.287$) or dermopterans ($t = -2.325$, $df = 7$, $P = 0.053$).

There are few differences among taxa for the fifth intermediate phalanx ratio (Fig. 7.14). None of the xenarthrans studied here have a fifth digit so they could not be included here. Still, dermopterans and bats both have values of over 100 for this character. When considering the data partitioned by locomotor category we find that both flying and gliding taxa have higher values than the arboreal taxa ($p < 0.001$). Among gliding mammals the dermopterans have significantly higher values than any of the other gliding mammals ($p < 0.001$). There were no significant differences among diprotodontians ($F = 7.454$, $df = 3$, $P = 0.008$) or among dermopterans ($t = -2.166$, $df = 6$, $P = 0.073$).

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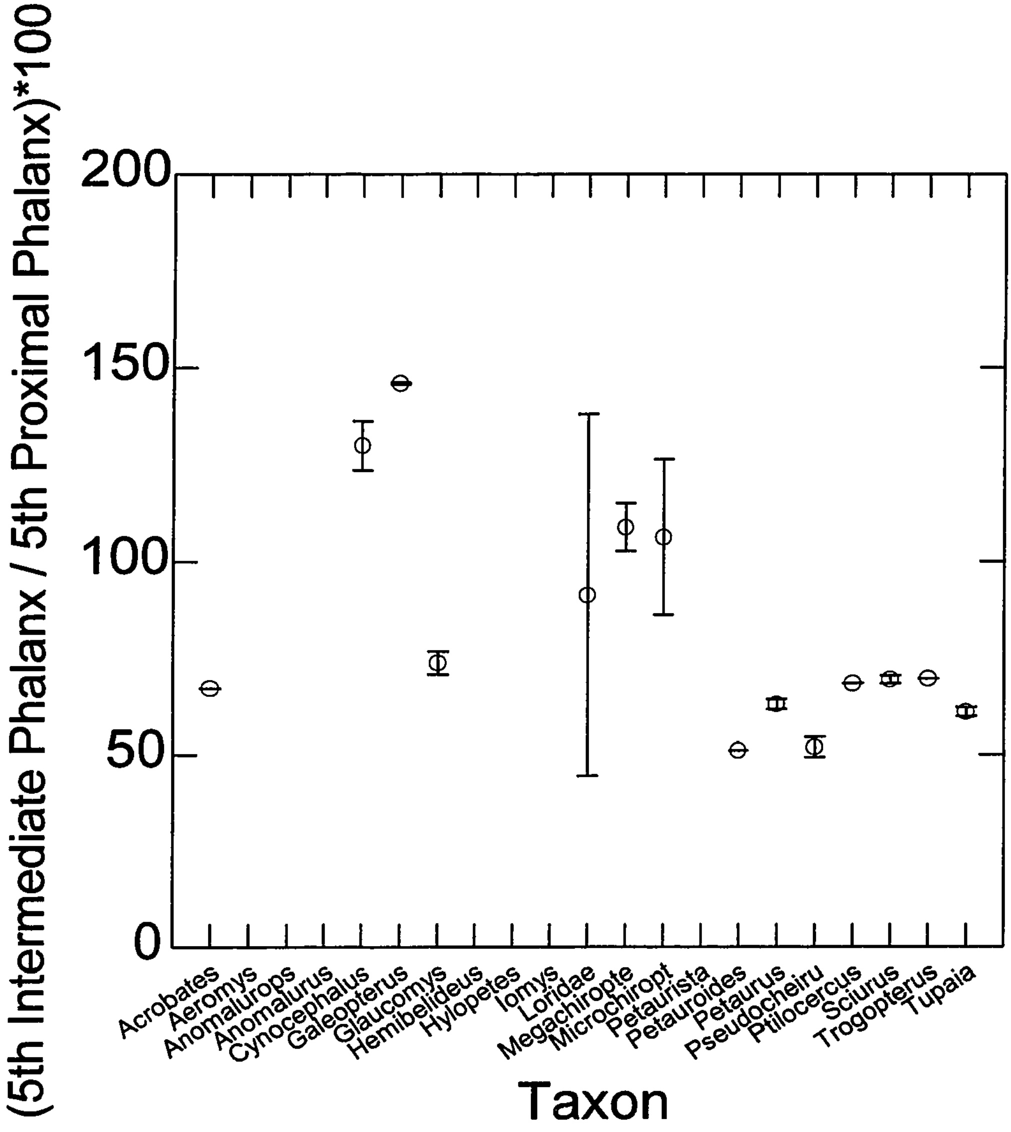

Figure 7.14: Fifth intermediate phalanx index in some mammals. Error bars equal one standard error of the mean.

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CHAPTER 8: THE HINDLIMB

In this chapter the relative proportions of hindlimb limb elements are examined in an attempt to discriminate gliding mammals from nongliding mammals. Thorington and Heaney (1981) performed a similar analysis confined to flying squirrels as compared to tree squirrels. Their results showed that the flying squirrels do have generally longer limbs and than their non-gliding relatives, although at low body sizes the regression lines for some comparisons crossed.

Relative hindlimb length.—Differences in relative hindlimb lengths (Fig. 8.1) show a different pattern than relative forelimb lengths did. Here, the microchiropterans and Galeopterus are most different from the other taxa but Acrobates and Cynocephalus also cluster near the upper end of relative hindlimb lengths. All of these taxa have relative hindlimb lengths over 100, while all other taxa studied here have relative hindlimb lengths below 100. Bats, gliding mammals, and climbing mammals generally have longer hindlimbs than either arboreal quadrupeds or suspensory taxa although these differences are not always significantly different. However, gliding rodents ($t = -3.85$, $df = 41$, $p < 0.001$) and marsupials ($t = -7.02$, $df = 19$, $p < 0.001$) do have relatively longer hindlimbs than their nongliding relatives. There is no significant difference in relative hindlimb length among dermopterans ($t=-3.33$, $df=13$, $p = 0.005$).

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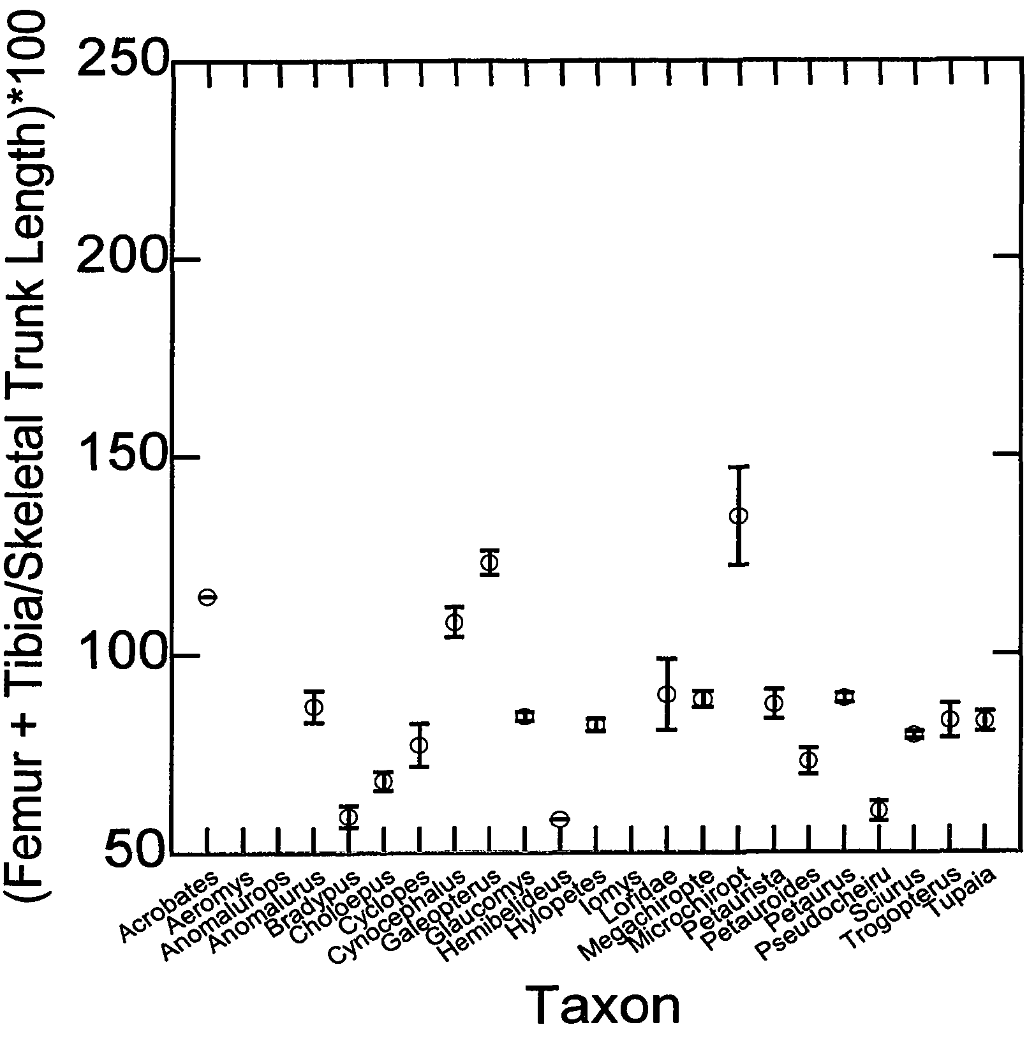

Figure 8.1: Relative hindlimb length in some mammals.

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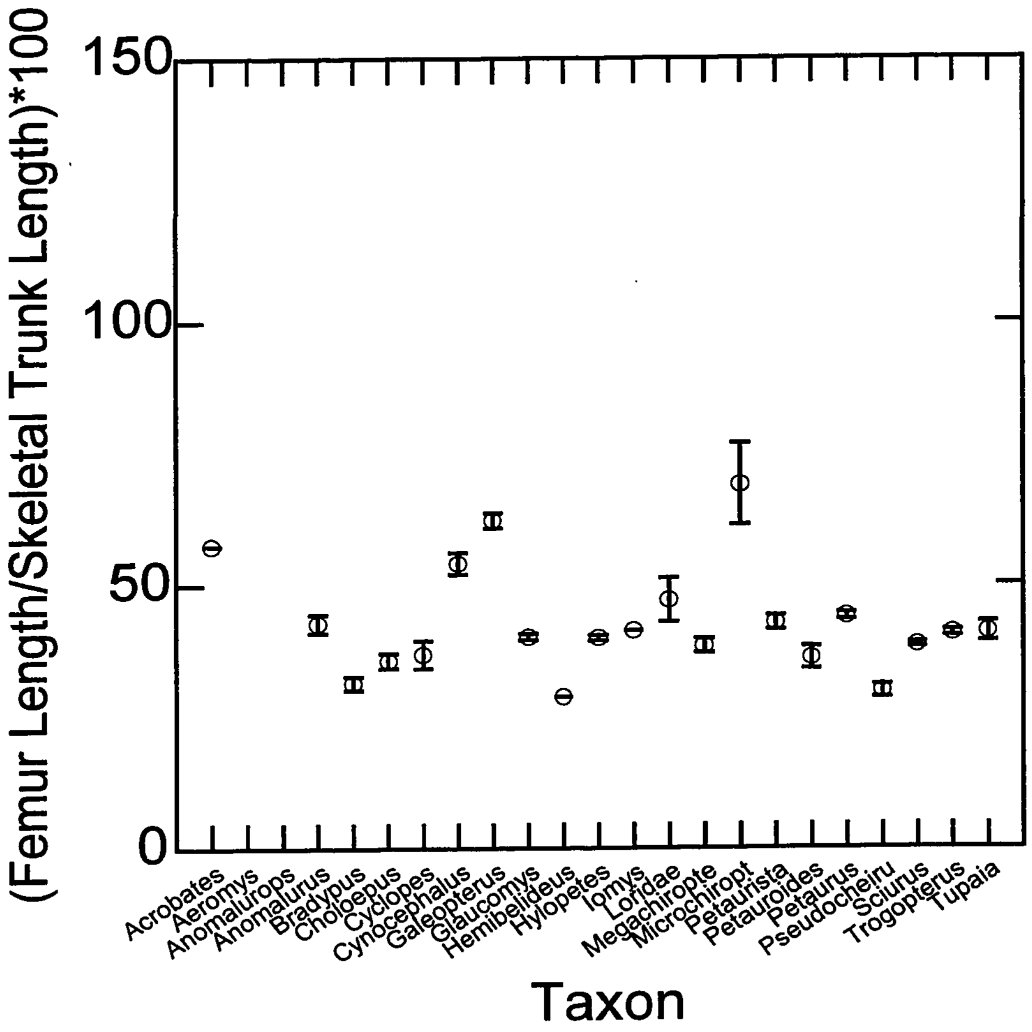

Figure 8.2: Relative femur length in some mammals.

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The femur.—Relative femur length generally tends to distinguish the microchiropterans and Galeopterus from all of the other mammals (Fig. 8.2). However, when taxa are grouped by locomotor category, the only significant difference is between the bats and arboreal taxa ($p < 0.001$), with the bats having relatively longer hindlimbs. However, bats, gliding mammals, and the lorids all have femur indices averaging from 45 - 50 while arboreal and suspensory taxa average only from 35 - 40. When only the gliding mammals are analyzed the dermopterans ($p < 0.001$) and Acrobates ($p < 0.001$) show significantly longer femora than most of the other taxa studied here. However, among rodents ($t = 3.70$, $df = 47$, $p < 0.001$) and marsupials ($t = -6.79$, $df = 19$, $p < 0.001$), the gliding taxa do have relatively longer femora. When examining only the dermopterans, xenarthrans, and lorids we see that the dermopterans have significantly longer femora ($p < 0.001$) than either of the two sloths, and that the lorids occupy an intermediate position between the dermopterans and xenarthrans, being statistically different from neither. Among the dermopterans there is no significant difference in relative femur length ($t = -.64$, $df = 13$, $p = 0.003$).

An analysis of $\mathbf{TCSA}_{\mathrm{Femur(STL)}}$ revealed no statistically significant differences among the taxa studied here ($F = 2.01$, $df = 20$, $p = 0.013$). The only subsequent data partitioning that revealed statistically significant differences was a comparison of dermopterans, lorids, and xenarthrans (i.e., suspensory taxa in a broad sense). In this comparison Cyclopes had a larger femoral

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cross sectional area than any of the other taxa ($p < 0.001$). Consequently, an analysis of polar moments of the femur also revealed no differences.

There were also no significant differences in relative $I_{ML,Femur(STL)}$ ($F = 0.74$, $df = 19$, $p = 0.768$), or in relative $I_{AP,Femur(STL)}$ ($F = 2.33$, $df = 20$, $p = 0.003$) among taxa. When grouped by locomotor category the suspensory taxa have higher $I_{AP,Femur(STL)}$ than all other categories ($p < 0.001$) and the arboreal taxa have higher values than the flying and gliding mammals ($p < 0.001$). These patterns also hold when $I_{AP,Femur(STL)}$ is corrected for femur length, $I_{AP,Femur(Fem)}$, rather than body size (rodent gliders vs. nongliders, $t=13.74$, $df=53$, $p<0.001$; marsupial gliders vs. nongliders, $t=11.69$, $df=19$, $p<0.001$). There are no significant differences among dermopterans ($t = 3.25$, $df = 15$, $p = 0.005$).

The Tibia.—Differences in relative tibia length generally parallel those that were seen in relative femur length (Fig. 8.3). Galeopterus and the microchiropterans have significantly longer tibia than all other mammals ($p < 0.001$), and although Acrobates and Cynocephalus are not statistically different from most of the other taxa in the sample, they do show relatively long tibia. When taxa are grouped according to locomotion, bats show significantly longer tibia than all other taxa ($p < 0.001$) and gliding mammals have significantly longer tibia than the arboreal taxa ($p < 0.001$) and the xenarthrans ($p < 0.001$). Among gliding mammals, the dermopterans have significantly longer tibia than all other gliding mammals ($p < 0.001$) except Acrobates. Among the rodents, there were no significant differences in

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relative tibia length ($F = 3.538$, $df = 5$, $p = 0.010$). However, <u>Acrobates</u> has a relatively longer tibia than all of the other marsupials studied here ($P < 0.001$), and <u>Petaurus</u> has a significantly longer tibia ($p < 0.001$) than all of the nonacrobatid marsupials. There were no differences in relative tibia length among dermopterans ($t = -3.20$, $df = 14$, $p = 0.006$).

$I_{AP,Tibia(Tib)}$ does show some differences among taxa. <u>Bradypus</u> has a significantly higher $I_{AP,Tibia(Tib)}$ than many of the other taxa studied here ($p < 0.001$), and <u>Pseudocheirus</u> ($p < 0.001$)and <u>Sciurus</u> ($P < 0.001$) are also higher than many of the other taxa studied here. When grouped by locomotor category arboreal taxa have higher values for $I_{AP,Tibia(Tib)}$ than flying and gliding taxa, and suspensory taxa have higher values than climbing, flying, and gliding taxa.

Our discussion of limb properties has up to this point focused on aspects of the limbs in relation to the size of the animals. In such comparisons, it has become apparent that bats generally are different from all other mammals and that dermopterans, sloths, and sometimes the lorids often differ in similar ways although not to the same magnitude as the bats. In may cases it is also evident that the dermopterans are quite different from all other gliding mammals. In these cases though it is possible that body size estimators do not give us a clear functional picture of what is going on here. Specifically, since bats seem to have relatively long and robust limbs it is possible that the changes in one of these parameters is required to maintain functional equivalence.

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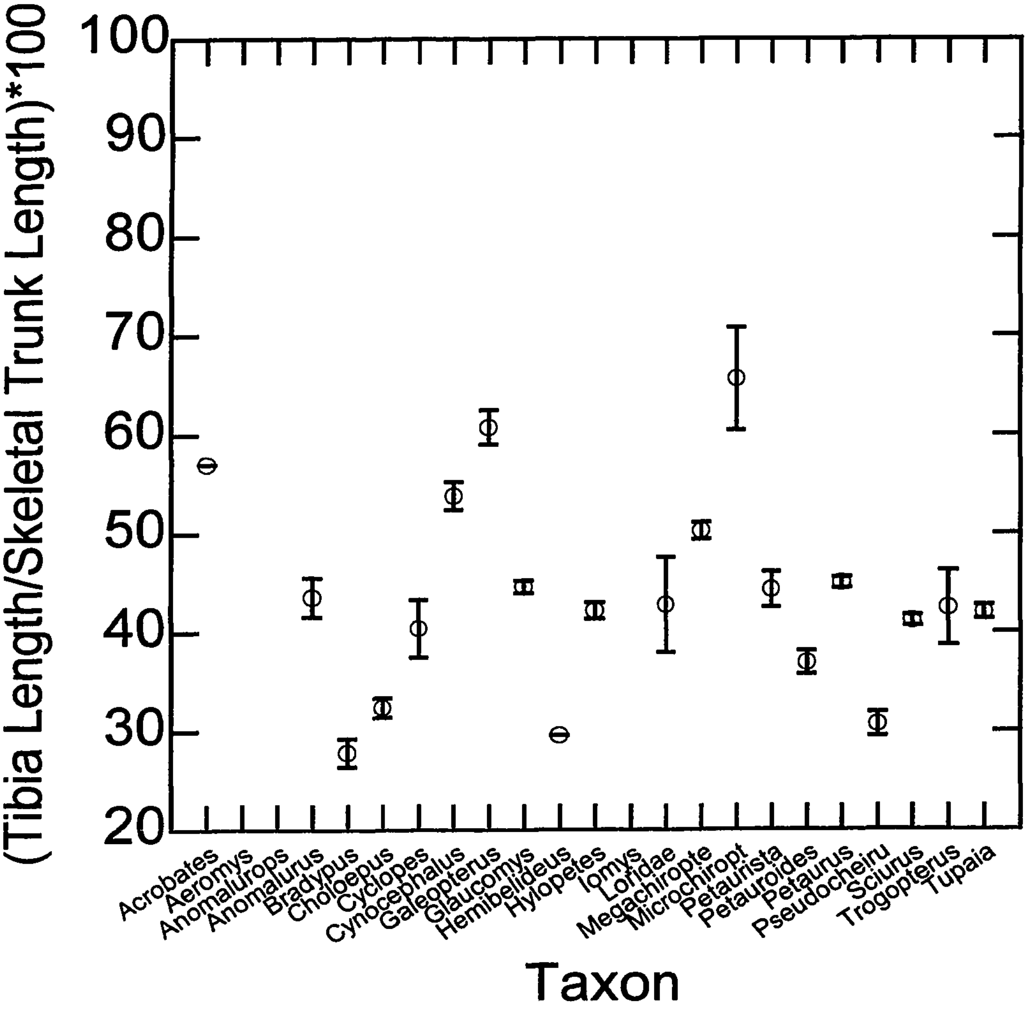

Figure 8.3: Relative tibia length in some mammals.

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CHAPTER 9: AERODYNAMIC THEORY

Aerodynamics are critical to any evaluation of the functional morphology of gliding or flying animals. A few definitions are required before we can proceed to discuss aerodynamics in gliding mammals. The aerodynamics needed to understand mammalian gliding can be found in standard aerodynamic texts (Anderson, 1985, von Mises, 1945, and Perkins and Hage, 1949). The discussions that follow are largely based on these works and that of Norberg (1991). There has been a substantial amount of work done on powered flight in vertebrates (for bats see: Farney and Fleharty, 1969; Findley et al., 1972; Hermanson, 1981; Meyers and Hermanson, 1994; Norberg, 1972a & b, 1981, 1985, 1986; Norberg and Rayner, 1987; Pirlot, 1977; Scholey, 1986; Struhsaker, 1961; Templin, 1977; Vaughan, 1959, 1966, 1970; Vaughan and Bateman, 1970. For birds see: Bock, 1965; Capel et al., 1983; Norberg, 1981, 1985; Ostrom, 1974, 1979; Padian, 1982; Pennycuick, 1971, 1972, 1975; Rayner, 1979, 1981, 1985; Yalden, 1985. For Pterosaurs see Brower, 1983; Padian, 1983, 1985; Unwin, 1987). Some work has also been done on gliding (Mammals; Ando and Shiraishi, 1991; Ando and Shiraishi, 1993; Nachtigal, 1979a, 1979b, 1986; Scholey, 1986; Thorington and Heaney, 1981: Reptiles; Carrol, 1978; Colbert, 1970; Evans, 1982; Gans et al., 1987: Amphibians; Emerson and Koehl, 1990; Emerson, et al., 1990; Emerson, 1991).

The main aerodynamic issues that will be dealt with here are aspects of performance, stability, and control. However, there are a few aerodynamic

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points that should be remembered throughout this discussion. First, any aircraft moving through the air has its flight path largely determined by four elements; the Earth's gravitational field, the aircraft's inertia characteristics, the aircraft's propulsive force, and the aerodynamic forces and moments that the aircraft itself creates as it moves through the air.

In the case of gliding mammals the gravitational acceleration is a constant (9.81 m/sec^2). This acceleration provides some propulsion for a gliding mammal as the animal trades the potential energy stored in its altitude for forward motion. The aerodynamic forces and moments acting on the aircraft are determined by this forward motion of the aircraft (its velocity, unknown for most gliding mammals), the density of the air (for our purposes assumed to be 1.225 kg/m^3 at 15^0 C and 1 atmosphere), the geometry of the aircraft (highly variable among mammalian gliders, and probably highly variable within a single glide since mammalian gliders have the ability to alter the geometry of their wing in flight.), and the angle that the relative wind makes with the aircraft (also unknown for most mammalian gliders).

For mammalian gliders these aerodynamic forces determine the flight path of the animal. For a man made aircraft, other limiting factors are the strength of the propulsive system and the strength of the airframe. In mammalian gliders the propulsive force comes from the initial leap or drop of the animal, and from trading potential energy for velocity. For our purposes, this can probably be considered constant across mammalian gliders. Similarly, skeletal (i.e., airframe) strength is unlikely to vary significantly among gliding mammals. However, both

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of these assumptions need further study, and may not in fact hold true for all mammalian gliders.

The term **AIRCRAFT** may refer to either man made flying vehicles or to flying or gliding mammals. A distinction will be made between gliding mammals and bats where necessary. This distinction corresponds to the distinction between **GLIDING** or unpowered flight, and **POWERED** or flapping flight in mammals. This is necessary because **FLIGHT** generally refers to all methods of moving through the air, and sometimes the water, where lift is generated from a wing, and thrust offsets the effects of drag on the wing. The **WING** is the lift, and sometimes thrust, producing component of the aircraft and any wing has a definite shape or **PLANFORM** when viewed from above. An **AIRFOIL** is a section through the wing taken parallel to the direction of flow of the medium through which the wing is passing (Fig. 9.1).

Any aircraft responds to four translational forces (Fig. 9.2) and three rotational forces (Fig. 9.3). The four translational forces are lift (**L**), weight (**Mg**), thrust (**T**), and drag (**D**). The lift (**L**) and drag (**D**) forces produce a resultant force (the aerodynamic force, (**R**) that acts perpendicular to the chord of the airfoil (Fig. 9.4). An airfoil is simply a section through the wing and has a certain thickness, cord and camber. **Camber** is measured by the maximum distance between the mean camber line and the chord line. The **chord** line is simply a line connecting

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Figure 9.1: Wing terminology used in this study a) **planform**, b) **airfoil**. Planform is the shape of the wing in dorsal profile. As illustrated in a, planform can change drastically by moving wing components. The aerodynamic characteristics of the two planforms illustrated are very different, even though they both have the same area and component shapes. As illustrated in b, an airfoil is a section through the wing. The shape of the airfoil is important in determining the behavior of the slipstreams that move around the airfoil. Airfoil shape may not be constant across the span of the wing.

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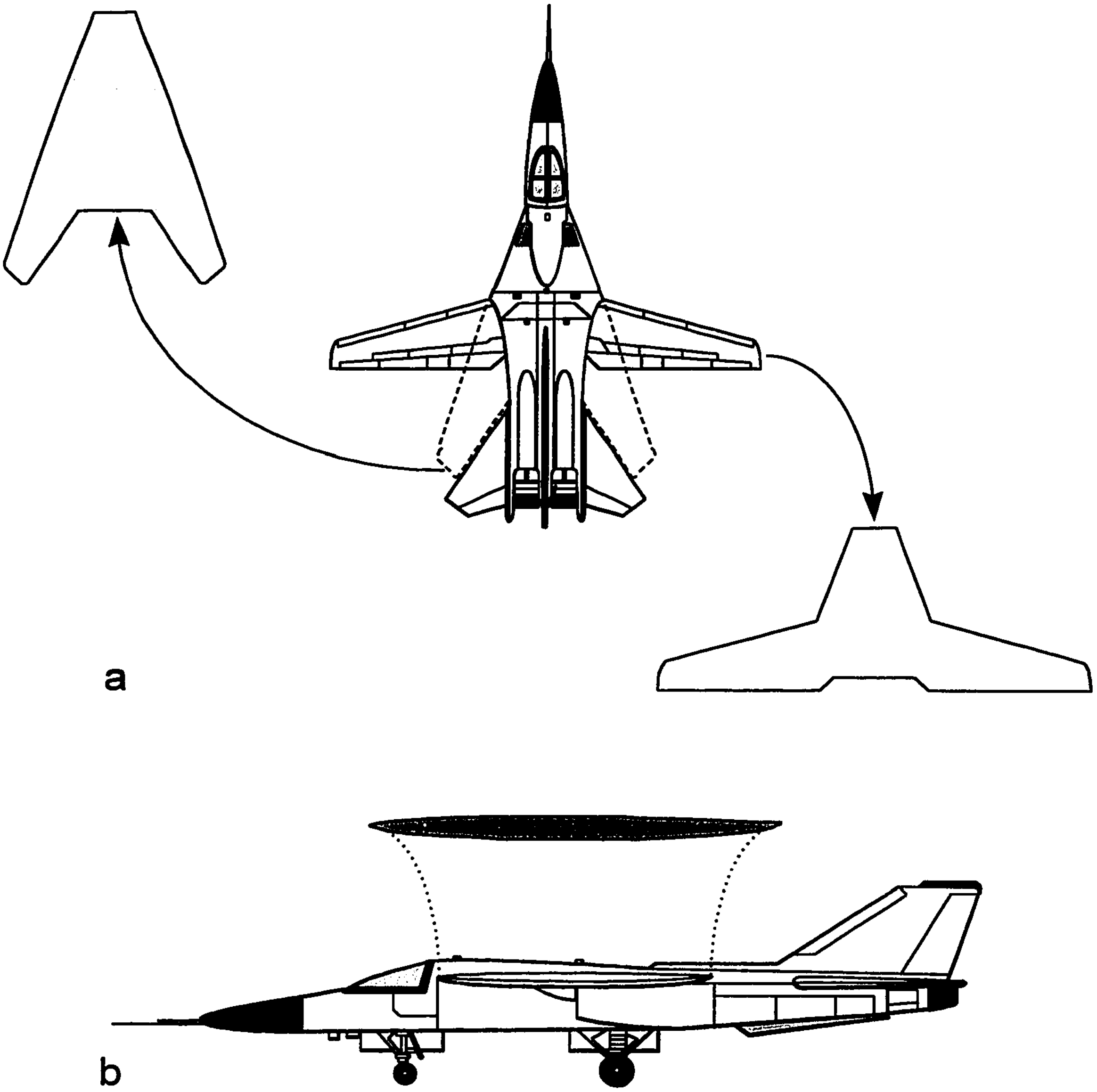

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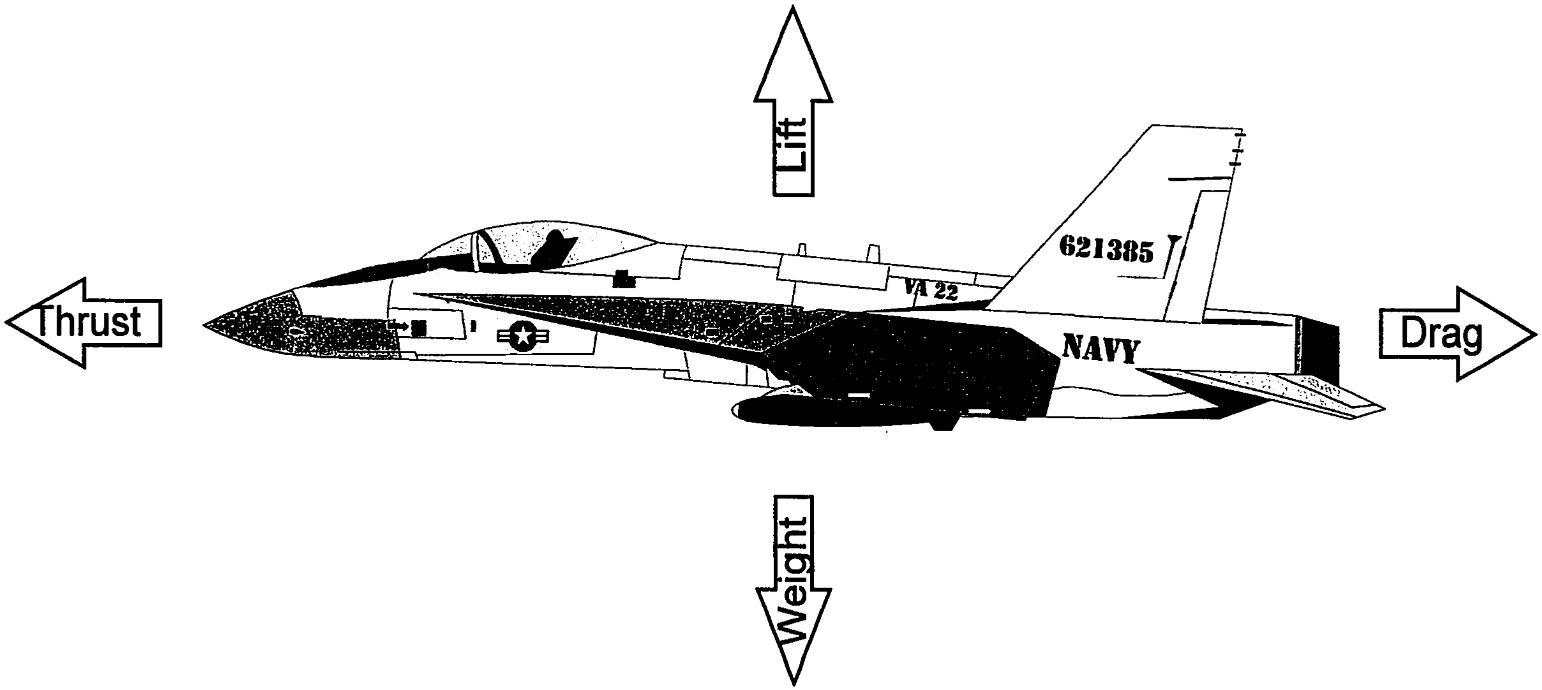

Figure 9.2: Translational forces acting on an aircraft.

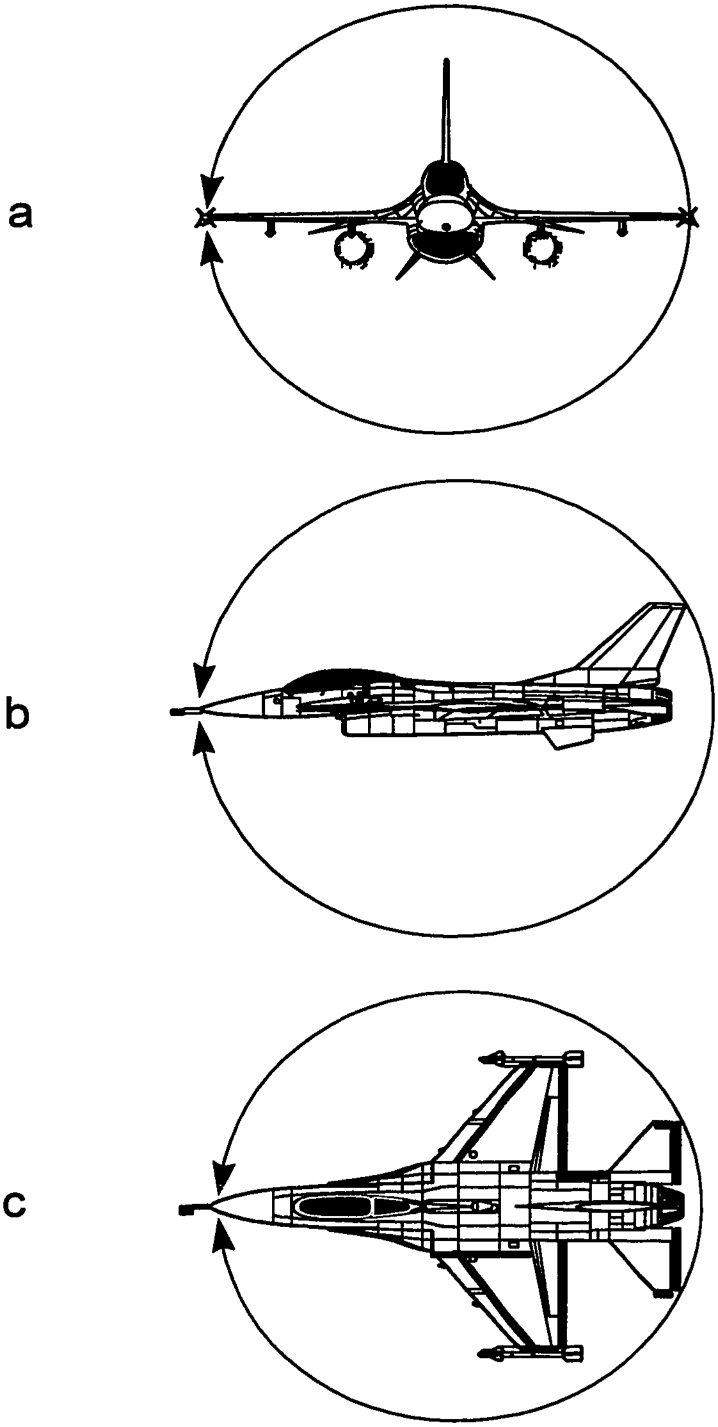

Figure 9.3: Moments acting on the aircraft a) roll, b) pitch, and c) yaw.

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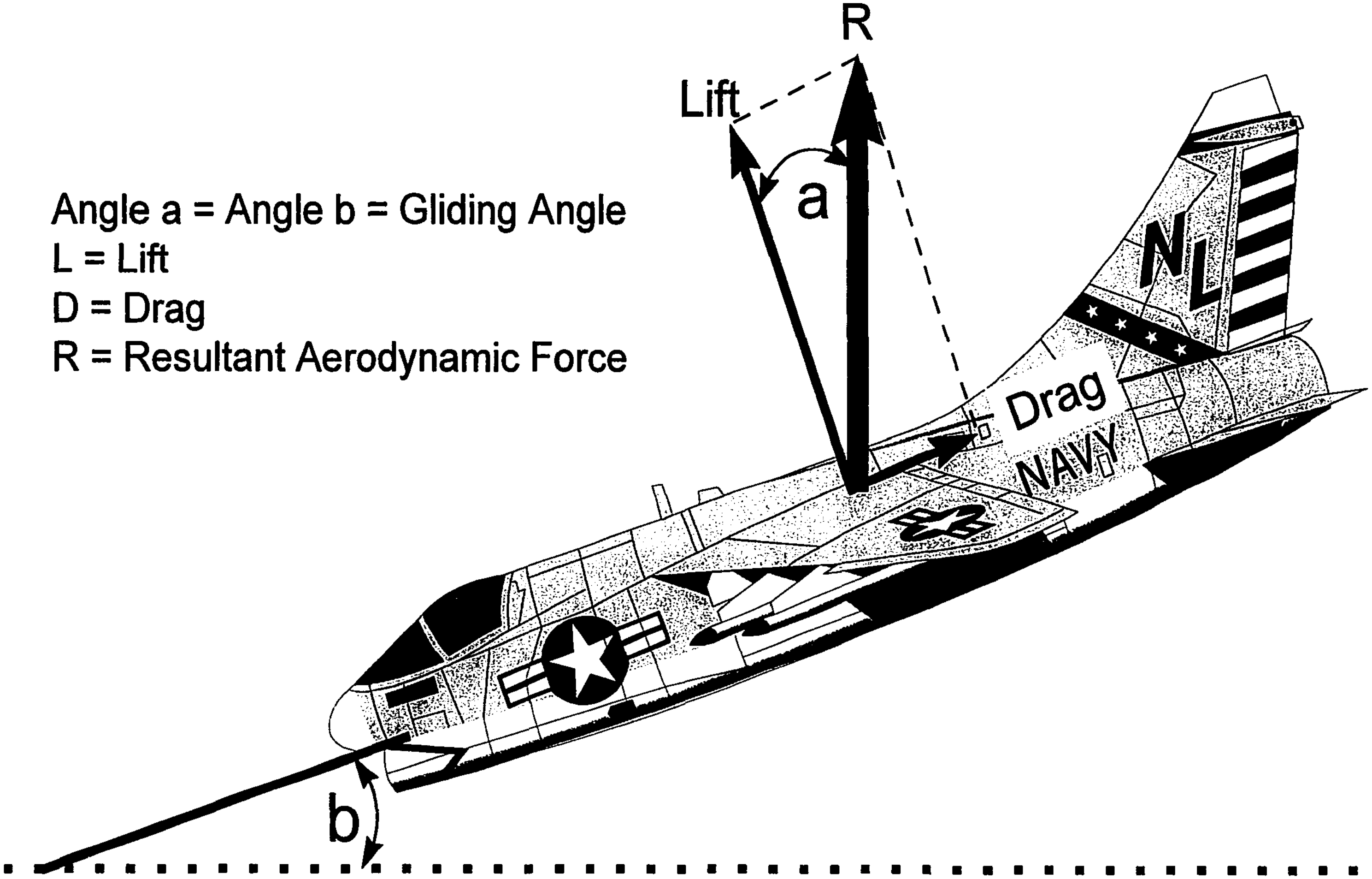

Figure 9.4: Forces acting on an aircraft during gliding flight.

the leading edge of the airfoil with the trailing edge of the airfoil. The **mean camber line** however is a line connecting the points that are exactly half way between the upper and lower surfaces of the airfoil (Fig. 9.5). As noted by Anderson (1985, p. 175) "[t]he camber, shape of the mean camber line, and to a lesser extent, the thickness distribution of the airfoil essentially control the lift and moment characteristics of the airfoil."

Within the context of this study the main aerodynamic concerns are with elements of **PERFORMANCE**, and principles of **stability and control.** Performance elements are those that have mostly been dealt with in previous studies of gliding and flying animals (Norberg and Rayner, 1987; Scholey, 1986; Thorington and Heaney, 1981), while principles of stability and control have largely been ignored (but see Norberg, 1991). This is a critical omission, as these principles may have as great an impact on overall gliding ability as general parameters of performance.

PERFORMANCE can be defined as the movement of the wing as it responds to lift, weight, thrust, and drag (Anderson, 1985; von Mises, 1945; Figure 1). In gliding the propulsive thrust comes from the initial leap into the glide and from gravity. The study of performance deals with the translational motion of the wing through the air in response to forces that are either perpendicular or parallel to the flight path (i.e. lift & weight, and thrust & drag). Aspects of airplane performance include maximum speed, rate of climb, range, endurance, service ceilings, and take off and landing

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Figure 9.5: Angle of attack (α) is the angle between the cord line and the relative wind. **Camber** is defined by a line exactly half-way between the upper and lower wing surfaces. **Cord** is the width of the airfoil. It is important to remember that α, **camber**, and **cord** can all change depending on the location of the airfoil section in the wing.

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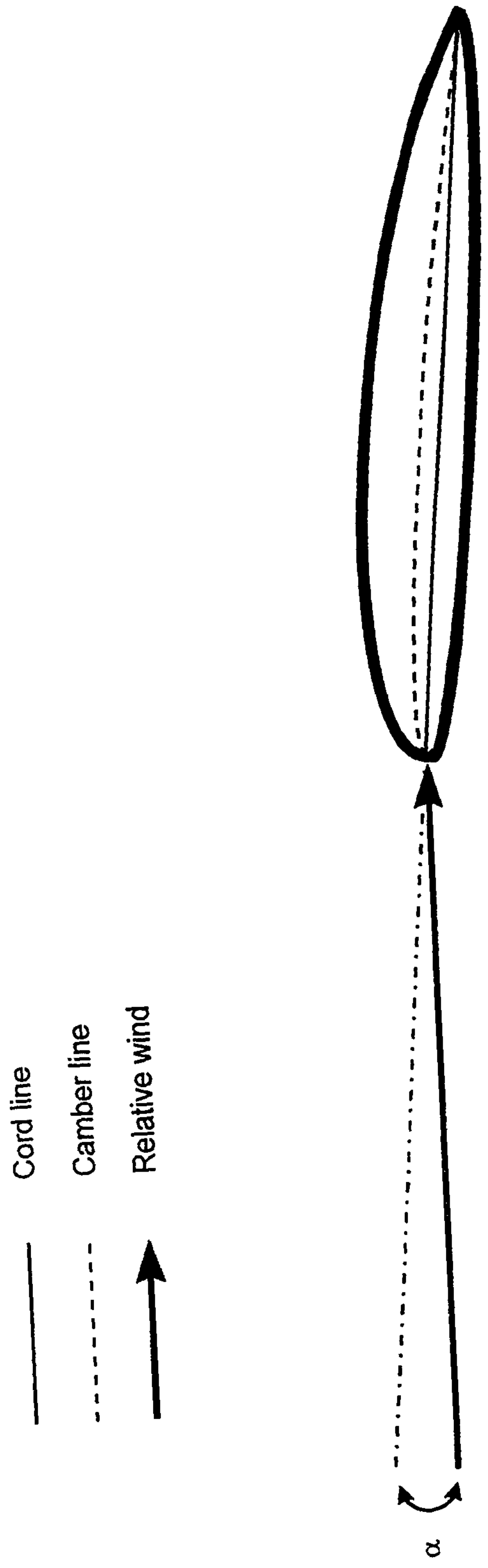

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performance. For gliding mammals performance aspects would include minimum gliding velocity, minimum gliding angles, maximum lift to drag ratios (**L/D**$_{max}$), and maximum coefficients of lift (**C**$_{L,max}$). Lift to drag (**L/D**) ratios have an important role in determining performance parameters, as do the shapes of the wings being compared. These parameters are affected by parameters of the wing such as aspect ratio (**AR**) and wing loading (**WL**), and by the more subtle aspects of wing shape discussed in the next chapter.

Principles of **stability and control** deal with the rotational motion of the wing in response to moments about the center of gravity (Fig. 9.3). There are two kinds of stability, static stability and dynamic stability. **Static stability** can be defined as the condition that exists when the forces and moments on a wing that has been disturbed from equilibrium tend to *initially* return the body toward its equilibrium position. Such a wing would have positive static stability. A wing would be **STATICALLY UNSTABLE** if the forces and moments that act on it when it has been disturbed from equilibrium *initially* continue to move the wing away from its equilibrium position. Such a wing would have negative static stability. A **NEUTRALLY STABLE** wing would be one where the wing is still at equilibrium after being disturbed from an initial equilibrium position. Anderson (1985) notes that neutrally stable wings are very rare, and emphasizes that static stability and instability only deal with the initial tendencies of the wing after it has been disturbed from equilibrium. Longitudinal static stability (stability around the pitch axis) has been shown in wind tunnel tests of aircraft (Anderson, 1985) to be relatively

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more important than either lateral (roll) or directional (yaw) stability. As we will see, gliding mammals have mechanisms for increasing static stability in all of these axes.

Whether or not the wing ever returns to its initial equilibrium position, and how it reattains that position, are the realm of dynamic stability. "**Dynamic stability** deals with the *time history* of the vehicle's motion after it initially responds to its static stability." (Anderson, 1985 p. 345; bold added). Therefore, a wing would be considered dynamically stable if it eventually returns to and maintains its equilibrium position. A dynamically unstable wing would never maintain its equilibrium position for any period of time after it is disturbed from equilibrium, if it even has an equilibrium position. If the wing were oscillate with a constant amplitude about the equilibrium position it would be **dynamically neutral**. Anderson (1985 p. 347) notes that "...such a case is of little practical interest...", presumably because it never occurs.

The combinations of static and dynamic stability in a given aircraft can be complex. For example, a dynamically stable aircraft must always be statically stable. If it were to initially continue away from its initial equilibrium position it will not be able to return to its initial equilibrium position. Similarly, a statically unstable wing must always be dynamically unstable. However, a dynamically unstable wing may also be statically stable.

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Control deals with the deflection of control surfaces necessary to produce the forces needed to change the wing from one equilibrium position to another, or "...to produce nonequilibrium accelerated motions...", i.e. maneuvers (Anderson, 1985). Therefore, stability is concerned with the ability of an airfoil to maintain or return to its equilibrium position, while control is concerned with the ability of an airfoil to change its equilibrium position. Consequently, studies of stability and control are necessarily linked, and focus on moments. In airplane aerodynamics these moments are concentrated about the center of gravity of the vehicle, but can be reduced to moments about the aerodynamic centers of the wings and control surfaces. When the moments about the center of gravity ($\mathbf{M}_{cg}$) are zero the wing is in equilibrium and is said to be trimmed. In our discussion of mammalian aerodynamics we will only be concerned with moments about the center of gravity because there is presently no way of determining the aerodynamic centers of the various wing components. Such a determination requires expensive, time consuming, and detailed wind tunnel testing.

As mentioned above, lift and drag are two parameters which have a large impact on performance and all wings generate both lift and drag. Exactly how they generate lift is still being debated. There are two competing theories, the Bernoulli theory and the Newtonian theory. Under the Bernoulli theory, an airfoil generates lift largely because it creates a pressure differential, while the Newtonian theory is more concerned with the downward deflection of air produced by an airfoil at some angle of attack.

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Because the Newtonian theory is usually discussed in standard aerodynamic texts along with (if not as a part of) the Bernoulli theory the two theory are not differentiated here.

The **ANGLE OF ATTACK** (α) is the angle between the chord line of the airfoil and the vector of the slipstreams (Fig. 9.5). The kinetic energy imparted through the downward deflection of air (i.e., the Newtonian theory) is usually of little importance for most aerodynamic situations because the angles of attack tend to be relatively low. The manner in which the airfoil creates this pressure differential is described by Bernoulli's theorem which describes steady flow along a streamline in an incompressible (i.e. constant density) fluid. Steady flow is maintained when the velocity of flow is constant at every point in space even though the velocity of the fluid may change at different points. A streamline is a curve that has the same direction of flow as the fluid. Therefore, in a steady flow a molecule will follow the whole course of the streamline from upstream to downstream. Explanations of the effects of this theorem usually consider the flow of some medium (fluid or gas) through a pipe. Because the mass of fluid or gas moving through any section of the pipe is constant, the condition of continuity is given as

$$p_1 V_1 A_1 = p_2 V_2 A_2$$

where p is the density of the fluid or air, V is the velocity of the flow, and A is the area of the section through which the fluid or air is moving. From this

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we see that if l is the length of the cylinder and A is the cross-sectional area of the cylinder through which the flow is passing, then

$gplA$ = the mass of the air in the cylinder,

where g is the gravitational acceleration (9.81 m/sec^2). Given that the mass at any section of the flow is constant, an increase in the length over which a slipstream must travel must entail a drop in pressure where gravity and cross sectional area are constant. Gravity is certainly constant for all flying mammals and most man-made aircraft. Similarly, the cross section of the "pipe" within which these aircraft are moving is functionally infinity. Velocity is also constant across the airfoil at any time t for gliding mammals and man-made aircraft. This is not true for bats, and they are better modeled under the principles of unsteady aerodynamics. Therefore Bernoulli's equation for an incompressible steady flow can be expressed as

$V^2/2 + p/p$ = constant along each streamline.

If we place an asymmetrical airfoil, or a symmetrical one of some angle of attack into the middle of our "pipe" we create an interesting situation. Since the molecules of the medium (in this case air) are incompressible and are assumed to have constant velocity, the only parameter that can change in Bernoulli's equation is the pressure of the air. Remember, the longest distance is over the top half of a cambered airfoil. Because the mass of air in any section of the flow is constant the distance between air molecules on the top of the wing increases, creating a low pressure system above the

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wing and a high pressure system below the wing. Lift is the force that results from the pressure differential above and below the wing. Lift is also generated by the downward deflection of the air passing over a wing at some angle of attack, but this force has little input into the total lift force. Mathematically lift (**L**) is defined as

$$L = p/2V^2SC_L$$

where p is the density of the air, **V** is the velocity of the flow, **S** is the area of the wing, and C_L is the coefficient of lift.

Drag results from the movement of the slipstreams over the airfoil (the wing through the air). Drag acts parallel to but in the opposite direction from the flow of the fluid. The total drag (D_{tot}) on any aircraft is the sum of the parasite drag (D_{par}), the profile drag (D_{pro}), and the induced drag (D_{ind}).

$$D_{tot} = D_{par} + D_{pro} + D_{ind}$$

Parasite drag is simply the drag incurred due to frictional forces acting on the non lift generating surfaces of the aircraft. In man-made aircraft this is the drag incurred by the fuselage, landing gear, etc. Profile drag has three distinct components, skin friction drag (D_f), pressure drag due to flow separation (D_p), and wave drag (D_{wave}).

$$D_{pro} = D_f + D_p + D_{wave}$$

Wave drag is only a factor at transonic and supersonic speeds and need not be considered in a discussion of flying mammals. Therefore, for flying

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mammals, and indeed most man-made aircraft, the profile drag on a wing can simply be defined as

$$D_{pro} = D_f + D_p.$$

Skin friction drag is the drag component that results from the shearing forces generated as the slipstreams move over the airfoil. Because the flow over an airfoil is not frictionless, the slipstream closest to the airfoil adheres to the surface. In theory, the flow velocity right at the surface is zero. As you move away from the surface of the airfoil, the retardation of the flow due to friction becomes less, until the velocity of the slipstreams again reaches $\mathbf{V_{inf}}$ (the velocity of the slipstream at an infinite distance from the airfoil). The region of viscous flow between the airfoil surface and the point where the slipstreams again reach $\mathbf{V_{inf}}$ is called the boundary layer. The flow field can therefore be separated into two regions, the boundary layer, where friction is important, and an outer layer of frictionless flow. This boundary layer becomes thicker as the slipstreams progress over the airfoil.

To make things more interesting, there are two types of viscous flow, laminar flow and turbulent flow. **Laminar flow** is characterized by streamlines that are "...smooth and regular and a fluid element moves smoothly along a streamline..." (Anderson, 1985, p. 134). **Turbulent flow** is characterized by streamlines that "...break up and a fluid element moves in a random, irregular, and tortuous fashion." (Anderson, 1985, p. 134). These two types of flow have very different characteristics. In a turbulent

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boundary layer the velocity within the layer is very close to $\mathbf{V_{inf}}$ except for very close to the surface of the airfoil, where velocity rapidly decreases to zero. In laminar flow however, velocity gradually decreases from $\mathbf{V_{inf}}$ to zero as you approach the surface of the airfoil. The result is that there is less shearing stress incurred for laminar flows, and this translates into reduced profile drag. The thickness of the laminar boundary layer also grows at a parabolic rate $x^{1/2}$, while a turbulent boundary layer grows at a much larger rate $x^{4/5}$.

Profile drag has another component that we are interested in and that is **pressure drag due to flow separation.** At some distance from the leading edge of the airfoil the slipstreams have a tendency to separate from the airfoil. This is particularly the case for an airfoil at high angles of attack, where there is a rapid decrease in lift, and a rapid increase in drag. When the L/D ratio reaches a point where the lift force can no longer offset the effects of gravity, stalling is said to occur. In effect, the aircraft falls out of the sky. The flow separates from the airfoil because as the slipstream moves across the airfoil it is retarded due to the forces of skin friction drag. As this happens the pressure differential between the top of the airfoil and the freestream pressure begins to decrease. In effect pressure increases as the slipstreams move from the leading edge to the trailing edge of the airfoil. When the flow is attached there is an area of very low pressure near the leading edge of the airfoil. This translates into an area of much higher

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pressure near the trailing edge of the wing. When the flow is separated the area of low pressure at the leading edge of the wing is of a much higher pressure and there is not as steep a transition to high pressure near the trailing edge of the wing. There are two effects related to a separated flow. First, lift is reduced because the pressure differential across the airfoil is reduced. Second, there is an added drag component incurred from the greater horizontal vectors imparted by the separated flow.

There is an interesting trade off between these two components of drag. D_f is minimized when a laminar (i.e. nonturbulent) flow is maintained across the wing. Conversely, D_p is minimized when there is a turbulent boundary layer about the wing because this helps to prevent flow separation. A turbulent boundary layer can do this because at a given distance from the surface of the airfoil it maintains a higher velocity than a laminar flow. This means that there is greater kinetic energy in the flow near the airfoil surface, and this helps prevent the flow from separating. It is important to remember that neither laminar nor turbulent flow are in any sense "better" than the other. On a blunt object like a sphere, D_p is the major contributor to profile drag and a turbulent boundary layer is preferable for reducing drag. Hence the dimples on a polo ball or a golf ball. However, for a slender object like an airfoil at a low angle of attack, D_f is the larger contributor and a laminar boundary layer is more appropriate for reducing drag. Finally, no airfoil is characterized by solely laminar or solely turbulent flow. On any airfoil, the

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flow begins as laminar, but then becomes turbulent as it proceeds across the airfoil.

Induced drag (**D_i**) is another component of drag that acts on the wing. Whereas profile drag is the result of the action of viscous forces on the wing, induced drag results from the fact that all wings are of a finite span. In other words, they have wing tips. As a result of this, and the fact that lift is created via a pressure differential across the wing, there is a tendency to lose lift at the wing tips. In effect, some of the high pressure from under the wing "leaks out" around the wing tip, reducing the pressure differential and altering the flow of the slipstreams about the wing at the wing tips (Fig. 9.6a). The result is the creation of wing-tip vortices extending back along the flight path from the wing tips (Fig. 9.6b). This is what is commonly referred to as the downwash of an aircraft. The overall effect of induced drag is to introduce a small downward vector to the wing at the wing tips. This has two important effects; first, this acts to effectively reduce the angle of attack of the wing tips; and second, there is an increase in drag.

Why this circulation of air at the wing tips should be manifest as increased drag is not entirely clear, but it has been experimentally verified and may be related to three factors. First, the wing-tip vortices alter the flow of the slipstreams so that the pressure distribution over the wing changes in the direction of increased drag. It could do this if the downward component of the rotation were greater at the leading edge of the wing and less as it

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Figure 9.6: **Induced drag** results from a) high pressure from under the wing “leaking” into the area of low pressure above the wing at the wing tips. This produces vortices of disturbed air b) that trail from each wing tip.

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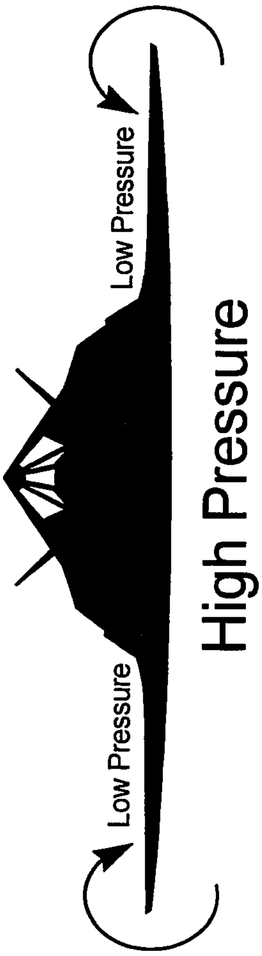

a

b

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approached the trailing edge. If this were the case then $\mathbf{D_i}$ would be effectively mimicking $\mathbf{D_p}$ because it would reduce the pressure differential at the leading edge of the wing. Just as in $\mathbf{D_p}$ this would add to the horizontal vectors of these forces above the wing and be manifest as increased drag. Another interpretation is that the downward vector of the wing-tip circulation changes the effective angle of attack of the wing by changing the direction of flow in the vicinity of the wing. Therefore, "...the lift vector itself is 'tilted back,' hence it contributes a certain component of force parallel to V_{inf} [relative wind], that is, a drag force..." (Anderson, 1985, p. 211). Finally, because there is kinetic energy contained within the wing-tip vortices, and this energy has to come from somewhere, it must be supplied by the thrust of the aircraft. Therefore if thrust is being applied to counter its effect, it is by definition a drag force. To some degree all of these explanations of induced drag are interchangeable, and what is important to remember is that induced drag results from the circulation of air at the tips of the wings that reduces the pressure differential across the wings.

Although flapping flight may not meet the assumptions of Bernoulli's theorem gliding flight does. Therefore it is appropriate to model gliding mammals as "static airfoils". This does not mean that the wing is a fixed and immutable structure. It only means that we are considering performance where acceleration is zero. Unstable aerodynamic theory would be needed to analyze flight where acceleration plays a major role in wing performance, i.e.

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where the rotation of variable pitch propellers or rotor blades are important, or where thrust is being generated through the flapping of wings.

Aspect ratio describes the general shape of the wing, and is a ratio of the wingspan to the chord of the wing (Fig. 9.7). Because with flying mammals we are dealing with complex shaped wings it is more appropriate to use the formula $\mathbf{AR} = \mathbf{b^2/S}$ (S = wing area). A perfectly square wing would have $\mathbf{AR} = 1$, a wing with the chord greater than the wingspan would have $\mathbf{AR} < 1$, and a wing with a wingspan greater than the chord would have $\mathbf{AR} > 1$. Even something as simple as this has profound effects on flight parameters and wing performance.

Coefficients of lift are a means for comparing the relative lift produced for wings of different sizes and shapes, and is a very useful concept. For example, a flat rectangular plate with an aspect ratio of 1 and an area of 10 cm^2 will produce some lift force L at angle of attack α. A flat rectangular plate with an aspect ratio of 1 and an area of 20 cm^2 will produce some lift force **2L** at angle of attack α. Although the second wing produced twice as much lift as the first wing we can in fact treat them as the same wing because their coefficients of lift ($\mathbf{C_L}$) are equal. Coefficients of lift are defined as

$$\mathbf{C_L = L/\mathit{q}S}$$

where q is the dynamic pressure of the fluid, and **S** is the surface area of the wing. The coefficient of drag ($\mathbf{C_D}$) has a similar equation

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Figure 9.7: Wing loading and aspect ratios influence performance, control, and stability. Highly loaded wing are less maneuverable and must fly fast to remain airborne. High aspect ratio wings have lower drag, but also stall at lower angles of attack. Agility depends on a number of factors. High aspect ratio wings with control surfaces located near the wing tips should be able to effect larger moments about the center of gravity for any given control surface movement. However, the larger dampening moments of high aspect ratio wings may counteract these forces.

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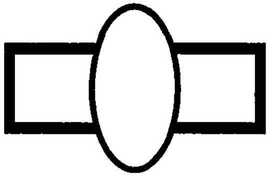
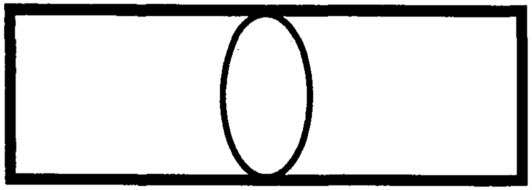
Wing Loading (WL) = Mg / S

Higher Wing Loading



Mg = 500, S = 5, WL = 100
- Must fly faster
- Less maneuverable

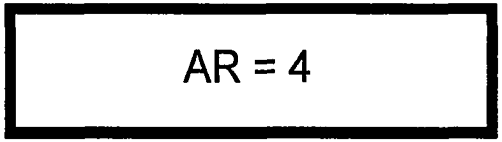
Lower Wing Loading



Mg = 500, S = 10, WL = 50
- Slower flight
- More maneuverable

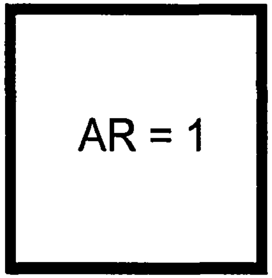
Aspect Ratio (AR) = b^2 / S

High Aspect Ratio



b = 4, S = 4
- Low drag
- More agile?
- Stall at low angle of attack

Low Aspect Ratio



b = 2, S = 4
- High drag
- Less agile?
- Stalls at higher angle of attack

$$C_D = D/qS$$

and reflects similar factors.

High aspect ratio wings produce a greater coefficient of lift at angles of attack above about -5 degrees (von Mises, 1949). This is largely due to the fact that high aspect ratio wings produce less drag. Given what we now know about drag it is easy to see why this is so. Profile drag is the result of viscous forces and the longer a distance over which such forces have to act, the greater magnitude they will have. Therefore low aspect ratio wings (those with a relatively thick chord) will produce greater relative profile drag. Similarly, a low aspect ratio wing with a relatively long chord also has longer wing-tips (usually, see below for the correction for elliptical wings). Consequently, the momentum imparted by the wing tip vortices will have a relatively greater magnitude in low aspect ratio wings.

Wings with high aspect ratios will therefore have higher L/D ratios and this translates into greater gliding distances for a gliding mammal. Gliding mammals, however, tend to have very low aspect ratios, and low aspect ratio wings have their benefits as well. The conventional explanation for low aspect ratios in gliding mammals has been that at high angles of attack low aspect ratio wings actually produce relatively more lift, and resist stalling better than low **AR** wings. In fact, wings with **AR** 2-7 reach $\mathbf{C_{L,Max}}$ before or just after α 15^0 (von Mises, 1949), while wings of AR 1 and 2, however have not yet reached $C_{L,Max}$ at α 15^0.

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This factor (**$C_{L,Max}$** reached at a higher α for low aspect ratio wings) may have to do with another property of low aspect ratio wings, their higher Reynolds numbers. **Reynolds number** is a dimensionless number that describes the circulation of air about the wing. It is defined as

$$\mathbf{Re} = pVl/u$$

where ***p*** is the air density, **V** is the velocity of the flow, ***l*** is the chord of the wing, and ***u*** is the viscosity of the air. For our purposes, velocity, air density, and viscosity can be considered constant, and therefore **Re** depends largely on the chord of the wing. In effect, high Reynolds numbers indicate a strong circular flow about the airfoil. This prevents the slipstreams from separating from the upper surface of the wing at high angles of attack. The soft downy fur of mammalian gliders may also act as a "dead space" that also helps to preserves laminar flow. Reynold's number has an impact on many aerodynamic properties. Both the thickness of the boundary layer and the skin friction coefficient are inversely proportional to the square root of the Reynolds number.

The final important factor to consider about low aspect ratio wings is to consider what happens at negative angles of attack. Von Mises (1949) shows that low aspect ratio wings reach **C_L** = 0 at a more negative angle of attack than higher aspect ratio wings, and that below ~-5 degrees angle of attack the low **AR** wings produce the greater (although negative) **C_L**. Similarly, for moderate Reynolds numbers **C_L** is essentially the same for all

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wings, but at high and negative angles of attack the high **Re** wings outperform the lower **Re** wings (i.e., the low aspect ratio wings outperform the high aspect ratio wings).

Aspect ratio has also been proposed to have an effect on the maneuverability of bats (Struhsaker, 1961; Dwyer, 1965; Vaughan, 1966; Strickler, 1978) and although this is a bit of a generalization that requires some strict boundary conditions it is true (contra Norberg and Rayner, 1987). The main boundary condition that must be met is that the two aircraft being compared have the same wing loading (see below). The two aircraft should also be traveling at the same velocity for the comparison to be valid. We also need to make a distinction (as Norberg and Rayner, 1987 do) between maneuverability and agility. **Maneuverability** refers to the space required to change the flight path and is often expressed as a turning radius. Animals with a smaller turning radius at a given speed would be more maneuverable. **Agility** refers to the acceleration about the center of gravity needed to initiate maneuvers and is expressed as the rapidity with which an animal can initiate maneuvers.

Wing loading (**WL**) simply describes the amount of weight born by the wing and is expressed as Newtons per meter squared (**N/m^2**). Wing loading has important performance correlates as well. Theoretically, wing loading does not affect glide angle or gliding distance but we will see later that operationally this may be very important for gliding mammals. Wing loading does, however, effect stalling speed, or the speed at which the wing stops

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producing enough lift to offset the weight of the aircraft. This minimum velocity is proportional to the square root of wing loading.

$$V_{Min} = (2N/\rho SC_L)^{1/2}$$

Therefore, as wing loading doubles the minimum velocity at which the aircraft must fly to remain airborne increases by 1.41 times. Wing loading is also inversely correlated with maneuverability. Animals with high wing loading are less maneuverable than animals with low wing loading. Again, maneuverability is defined by the minimum turning radius for any given aircraft at a certain velocity. Turning radius is directly proportional to wing loading [$r = 2Mg/(SC_L\rho\sin\Phi)$], all other factors being equal.

The principles discussed above form the framework within which the aerodynamics of gliding mammals can be discussed.

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CHAPTER 10: COMPARATIVE AERODYNAMICS OF GLIDING MAMMALS

Gliding has evolved at least six times in extant mammals and at least twice in fossil mammals (Fig. 1.1). The degree of convergence seen in these gliders is considerable. The specializations associated with gliding include elongate and gracile limbs, and unique patagial suspensory mechanisms. However, most studies of gliding mammals have focused on relative wing size (wing loading, **WL**) and general wing shape (aspect ratio, **AR**) as means of evaluating gliding adaptations and comparing gliding abilities across taxa. These measures are important aerodynamic parameters, but extant gliders generally fall within a narrow range of wing loadings and aspect ratios. Finer details of wing shape may also represent convergent adaptations that play important roles in gliding. Specifically, dorsiflexed wing tips function to reduce the coefficient of induced drag ($\mathbf{C}_{D,i}$) (Thorington et al., 1998) and to increase lateral and directional stability in the colugos (Dermoptera, Cynocephalidae), flying squirrels (Rodentia, Sciuridae), and yellow-bellied, sugar, mahogany, and squirrel gliders (Diprotodontia, Petauridae) (Stafford and Thorington, 1997). A reduction of $\mathbf{C}_{D,i}$ provides a higher lift to drag (**L/D**) ratio, and translates into longer gliding distances. Winglets may also play an important role regarding control and maneuverability issues. The dorsiflexion of the winglets provides a more stable configuration about the roll axis and enhances static stability. Likewise, these winglets may also enhance directional stability. The winglets are also highly mobile, under voluntary control, and located far enough from the center of

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gravity (CG) that slight movements could produce significant moments around the CG. These hypotheses are consistent with aerodynamic theory but require testing in the specific taxa. The first step is the collection of detailed kinematic data on the roles these structures play in gliding. The second step consists of tests designed to determine how the structures function. A consideration of function and role will then allow us to evaluate adaptive scenarios explaining the acquisition of these features in independent lineages.

Gliding has evolved three times in the marsupials (in the Pseudochirini, the Petaurini, and the Acrobatini), once in the flying squirrels (the Pteromyinae), at least once in the scaly-tailed "flying squirrels" (the Anomaluridae), probably once in the common ancestor of the bats and the “flying lemurs” (the Chiroptera and the Dermoptera). If one considers the bats and dermopterans to be unrelated phyletically, then gliding has evolved seven times in extant mammals. Gliding has also evolved in fossil dormice (the Gliridae, Mein and Romaggi, 1991) and in the Eomyidae (Storch et al., 1996), a well known family of fossil rodents that have been linked to the Anomaluridae in the past (Stehlin and Schaub, 1951). Szalay and Sargis (in preparation) inform me also that the appendicular skeleton of an undescribed Paleocene marsupial from South America shows the hallmarks of gliding adaptations. All totaled then, gliding has evolved eight or nine times in mammals and, contrary to popular opinion, it is a fairly common adaptation among mammals and other vertebrates.

Given that gliding flight has been acquired independently in these different lineages it is possible that gliding has also evolved in different ways. Each taxon

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would have been constrained differently by its respective ancestry, and each taxon may have been subject to different selective pressures that led to gliding. Even so, each lineage would have encountered similar physical problems (i.e., problems related to physics) during their acquisition of flight. Therefore, gliding mammals may have evolved similar structures to deal with similar physical problems. All gliding mammals are specialized compared to their closest nongliding relatives. Many gliding mammals also possess unique structures that are homoplasious and function analogously to similar structures in other gliding lineages. This is often the result of natural selection acting on different structures that are performing similar functions and roles (see Bock and von Wahlert, 1965). These structures are convergent adaptations.

The definition of an airplane as a series of compromises flying in close formation is often jokingly offered by aeronautical engineers and pilots when asked to define an airplane. However, this definition is particularly appropriate for describing gliding mammals. Like man made aircraft, gliding mammals must function under a wide range of aerodynamic conditions and there are a series of trade-offs that must be maintained between **performance**, **stability**, **agility**, and **maneuverability**. Unlike man made aircraft gliding mammals must also be able to execute a wide range of nonarial positional behaviors that also exert selective forces on their postcranial anatomy.

Wing components.—All mammalian gliders have one wing component in common (Table 10.1), the plagiopatagium. This is the part of the wing that stretches between the forelimbs and the hindlimb and it is variably developed

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Table 10.1: Wing components present in extant gliding mammals.

	Plagiopatagium	Propatagium	Uropatagium	Patagial Extension
Diprotodontia				
Acrobatidae				
Acrobates pygmaeus	Yes	No	No	None, plagiopatagium extends from elbow to knees.
Pseudocheiridae				
Petauroides volans	Yes	?[1]	?[2]	None, plagiopatagium extends from elbow to ankle.
Petauridae				
Petaurus	Yes	?[1]	?[2]	Plagiopatagium extends onto ulnar aspect of fifth digit.
Dermoptera				
Cynocephalus volans	Yes	Yes	Yes	Dactylopatagium
Galeopterus variegatus	Yes	Yes	Yes	Dactylopatagium
Rodentia				
Sciuridae				
Petaurista	Yes	Yes	Yes	Stylopatagium
Biswamoyopterus	Yes	Yes	Yes	Stylopatagium
Aeromys	Yes	Yes	Yes	Stylopatagium
Eupetaurus	Yes	Yes	No	Stylopatagium
Pteromys	Yes	Yes	No[3]	Stylopatagium
Glaucomys	Yes	Yes	No	Stylopatagium
Hylopetes	Yes	Yes	No	Stylopatagium
Eoglaucomys	Yes	Yes	No	Stylopatagium
Petinomys	Yes	Yes	No[3]	Stylopatagium
Aeretes	Yes	Yes	No	Stylopatagium
Trogopterus	Yes	Yes	No	Stylopatagium
Belomys	Yes	Yes	No	Stylopatagium
Pteromyscus	Yes	Yes	No	Stylopatagium
Petaurillus	Yes	Yes	No	Stylopatagium
Iomys	Yes	Yes	No	Stylopatagium
Anomaluridae				
Anomalurus	Yes	Yes	Yes	Olecropatagium[4]
Idiurus	Yes	Yes	Yes	Olecropatagium[4]

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[1] Johnson-Murray (1987) identifies *M. sphincter colli profundus pars propatagialis* in these taxa, but I have been unable to identify any appreciable propatagium in the specimens available.

[2] Johnson-Murray (1987) identifies *M. semitendinosus* in the uropatagium of these taxa, but I have been unable to locate any appreciable uropatagium in the specimens available.

[3] Johnson-Murray (1977) identifies *M. semitendinosus* in the uropatagium of these taxa, but I have been unable to locate any appreciable uropatagium in the specimens available.

[4] The olecranon cartilage does not extend the patagium distally in these taxa.

Figure 10.1: Schematic illustrations of the planforms of gliding mammals. Solid lines illustrate the extent of the patagium without the contribution of patagial extensory mechanisms. Dashed lines illustrate the patagial extensory structures, dash-dotted lines show the extent of the patagium resulting from these structures. Patagial subsections that have not been confirmed are marked with a question mark.

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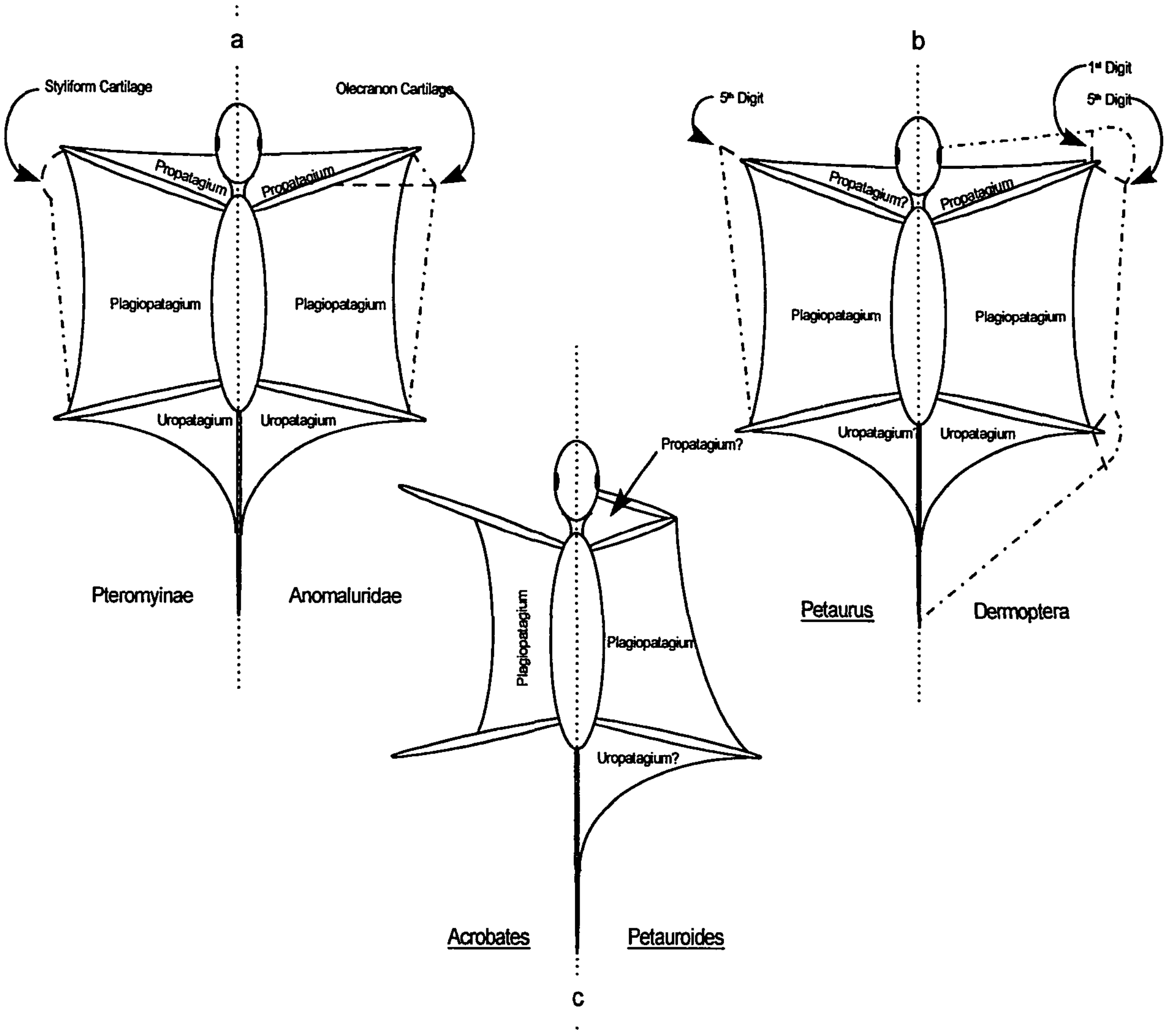

among gliding taxa. In addition, many gliding mammals have a membrane anterior to the forelimb, the propatagium, or a membrane between the hindlimbs that encloses the tail to some degree, the uropatagium. Many gliding mammals also have distal extensions of the gliding membrane supported by a variety of structures (Fig. 10.1), and these produce a variety of planforms among gliding mammals. Petaurus has an extension of the plagiopatagium onto the ulnar aspect of the fifth intermediate manual phalanx. This is not really a manual dactylopatagium, but it does qualify as a wing tip extension. The other gliding marsupials have no wing tip extensions. In Petauroides volans the leading edge of the wing only extends to the elbow, although the trailing edge extends almost onto the tarsus. In Acrobates the wing really only extends to the elbow and the knee although it may continue distally very close to the limbs. The dermopterans have webbing between the manual and pedal phalanges, true manual and pedal dactylopatagia. Anomalurus also has interdigital webbing, but this is not associated with the gliding membrane. Anomalurids have a cartilaginous strut articulating with the olecranon process that helps to suspend the plagiopatagium. The degree to which this strut extends the gliding membrane distally is debatable and largely depends on limb positioning, but the portion of the patagium between the olecranon cartilage and the forelimb is here considered as a separate patagial component, the olecropatagium. The true flying squirrels also extend the gliding membrane distally by suspending it from a cartilage, but this styliform cartilage articulates with the pisiform at the wrist (Thorington et al., 1998). The wing tip extension in the Pteromyinae is the stylopatagium. Although the

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patagial extensions do increase the lifting area of the animal, they only do so to a minimal extent (Table 10.2) in most taxa and may also serve other functions. Specifically they may serve to reduce drag, enhance stability, or to control the glide.

Capel et al. (1983), dealing with the acquisition of powered flight from the ground up, have questioned the effect that relatively small increases in the surface area of the wing have on generating lift. These authors hypothesize that wings initially function in control and stability during leaping. However, in some gliding mammals, most notably the dermopterans, wing tips and the patagial extensions associated with them do make up a significant proportion of the wing (Table 10.2). Norberg (1985) responded to Capel et al. (1983) by showing that even slight flapping movements in a gliding animal could produce enough **thrust** to significantly increase the glide angle. Thrust offsets drag, increases lift to drag ratios and increases glide angle. The acquisition of powered flight is not a consideration here, but both of these authors appear to be correct in certain particulars. Patagial extensions are not solely related to increasing lift. The plagiopatagium probably produces all of the lift necessary to be a glider and patagial extensions likely function in control and stability, and to increase performance. I would also agree with Norberg (1985) concerning the importance of offsetting the effects of drag, and suggest that wing tip extensions function in this role in gliding mammals. Whether or not these structures can later become co-opted to produce thrust remains unclear at this time.

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Table 10.2: Wing component area in gliding mammals[1].

	Plagiopatagium	Propatagium	Uropatagium	Wing Tip[2]	Plagiopatagial Extension[3]
Diprotodontia					
Acrobatidae					
Acrobates pygmaeus	100%	NA?	NA?	NA	NA
Pseudocheiridae					
Petauroides volans	100%	NA?	NA?	NA	4%
Petauridae					
Petaurus	100%	NA?	NA?	NA	16%
Dermoptera					
Cynocephalus volans	64%	9%	21%	6%	16%
Galeopterus variegatus	67%	10%	17%	6%	13%
Rodentia					
Sciuridae					
Petaurista	78%	3%	13%	6%	5%
Other Pteromyinae[4]	94%	5%	NA	2%	4%
Anomaluridae					
Anomalurus	75%	5%	18%	2%[5]	1%

---

[1] All comparisons presented here are for animals gliding with a forelimb angle of 90° and a hindlimb angle of 45°, with the exception of Petauroides volans. P. volans is modeled with the limbs perpendicular to the trunk.

[2] Wing tips include all wing tip structures not included in the plagiopatagium.

[3] This is the amount of plagiopatagial surface area added as a consequence of wing tip extensions. For *Petaurus* this includes the plagiopatagium between the manus and the pes. For dermopterans it is also the portion of the plagiopatagium that stretches between the manus and pes. For the flying squirrels it is the area added to the

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plagiopatagium due to the lateral expansion of the patagium onto the styliform cartilage. For the anomalurids it is the added surface area due to the olecropatagium. These values were arrived at by comparing models of patagial surface area computed with and without patagial extensions for each taxon.

[4] Average values for Trogopterus, Eoglaucomys, and Glaucomys. None of these taxa differed from each other by more than 1%.

[5] For Anomalurus the wing tip is the olecropatagium between the olecranon cartilage and the radius. In some configurations, the presence of the olecranon cartilage actually decreases total patagial surface area.

General body proportions.—The length of the animal's trunk and limbs constrain the shape and size of the wing. Gliding mammals tend to have relatively long and gracile limbs as compared to their nongliding relatives (see also Thorington and Heaney, 1981; Runestad and Ruff, 1992; Chapters 6, and 9). Specifically, the anatomical structures to which the patagial extensions attach appear to be particularly elongate and gracile. This has usually been interpreted as a means of increasing patagial surface area, thereby increasing lift. However, the wing loadings of many gliding mammals are not all that different from the hypothetical wing loadings calculated for their nongliding relatives (Fig. 10.2, Table 10.3). For example, the wing loading of Petauroides volans appears to be more similar to the hypothetical wing loading of the nongliding sciurids and the nongliding pseudocheirids than it is to the other gliding marsupials. Similarly, Sciurus deppei (a nongliding sciurine from Central America) has a hypothetical wing loading very close to that of Glaucomys sabrinus and Petaurus breviceps. However, the degree to which wing loading and aspect ratio can change based on the positioning of the limbs (Table 10.3) is remarkable.

There is some evidence that gliding mammals may have relatively longer vertebral columns than their nongliding relatives (Fig. 5.4b), but this may apply to only the larger gliding mammals (Fig. 5.4a). Such a situation would provide the larger gliding mammals with relatively longer wing cords. This would increase **Re** and thereby allow these taxa to attain higher angles of attack before

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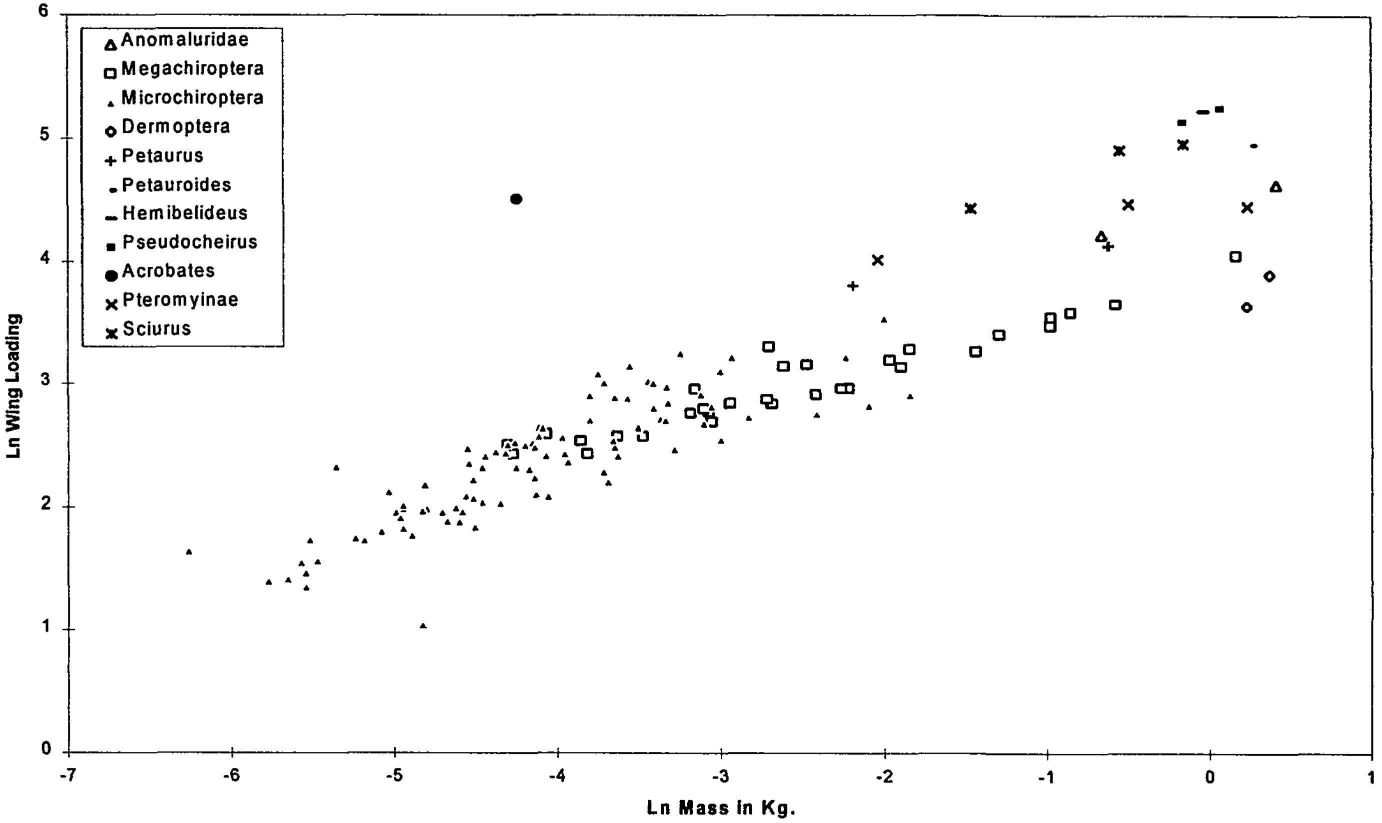

Figure 10.2: Wing loading in some mammals. The wing loadings presented here are based on animals gliding with the limbs held at 62.5 and 45 degrees to the midline, except for Petauroides, which is modeled with the limbs perpendicular to the midline (Table 10.3). Chiropteran data from Norberg and Rayner (1987). Note the relatively low wing loadings of the dermopterans.

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Table 10.3: Aspect ratios and wing loadings in some mammals.

	Forelimbs at 62.5^0 Hindlimbs at 45^0		Forelimbs at 90^0 Hindlimbs at 90^0		% Change	
	AR	WL	AR	WL	AR	WL
Petaurus australis	1.04	63	2.11	81	105%	30%
Petaurus breviceps	1.05	45	2.15	59	105%	31%
Petauroides volans	0.76	134	1.36	143	79%	7%
Acrobates pygmaeus	0.73	84	1.23	92	68%	10%
Cynocephalus volans	1.08	38	1.35	48	25%	26%
Galeopterus variegatus	1.36	49	1.94	71	43%	45%
Petaurista sp.	1.28	86	2.02	109	58%	27%
Trogopterus edithae	0.97		1.54		59%	
Eoglaucomys fimbriatus	0.98	88	1.69	95	73%	8%
Glaucomys sabrinus	1.04	56	1.83	61	76%	9%
Anomalurus derbianus	0.86	69	1.86	93	116%	35%
Anomalurus peli	0.85	103	1.80	139	112%	35%

stalling. However, many of the larger gliding mammals included in this study are dermopterans with disproportionately long necks. A more detailed study of vertebral column morphology in gliding mammals and their nongliding relatives is needed to clarify these issues.

Limb indices do indicate that in general the limbs of gliding mammals are relatively longer than those of their closest nongliding relatives and that the forelimbs of the dermopterans are much longer than all the other gliding mammals. Petauroides volans, however, does not have relatively longer forelimbs than the nongliding taxa studied here. A closer inspection of this issue shows that forelimb elongation in gliding mammals is largely due to a relatively longer radius, and that only the dermopterans appear to have relatively elongate humeri. It is not surprising that Anomalurus fits well within this pattern of forelimb and radial elongation in gliders. Nor is it surprising that Petauroides does not. Although Anomalurus has been characterized as an "elbow glider", due to the suspension of it's patagium from the olecranon cartilage, the patagium does extend all the way to the wrist in this taxon. However, the olecranon cartilage may not extend the patagium laterally in some wing configurations. This is not the case for Petauroides, where the patagium does not extend onto the antebrachium. Petauroides do appear to have relatively elongate humeri, but only in comparison to the nongliding pseudocheirids, which of course is the most appropriate comparison. As previously noted (Chapter 6), the regression lines for forelimb length of nondermopteran gliders and nongliders converge at lower body sizes (Thorington and Heaney, 1981; Runestad and Ruff, 1994). This may

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be the result of selection for elongate forelimbs in small arboreal animals utilizing relatively large supports (Cartmill, 1985; Jungers, 1977, 1979, 1985; Thorington and Thorington, 1989), and be relevant to the acquisition of gliding in mammals. The evolution of relatively long forelimbs as a consequence of locomotion on relatively large substrates represents a possible preadaptation for gliding.

The patterns of hindlimb elongation are much simpler to interpret with respect to patagial morphology. Dermopterans have longer hindlimbs than all other gliding taxa studied here. Nongliding pseudocheirins have shorter hindlimbs. This pattern in the pseudocheirins is most likely the result of hindlimb elongation in Petauroides rather than hindlimb shortening in Pseudocheirus and Hemibelideus. Similar patterns are seen for relative femur and tibial lengths. Dermopterans have longer femora and tibia than all the other taxa studied here, and Pseudocheirus and Hemibelideus have relatively shorter femora and tibia.

Wing loading.—Wing loading describes the relative amount of weight borne by a wing. Aircraft with high wing loadings (Fig. 10.3.) either have relatively heavier bodies, or smaller wings than aircraft with low wing loadings. Comparing wing loading across mammals can tell us something about performance and maneuverability. However, it is important to remember that general descriptors of performance, like wing loading, may only hold true for wings with generally similar planforms (see Fig. 9.1). In gliding mammals, which have voluntary control over the shape of their wings, such general descriptors may not adequately characterize relative performance among taxa. Similarly, as the

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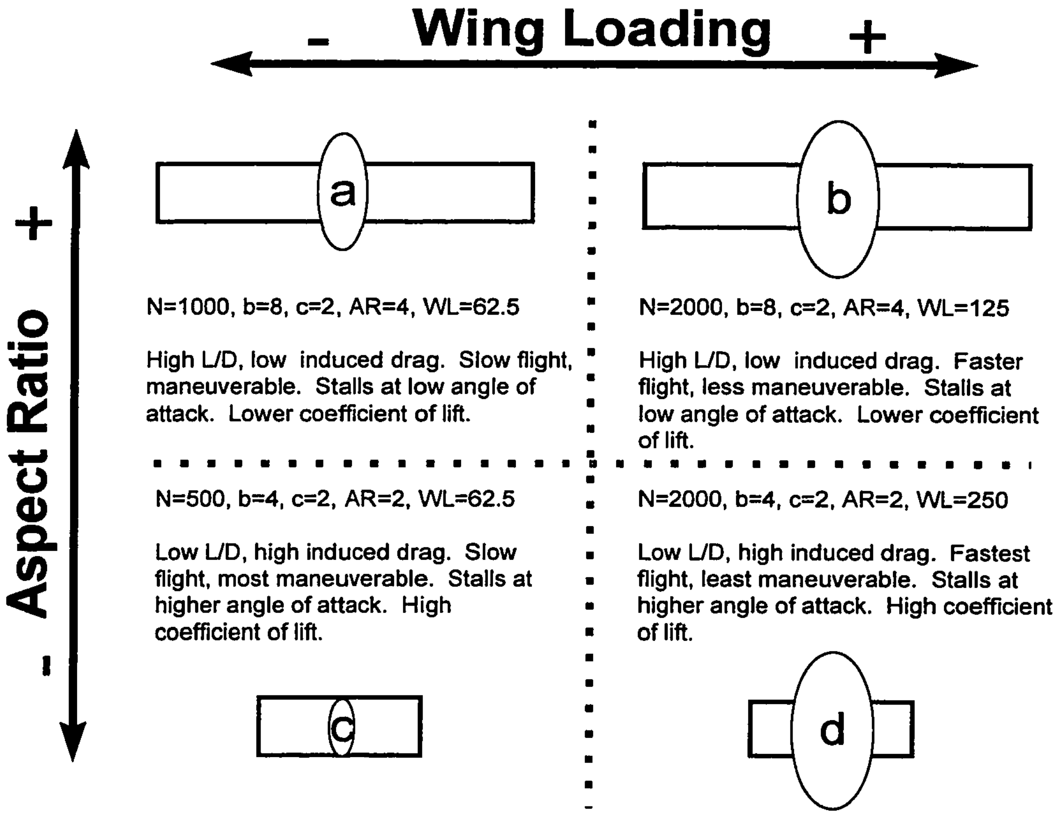

N=1000, b=8, c=2, AR=4, WL=62.5

High L/D, low induced drag. Slow flight, maneuverable. Stalls at low angle of attack. Lower coefficient of lift.

N=2000, b=8, c=2, AR=4, WL=125

High L/D, low induced drag. Faster flight, less maneuverable. Stalls at low angle of attack. Lower coefficient of lift.

N=500, b=4, c=2, AR=2, WL=62.5

Low L/D, high induced drag. Slow flight, most maneuverable. Stalls at higher angle of attack. High coefficient of lift.

N=2000, b=4, c=2, AR=2, WL=250

Low L/D, high induced drag. Fastest flight, least maneuverable. Stalls at higher angle of attack. High coefficient of lift.

Figure 10.3: The effects of aspect ratios and wing loading on performance of aircraft. N = weight, b = wing span, c = wing cord, AR = aspect ratio, WL = wing loading. Planforms do not change among models.

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shape of the wing changes dramatically during the glide, performance may be more radically affected than indicated by changes in wing loading, even within taxa. The long, gracile limbs of gliding mammals have usually been interpreted as mechanisms for increasing the surface area of the patagium and thereby increase the lift force. This would reduce wing loading which would permit slower gliding speeds and greater maneuverability. Greater maneuverability may be advantageous in predator or obstacle avoidance, and slower gliding speeds would allow the animal more time to react to obstacles, and provide a softer landing.

Wing loading is related to the speed at which an animal must fly in order to generate enough lift to remain airborne. Animals with high wing loading must fly faster to remain airborne than animals with lower wing loading. Stalling speed, the speed at which the wing stops generating enough lift to offset the weight of the animal, is proportional to the square root of wing loading ($V_{stall}=\sqrt{2Mg/\rho SC_{L,max}}$), and inversely proportional to maximum coefficient of lift. Consequently, Petauroides volans, with a wing loading of 143, must fly almost twice as fast as Petaurus breviceps, with a wing loading of 45, just to remain airborne, all other factors being equal (Table 10.3). Similarly, doubling the coefficient of lift allows an animal to fly 0.70 times slower.

Wing loading is also inversely correlated with maneuverability (Fig. 10.3). Animals with high wing loading are less maneuverable than animals with low wing loading. Maneuverability is defined as the minimum turning radius for any

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given wing at a certain velocity. Turning radius, often used as a measure of maneuverability, is directly proportional to wing loading [$\mathbf{r = 2Mg/(SC_L\rho\sin\Phi)}$], all other factors being equal. Table 10.3 shows the wing loading for the taxa studied here at maximum aspect ratios and at aspect ratios calculated based on published photographs of gliding mammals (Chapter 2).

Theoretically, increased wing loading does not decrease gliding angle or gliding distance, but animals with higher wing loading must glide faster at any given gliding angle to produce the same relative lift force and remain airborne. To do this a gliding mammal with high wing loading must either have a higher launching speed or it must glide at a steeper angle than an animal with lower wing loading. There is little data on launch speeds in gliding mammals that could be used to answer this question, and there is no anatomical evidence that more highly loaded gliders have greater leaping abilities. Mammalian gliders with high wing loading do not have relatively longer hindlimbs (Fig. 10.4a), or relatively higher crural indices (Fig. 10.4b). Therefore, heavily loaded mammalian gliders may have to glide at steeper angles than gliders with lower wing loadings. One would therefore expect selection to favor low wing loadings in gliding mammals. This correlates with reduced gliding angles and greater gliding distances. However, very low wing loadings also have disadvantages. Thorington and Heaney (1981) note that low wing loading may make animals particularly susceptible to tail winds. This is because even a slight tailwind can produce an effective airspeed below staling velocity for an animal gliding at low velocities.

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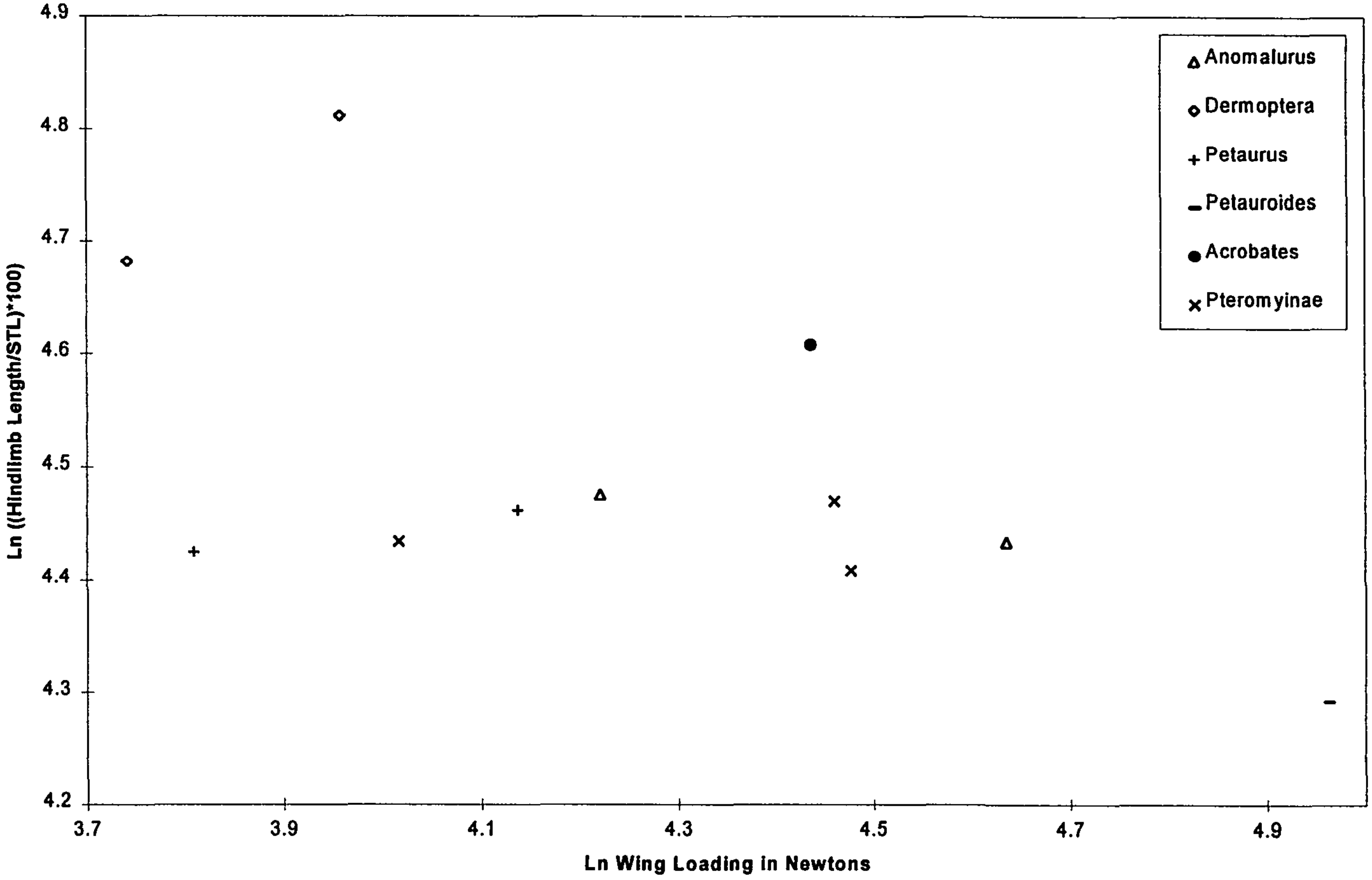

Figure 10.4a: Relative hindlimb length and wing loading is some gliding mammals. Note that taxa with high wing loading do not have relatively longer hindlimbs taxa with low wing loading. Note also the relatively high values of the dermopterans.

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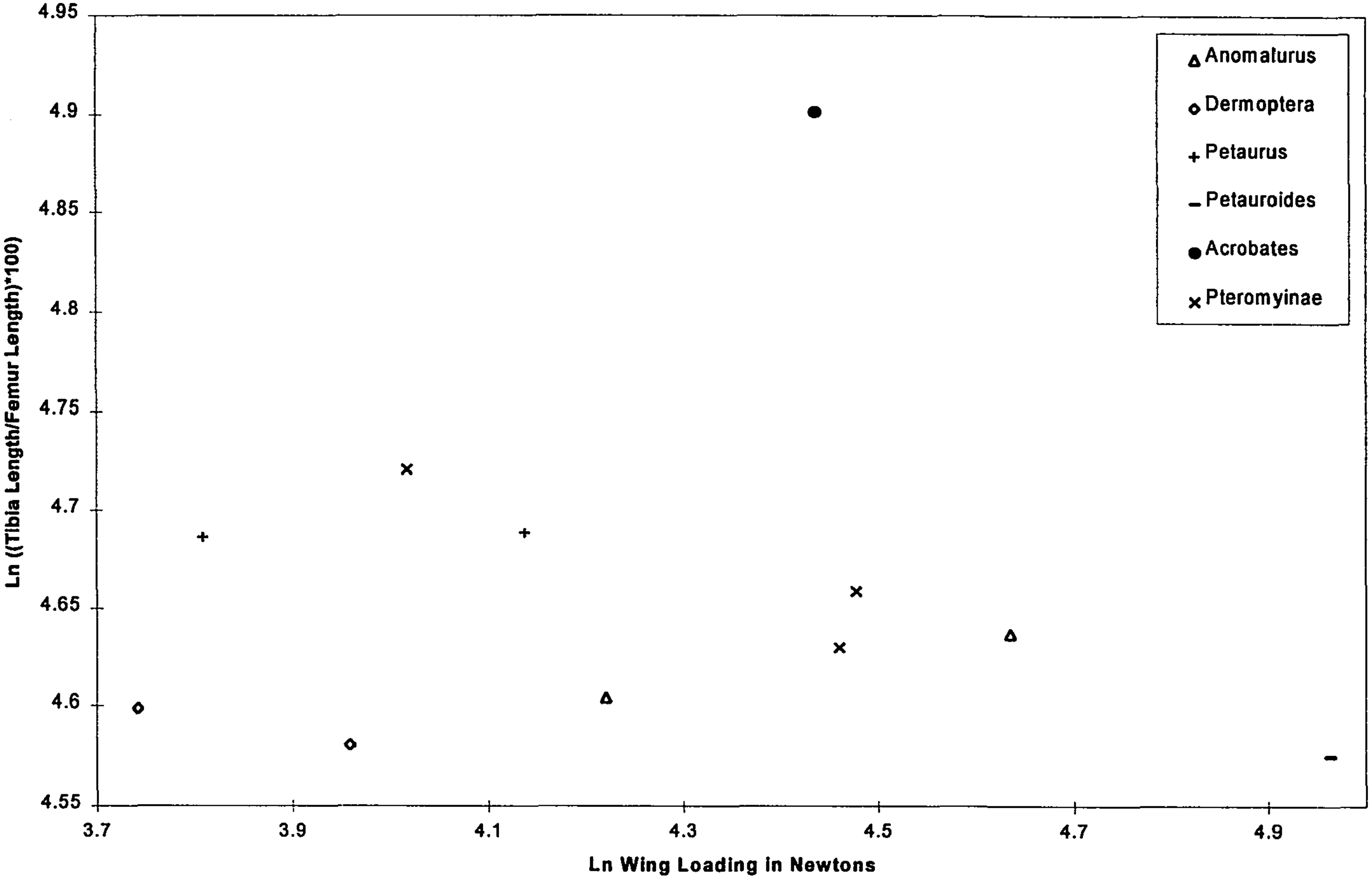

Figure 10.4b: Crural indices and wing loading in some gliding mammals. Note that taxa with high wing loading do not have relatively higher crural indices than taxa with low wing loading. Note also the extremely high value for Acrobates.

Given all the above factors, the dermopterans occupy an interesting place among the gliding mammals. Figure 10.5 shows that the dermopterans have relatively low wing loading for a gliding mammal of their size. In fact, dermopterans have a low wing loading for a bat of their size (Fig. 10.2). Compared to other gliding mammals of comparable size, dermopterans should be able to glide slower, glide at shallower angles, land at slower speeds, and be more maneuverable. How the dermopterans compare to bats of comparable size is difficult to answer. Powered flight is obviously very different from unpowered flight. Also, bats have a much higher degree of control over the shape and placement of their wings than do dermopterans. Finally, bats have much higher aspect ratio wings than do dermopterans.

Aspect ratio.—Aspect ratios describe the relative width of a wing and also have important aerodynamic correlates (Fig. 10.3, Chapter 10). High aspect ratio wings produce relatively less drag and therefore possess higher lift to drag ratios. High lift to drag ratios mean shallower glide angles and increased gliding distances. Therefore, selection should favor high aspect ratio, lightly loaded wings. Such a wing would maximize gliding distance. However, gliding mammals fall within a narrow range of low aspect ratios, and their wing loadings can be very high (Fig. 10.2, 10.5). Gliding mammals generally have very square wings with aspect ratios below 2, but their wing loadings can be as high as 143 Mg/m^2. By comparison, bats tend to fall within a wide range of aspect ratios but a more restricted range of wing loading (Fig. 10.5). Birds follow a similar pattern.

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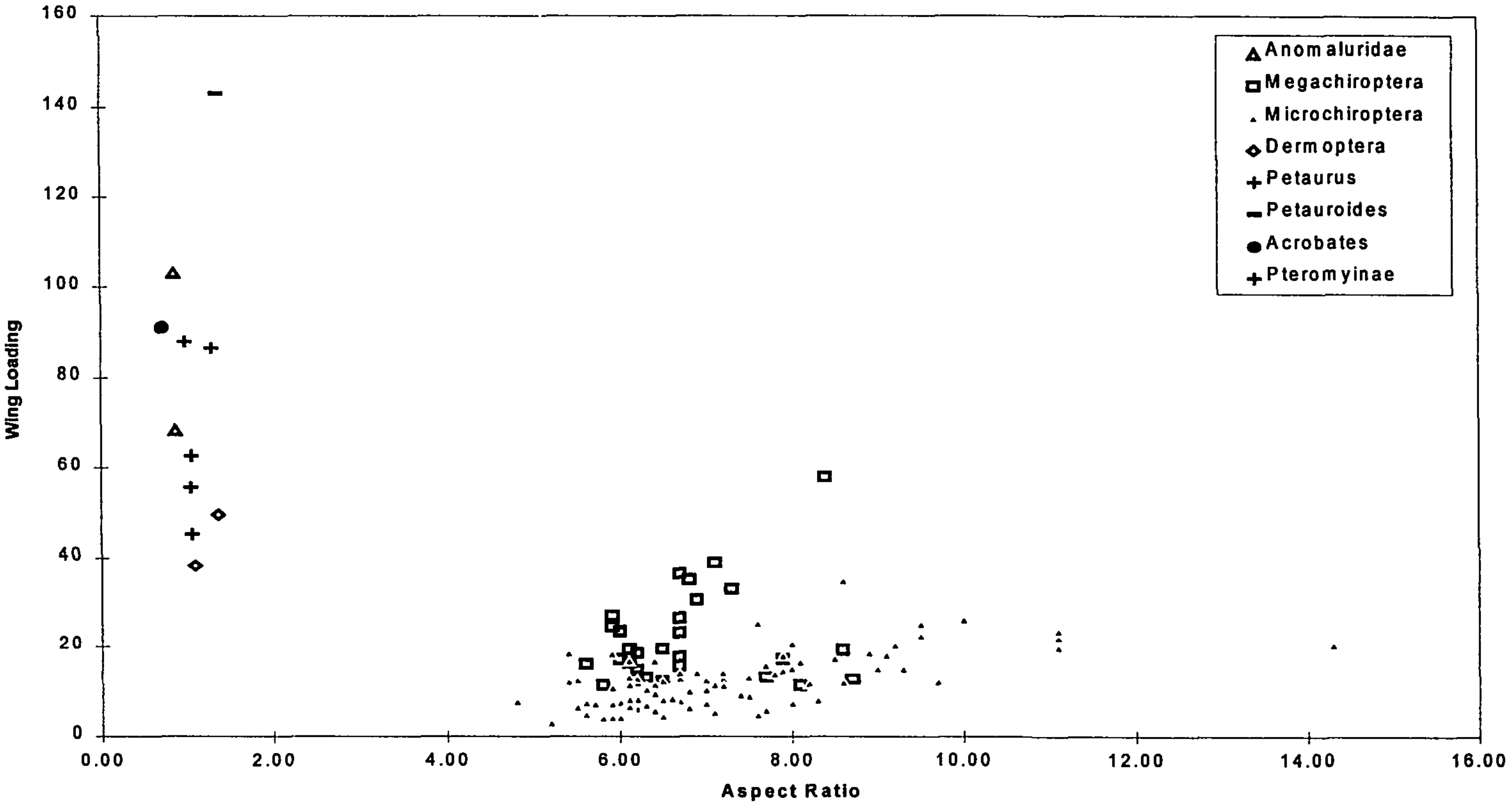

Figure 10.5: Aspect ratios and wing loading in some mammals. Gliding mammals fall within a narrow range of aspect ratios, and within a wide range of wing loadings. The situation regarding the bats shows the opposite. Bats fall within a wide range of aspect ratios, and a narrow range of wing loading. Note that the dermopterans, among the largest of the gliding mammals, fall at the lower end of the range of wing loading for gliding mammals.

The low aspect ratios of gliding mammals has been interpreted as an adaptation to maintaining lift at the high angles of attack reached by these animals in the terminal flaring phase of the glide. Low aspect ratio wings have high Reynold's numbers ($\mathbf{Re} = \rho \mathbf{Vl}/\mu$), and this prevents the slipstreams from separating from the wing at high angles of attack. However, once animals enter the landing phase of the glide it is unlikely that patagium produces any lift at all. If one accepts that the ability to maintain lift at high angles of attack during the terminal phase of the glide constrains gliding mammals to maintain relatively low aspect ratios, there are still ways that they might increase their lift to drag ratios and thereby their gliding distances. Specifically, gliding mammals may do this by reducing induced drag.

<u>Induced</u> <u>drag</u>.—Drag is produced as a result of frictional forces, and as a result of the pressure differential generated by the wing as it creates lift. The drag components due to frictional forces are parasite drag and profile drag. Parasite drag is incurred by the body while profile drag is incurred by the wings. Profile drag can be reduced for any wing of a given area by increasing the aspect ratio of the wing, thereby making it longer and narrower. Because lift is dependent on wing area ($\mathbf{L} = q\mathbf{SC}_L$) a high aspect ratio wing will have less drag, and a higher lift to drag ratio than a low aspect ratio wing of the same area. This results in higher lift to drag ratios for high aspect ratio wings, and this translates into longer gliding distances. However, as mentioned above, this avenue of

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reducing drag may not be open to gliding mammals because of the benefits of low aspect ratio wings at high angles of attack.

Induced drag, however, results from the fact that wings produce lift by creating a pressure differential between the top and bottom of the wing, and from the fact that all wings are of a finite span. At the wing tips the high pressure below the wing "leaks out" around the wing tip. This produces a downward component to the air velocity near the tip of the wing which imparts a downward force to the wing, the down-wash. This down-wash effectively reduces the angle of attack of the wing tip and produces and increase in drag that is called induced drag. Because induced drag produces a vortex trailing from the wing tip, planforms with relatively broader wing tips experience greater induced drag. Therefore, induced drag is inversely proportional to aspect ratio ($\mathbf{C}_{D,l} = \mathbf{C}_L^2/\pi e\mathbf{AR}$).

There are, however, means of reducing induced drag by altering wing shape without altering either aspect ratio or Reynold's number. The first of these is by creating a wing with an elliptical, rather than a square, planform (Fig. 10.6). This shape produces a uniform down-wash distribution across the wing and reduces the effect of induced drag. It does this because lift at each section of the wing is directly proportional to the chord of the wing at that point. Therefore, for wings with elliptical planforms the lift produced per unit of wing span produces an elliptical lift distribution (Fig. 10.6). Because lift production drops off rapidly as the wing tip is approached induced drag working at the wing tips has less of an

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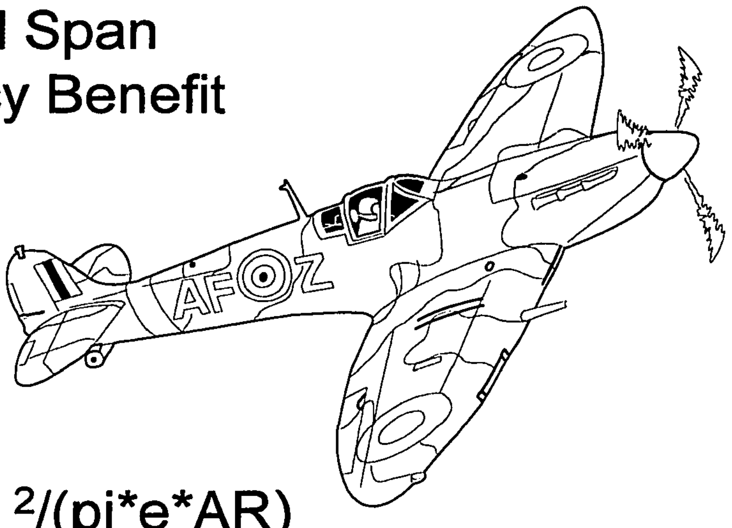
Elliptical Span Efficency Benefit



$C_{D,i} = C_L^2/(\text{pi}*e*AR)$

e = 1 for elliptical planforms

e < 1 for all other planforms

-------- = Lift per unit span as a function of distance along the span, the lift distribution.

-·-·-·-·-· = Downwash distribution resulting from the given lift distribution.

Figure 10.6: Elliptical planforms and the elliptical span efficiency factor. Elliptical planforms experiences less induced drag due to the elliptical span efficiency factor. This is a result of the downwash being evenly distributed across the wing span.

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effect on the wing. For elliptical planforms the span efficiency factor **e** = 1, while for all other nonelliptical planforms e < 1. flaring phase of the glide. Low aspect ratio wings have high Reynold's numbers (**Re** = ρ**Vl**/μ), and this prevents the slipstreams from separating from the wing at high angles of attack. However, once animals enter the landing phase of the glide it is unlikely that patagium produces any lift at all. If one accepts that the ability to maintain lift at high offset wing tip stall and a small elliptical wing tip may have large effects here, even though wing tip stall should not be a problem for wings where the taper ratio of the wing is one (λ = 1).

In any event, the orientation of the wing tip during gliding may be more important than the shape of the winglet in reducing induced drag (Thorington et al., 1998). The dorsiflexed wing tip that is seen in colugos (see MacKinnon, 1984), flying squirrels (Thorington, et al., 1998), and sugar gliders (see Suckling, 1995) is very similar to the wing-tip canards often seen on modern aircraft (Fig. 10.7). It has been experimentally determined that these winglets can reduce induced drag by ~20% and increase **L/D** by ~9% in man-made aircraft (Whitcomb, 1976). They do this by reorienting the downward component of the down-wash into a more laterally directed force (Fig. 10.8a). The wing tip vortices still alter the flow field, reorient the lift vector, and impart rotational kinetic energy, but because the vector is not oriented downward there is less of a realized effect on drag. Because the wing tips produce trailing vortices, the reorientation of these vortices at the leading edge of the wing may influence the rest of the wing

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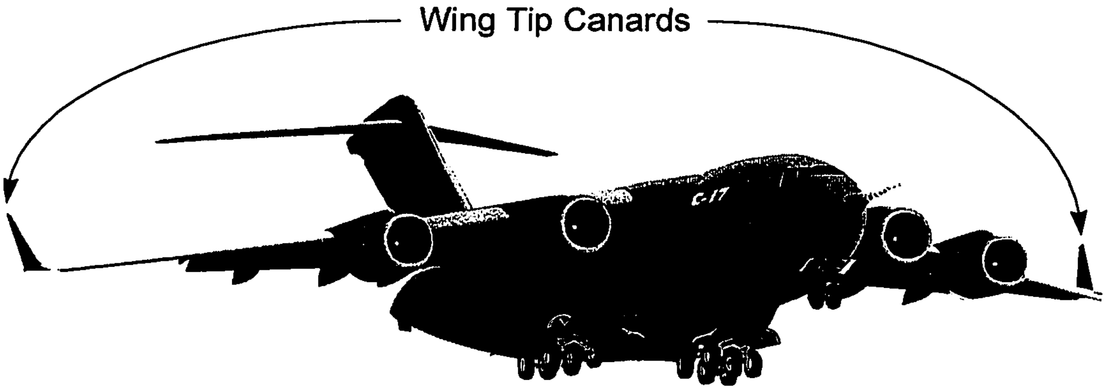

C-17 Globemaster

Figure 10.7 Wing-tip canards are used on modern aircraft to reduce induced drag and improve stability.

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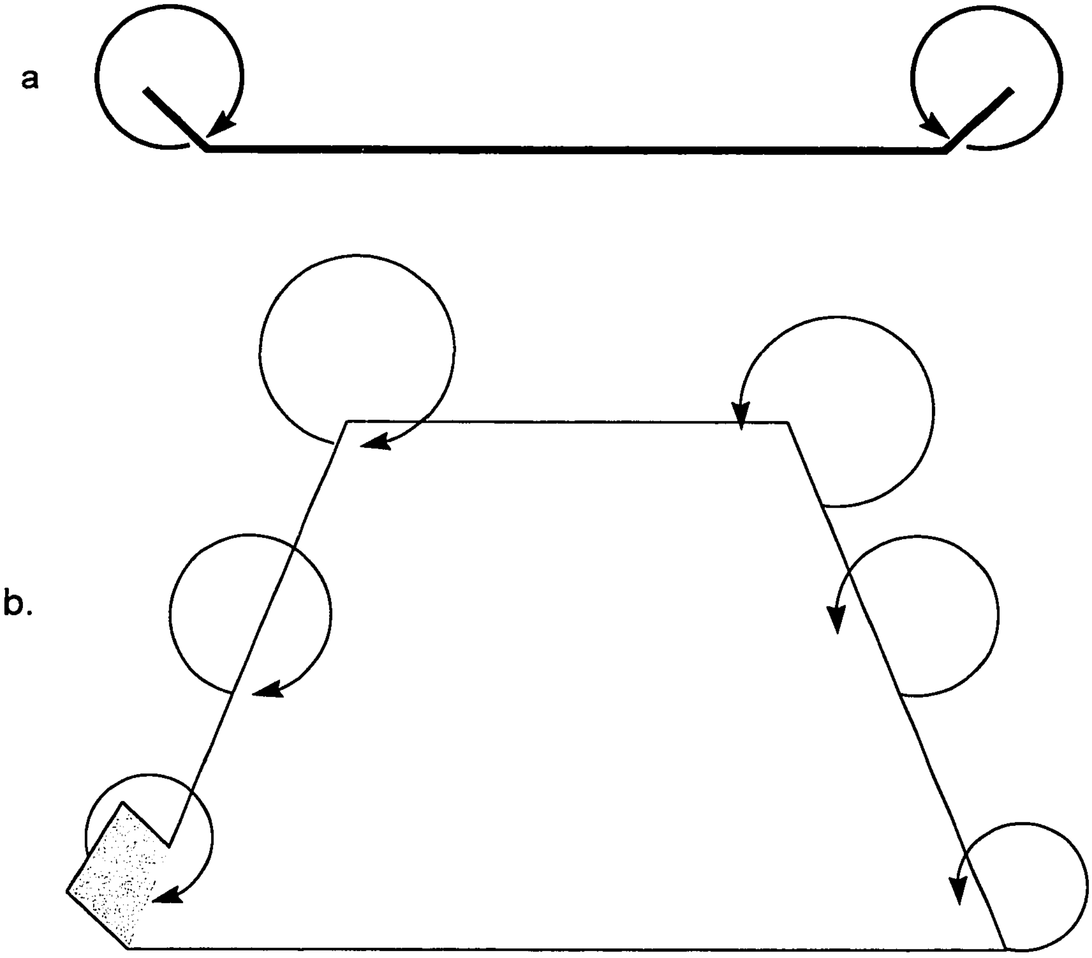

Figure 10.8: Wing-tip canards redirect the forces of induced drag laterally (a) rather than vertically. Because wings produce trailing vortices (b) wing-tip canards may be able to influence the vectors of induced drag forces along the entire wing tip. In (b), the left side of the wing would experience greater induced drag than the right side of the wing. Such a configuration in a living animal would induce rolling and yawing moments about the center of gravity.

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tip as well (Fig. 10.8b). This requires that the trailing vortices maintain the proper orientation along the rest of the wing tip and this may explain the incorporation of structures that are under a fine degree of voluntary control (i.e., the hands in dermopterans and Petaurus) into the flight system. This would allow the animal to maintain the trailing vortex in the proper orientation along the wing tip during flight.

This controllability of the wing-tip canards may also help maintain the function of these structures at high angles of attack. Induced drag varies as the square of the lift coefficient and is at it's highest at the maximum coefficient of lift, $\mathbf{C}_{\mathbf{L,max}}$. $\mathbf{C}_{\mathbf{L,max}}$ coincides with high angles of attack and results in wing-tip stall. Wing-tip stall is a condition where the wing tips lose lift before the rest of the wing as a consequence of induced drag. Man-made aircraft often have the wing tip rotated downward at the leading edge to provide the wing tip with a lower angle of attack than the rest of the wing and to help offset wing tip stall. Consequently, when induced drag is at its highest, winglets may be at their least effective. However, because the wing tips of gliding mammals are under voluntary control an anterior rotation, or pronation, of the forelimb (Fig. 10.9) coupled with ventral flexion of the neck could maintain a functional winglet angle even at high angles of attack. This would reduce induced drag and improve **L/D** ratios during the terminal, flaring portion of the glide.

However, as mentioned above, the degree to which wing tip stall is a problem for wings where $\lambda = 1$ may not be great. Pronation of the forelimb and ventral

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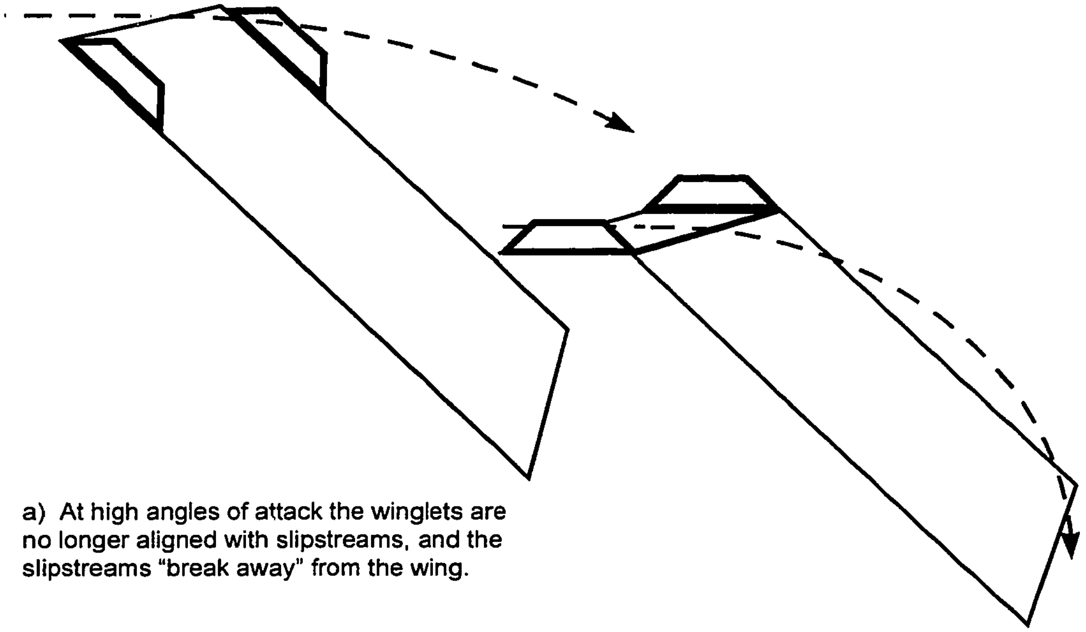

a) At high angles of attack the winglets are no longer aligned with slipstreams, and the slipstreams "break away" from the wing.

b) At high angles of attack the winglets maintain a functional angle of attack, and the slipstreams are more adherent to the wing.

Figure 10.9: Wing-tip canards at high angles of attack. It has been experimentally determined that at high angles of attack (a) (Anderson, 1985, Pamadi, 1998) wing-tip canards lose their effectiveness. At high angles of attack the slipstreams (dotted arrows) also break away from the wing and the wing stalls. The ability to ventrally flex the anterior portion of the wing (b), i.e., the propatagium, helps to maintain the adherence of the slipstreams to the wing and maintain lift. The ventral flexion of the propatagium would also maintain the wing-tip canards at a functional angle.

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flexion of the neck would also increase the camber of the wing and forestall flow separation, resulting in reduced profile drag as well. In this case, the propatagium is NOT acting as a leading edge slat. Such mechanisms are known to increase $C_{L,max}$ by a factor of 3 or more in man made aircraft (Anderson, 1985; McCormick, 1979), but function by allowing the air flowing through the slotted portion of the wing to accelerate. This accelerated air then moves further down the wing before separating from it (Perkins and Hage, 1949). Gliding mammals have no means of creating the slot in the wing necessary for this. Therefore, it is best to interpret the effects of forelimb pronation during landing in gliding mammals as a means of increasing the camber of the wing in a manner analogous to the use of trailing edge flaps in man made aircraft. At any given angle of attack the use of trailing edge flaps will increase the coefficient of lift and the uropatagia of the larger gliding mammals probably also functions in this way. Because stalling speeds are inversely proportional to the maximum coefficient of lift these mechanisms would reduce stalling speed.

The propatagia of the dermopterans and the anomalurids deserve special mention here. The dermopterans have a larger propatagium than the other gliders studied here (Table 10.2). This should allow them to reach even higher angles of attack than the other gliders by increasing the camber of the wing. The dermopterans also have the most extensive uropatatgium and this would also allow them to further increase the camber of the wing. These factors, considered together with the low wing loading of the dermopterans, further suggests an animals adapted to flying slowly and maintaining lift at high angles of attack. The

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propatagium of anomalurids is not much larger than that of the pteromyines, but when one considers the anomalurid propatagium along with the olecropatagium, these structures together are almost as extensive as that of dermopterans (Table 10.2). Given that the olecranon cartilage adds so little to the gliding membrane in anomalurids, this structure may function to support rather than extend the patagium. This would have the effect of incorporating this part of the plagiopatagium into the leading edge of the wing. The olecranon cartilage can obviously be extended from and retracted against the radius, but it is difficult to imagine how this structure could be dorsiflexed independently of the forelimb. However, pronation of the forelimb would accomplish this. Therefore, the olecropatagium may have been functionally incorporated into the leading edge propatagium in anomalurids.

Profile drag and mammalian hair.—Gliding mammals seem to have relatively soft and downy hair compared to other mammals. The effects of fur on drag and flow characteristics have been studied (Kokshaiskii et al., 1982; Nachtigall 1979b, 1986) but the results are somewhat equivocal. Kokshaiskii et al. (1982) found that "...fur as a passive covering on the internal surface of a tube of small diameter greatly increases its hydraulic resistance..." but that "...there are not sufficient grounds at present..." to conclude that hair actually increases drag. Nachtigall (1979b, 1986) found that placing the fur of Petaurus on a flat plate did increase coefficients of lift, especially at high angles of attack, but does not explore whether or not these increases in C_L were the result of reduced drag.

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Nachtigall (1979, 1986) does explain that other, nonglider, furs produced similar results, although not to the degree as was seen in Petaurus.

Both $\mathbf{D}_f$ (skin friction drag)and $\mathbf{D}_p$ (pressure drag due to flow separation) are probably important to gliding mammals, but during different phases of the glide. During the midphase of the glide (at low α) $\mathbf{D}_f$ is probably most important, but during the terminal flaring portion of the glide $\mathbf{D}_p$ is probably more important. In fact, Nachtigall (1979b, 1986) found that the greatest increase in lift for his furred models came at high angles of attack. This suggests that the fur of gliding mammals may be more efficient at ameliorating $\mathbf{D}_p$.

The above points raise the question of whether or not there is something fundamentally different about the hair of gliding mammals. Such a conjecture is strengthened by the well known highly specialized microstructure of microchiropteran hairs (Brunner and Coman, 1974; Sabnis, 1979). Figures 10.10 - 10.12 illustrate the results of a brief survey of mammalian hair. It is clear that there are few differences separating the gliding mammals from their nongliding relatives. Several points bear mentioning, and may warrant further study. First, the hairs of gliding mammals (Figs. 10.10a, 10.11a - c, 10.11g, 10.12a - f) seem to show less variability along their length than do nongliding mammals. There was also only one kind of hair represented in each gliding mammal sample, there were no guard hairs found in the gliding mammal samples. Second, although it appears at first glance that all gliding mammals have a simple coronal scale pattern, and this is true, the picture is more complex.

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Figure 10.10: Scanning electron micrographs of archontan hairs: a) Cynocephalus volans; b) Pteropus vampyrum; c), d) Myotis lucifugus; e), f), g) Ptilocercus lowii. Distal hairs are not illustrated for Cynocephalus volans and Pteropus vampyrum because the morphology of the distal hairs was not remarkably different from the mid-shaft morphology. Proximal hairs are not illustrated for Cynocephalus volans, Pteropus vampyrum, and Myotis lucifugus because the morphology of the basal hairs was not remarkably different from the mid-shaft morphology. Due to the sampling protocol, the hair from Pteropus vampyrum is a guard hair. No underhairs were sampled for this taxon.

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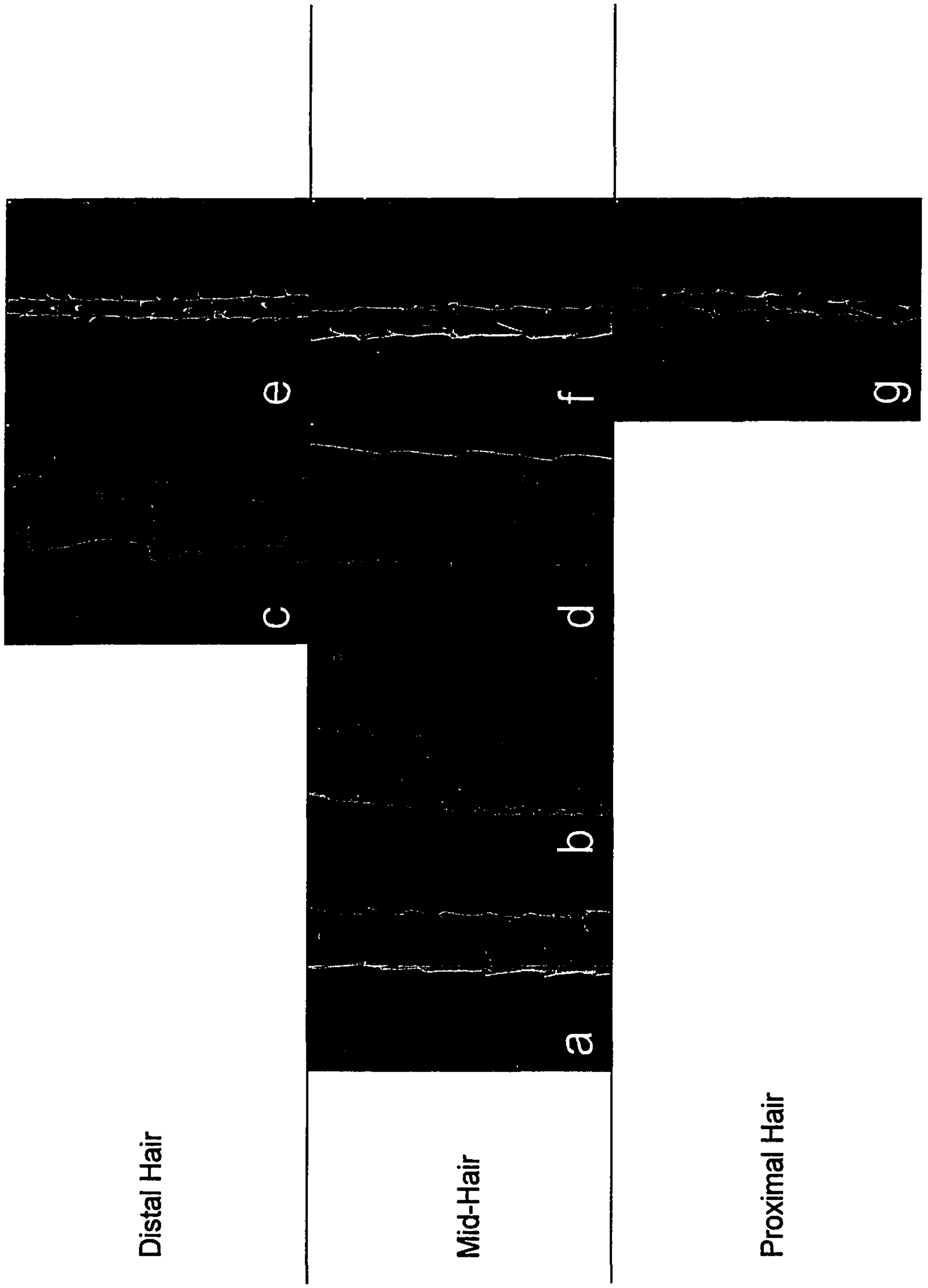

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Figure 10.11: *Scanning electron micrographs of some marsupial and sciurid* hairs: a), b), c) Acrobates pygmaeus; d), e), f) Hemibelideus lemuroides; g) Glaucomys sabrinus; h), i), j) Sciurus carolinensis underhair; k) Sciurus carolinensis guard hair. Distal hairs are not illustrated for Glaucomys sabrinus and the Sciurus carolinensis guard hair because the morphology of the distal hairs was not remarkably different from the mid-shaft morphology. Proximal hairs are not illustrated for Glaucomys sabrinus and the Sciurus carolinensis guard hair because the morphology of the basal hairs was not remarkably different from the mid-shaft morphology.

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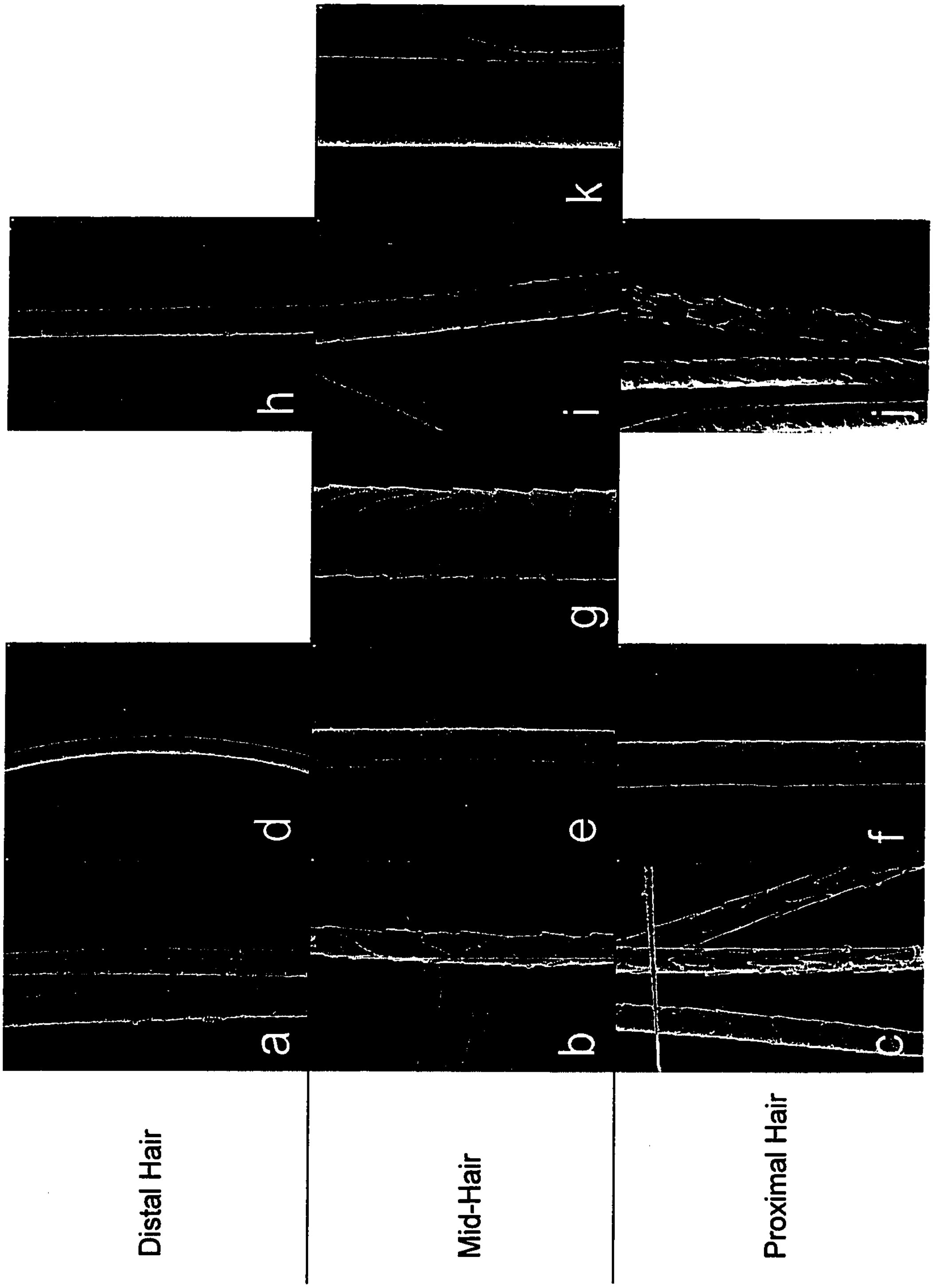

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Figure 10.12: Scanning electron micrographs of some other rodent hairs: a), b), c) Anomalurus peli; d), e), f) Idiurus macrotis; g), h), i) Glirulus japonicus.

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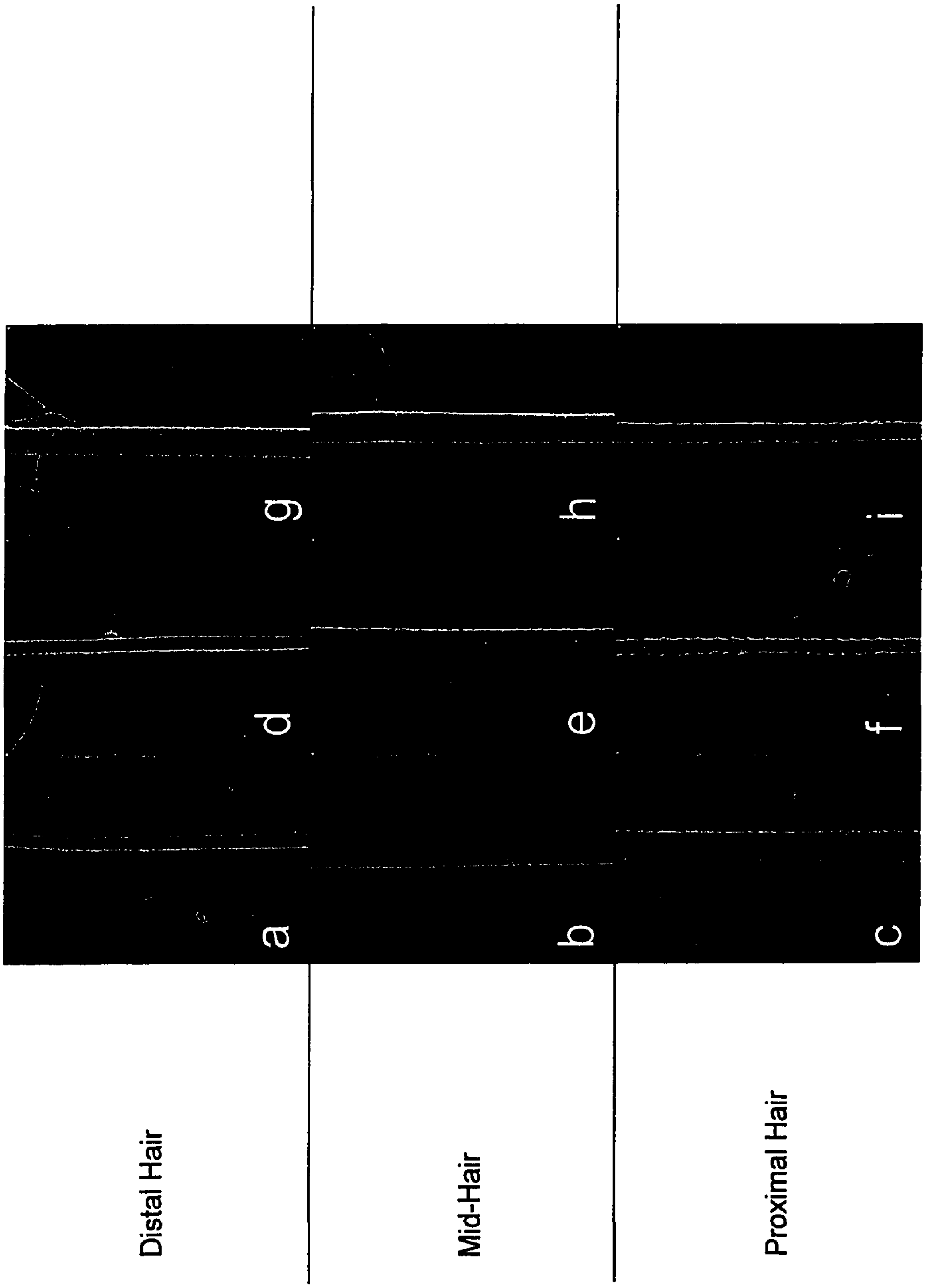

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Many mammalian hairs show a simple coronal pattern near the tip of the hair, whether they are gliders or not, and the presence of this scale pattern may be related to the size of the hair. No measurements were made on hair diameters, but gliding mammals may have relatively narrow hairs compared to nongliding mammals. These hypotheses require further investigation.

Given the geometrically complex hair morphology of many microchiropterans (Brunner and Coman, 1974; Sabnis, 1979), the morphology of the distal hairs of P. lowii is intriguing. However, a larger sampling of tupaiids, primates, and other eutherians is required here.

Longitudinal stability.—Longitudinal stability relates to the stability of an aircraft about the y axis, and to the moments of pitch about the center of gravity. Longitudinal stability is considered to be the most important static stability mode and usually receives the lion's share of attention in aircraft design and testing. Gliding mammals do not have separate horizontal stabilizers to influence longitudinal stability, but they do have tails and uropatagia. We are dealing with moments about the center of gravity when talking about control and stability issues, and this may explain why larger gliding mammals have uropatagia, while smaller ones have distichous tails. The moments about the center of gravity are defined by the forces acting on the wing. A large part of this determination also has to do with how far from the center of gravity forces are being applied.

Lateral stability.—Dorsiflexed wing tips may also have a role in increasing the stability of the wing. Because the canards are dorsiflexed they provide a self righting mechanism if the wing is disturbed about the roll axis (Fig. 10.13). This

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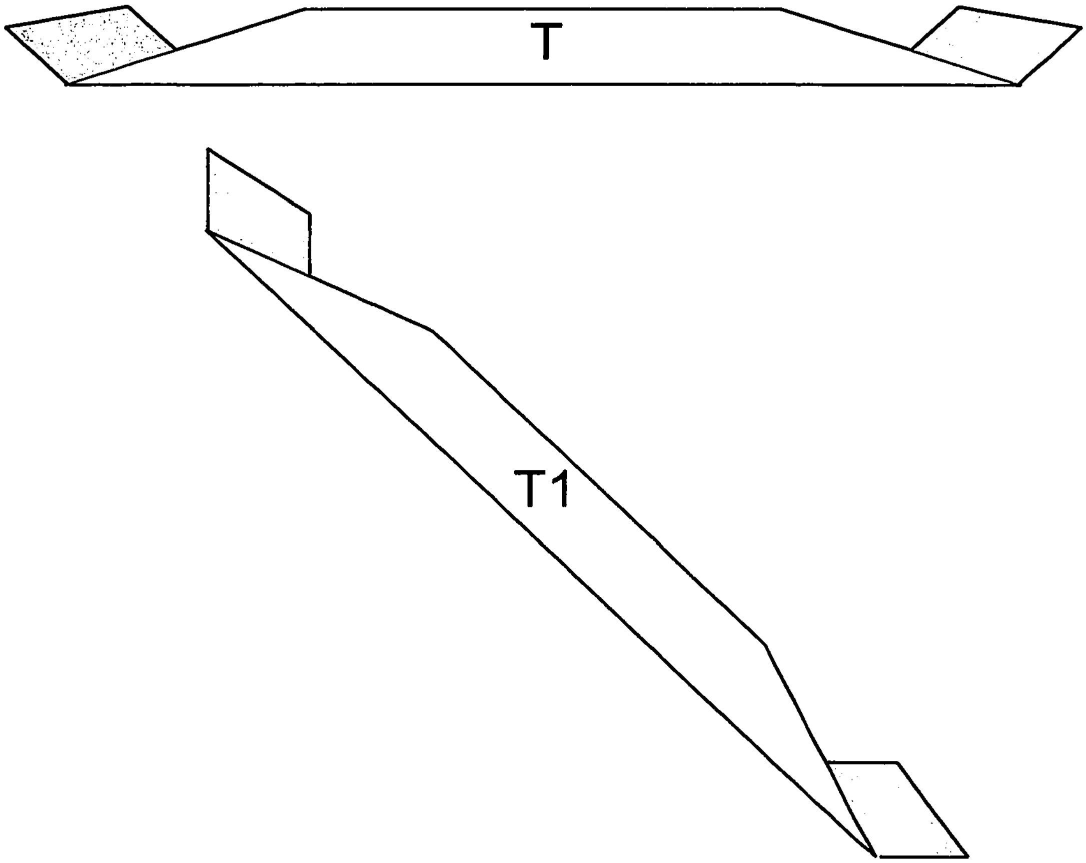

Figure 10.13: Dihedral and sideslip. As the wing at time T begins to roll to its left it experiences sideslip. Consequently, (T1) the lower portion of the wing begins to lag behind the upper portion of the wing. In such a case, vertically oriented wing tip provide a dihedral effect that serves to stabilize the wing.

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is known as the dihedral effect, and is not technically a form of static stability. Dorsiflexion of the forelimbs and hindlimbs would create an even larger dihedral effect. Consider a wing at equilibrium as shown here at time **T**, that is disturbed to the position indicated at time **T1**. A roll to the left will drop the left wing, raise the right wing, and induce a sideslipping motion to the left as well (a negative sideslip). Because the wing tips are angled, the sideslip that occurs during the roll will produce an increased functional angle of attack on the left wing tip and a reduced functional angle of attack on the right wing tip. The lower wing ends up producing more lift than the upper wing, and effects a positive rolling moment. This will initially tend to return the wing to a horizontal position. Although the forces generated by the wing tips are probably relatively small, they are acting at the maximum possible distance from the center of gravity and this maximizes their ability to effect moments about the center of gravity. Also, the animal could create a large dihedral effect simply by dorsiflexing the forelimbs and hind limbs. Because the initial tendency of the wing, after disturbance from equilibrium, is to return toward its equilibrium position these structures are said to enhance the static stability of the wing.

The exact manner in which this is accomplished is illustrated in Figure 10.14. Consider a gliding mammal with a dihedral angle δ. The vector **AB** of magnitude **V** represents the velocity of the aircraft. **AC** represents the zero lift direction for the wing at point **A** and therefore **∠CAB** is the angle of incidence when there is no sideslip. When sideslip (β) is present the vector **AB'** is the velocity vector. A

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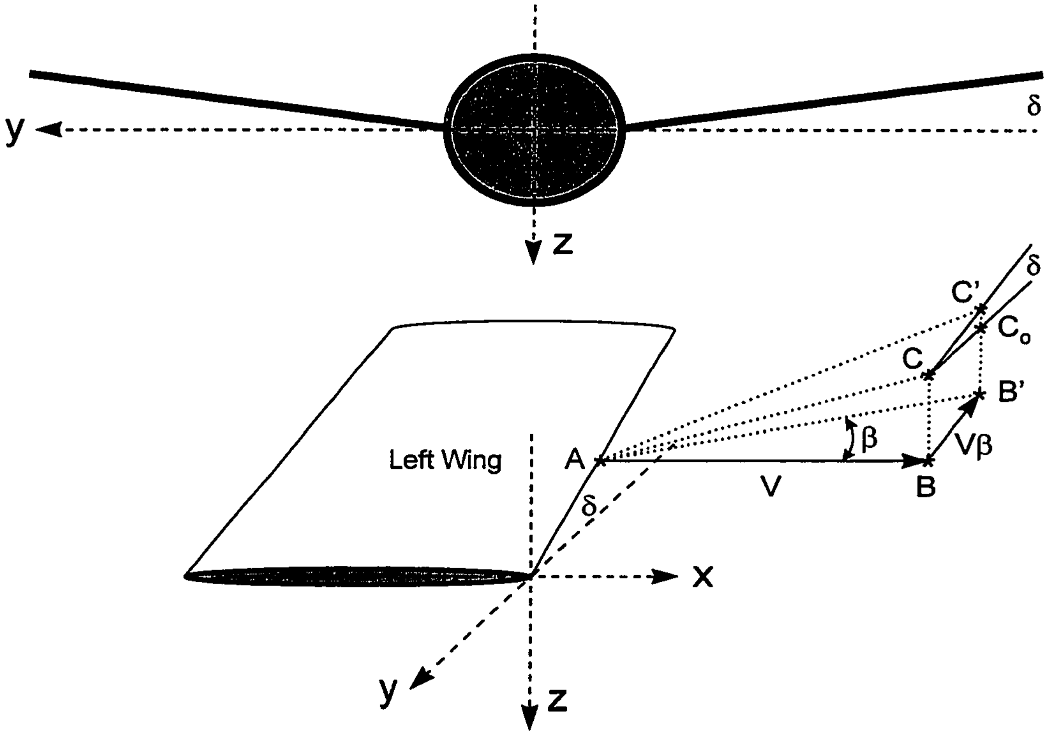

Figure 10.14: Dihedral angle δ and roll stability of the wing. The angle of attack of the wing in straight level flight is $\angle CAB$. As the wing rolls to the left it experiences some sideslip β. For a wing with no dihedral angle, the new angle of attack is $\angle C_oAB$. However, for the wing with dihedral angle δ, the new angle of attack is $\angle C'AB$. For wings wit a dihedral angle, there is a corresponding loss of effective angle of attack for the upper wing. This produces more lift on the downward rotated wing, and provides a self righting mechanism about the roll axis.

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line parallel to the z-axis of the aircraft drawn through **B'** intersects the plane of zero lift (defined by **ACC'**) at **C'**. When the wing has a positive (i.e., dorsiflexed) dihedral **C'** lies higher than **C** by an amount directly proportional to δ and β. In fact, the angle of incidence after sideslip is greater than the angle of incidence without sideslip by $\mathbf{C_0C'/AB = V\beta\delta/V} = \beta\delta$. The opposite is true for the starboard wing and "[t]he effect of a dihedral angle δ, when a sideslip β occurs, consists in reducing the incidence on the starboard side and raising it on the port by $\beta\delta$." (von Mises, 1945, p. 561). The interference between the wing and the fuselage may also help to increase lateral stability in dermopterans . The other gliding mammals probably receive no benefit here as they have mid wing configurations. A wing that is placed high on the fuselage will slightly increase the effective dihedral, a mid wing has little effect, and a low wing decreases the effective dihedral.

All gliding mammals could maintain lateral stability by holding their arms above their backs and creating some positive dihedral. Whether or not they do this remains to be seen. Similarly, dermopterans, pteromyines, and Petaurus may gain some stability benefits through having dorsally flexed wing tips. These wing tips are located at the maximal distance from the center of gravity and may, therefore, have large effects on moments about the center of gravity. However, the damping moments of the wings are likely so large that that may eliminate any such stability effects of the wing tips.

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Wing tips as ailerons.—The wing tip extensions of many mammalian gliders are under voluntary control and may also be used to effect moments about the center of gravity. In this way they may be used to actively control the angle of bank of the aircraft and initiate rolling moments. Because the damping moments of the wing are so large it is beneficial to locate the ailerons as far from the roll axis of the aircraft as possible. In the equation $\Delta\alpha_s = \boldsymbol{py/V}$, $\Delta\alpha_s$ is the change in the angle of roll from the horizontal, and $\boldsymbol{y}$ is the distance of the control surface from the center of gravity. Consequently, an animal flying very slow (i.e., low **V**) and with the control surfaces located very far from the center of gravity (i.e., high $\boldsymbol{y}$) will be very agile. That is, they will be able to initiate maneuvers very quickly.

Directional stability.—The dihedral effect may also be important to gliding mammals because they do not possess a vertical tail fin. Therefore they do not have a simple means to resist sideslip. Sideslip generally increases drag and would therefore reduce glide angle and glide distances for gliding mammals. Although swept back wings do have some directional stability straight wings do not, and forward swept wings are actually slightly directionally unstable. This may be a problem for gliding mammals because most gliding mammals have longer leading edges of the wing than trailing edges, and their planforms approximate an inverted delta wing (Fig. 10.1). As Perkins and Hage (1949, p. 315) note "[t]he problem of directional stability and control is first to insure that the airplane will tend to remain in equilibrium at zero sideslip and second to

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provide a control to maintain zero sideslip during maneuvers that introduce moments tending to produce sideslip."

Without a vertical tail fin gliding mammals may have problems maintaining directional stability. Thorington and Heaney (1981) have remarked on the distichous tails of the small flying squirrels and that these may function in control and maneuverability. However, larger flying squirrels, dermopterans, and anomalurids all have extensive uropatagia. The uropatagium appears to function to regulate longitudinal stability in dermopterans and may serve a similar role in the anomlurids and the larger flying squirrels. The distichous tail of the smaller gliding mammals may also be used to regulate longitudinal stability. If this is so, dorsally flexed wing tips may function as vertical stabilizers and provide directional stability in most gliding mammals.

The greater gliding possum does not have wing tip extensions but has a wing shape that may enhance directional stability. Their wing shape is similar to a delta or swept wing. Such wings are usually considered efficient in supersonic flight but produce a lot of drag a lower speeds. Certainly the greater marsupial gliders are not supersonic, but a swept wing of low aspect ratio may provide enhanced directional stability. As the wing begins to yaw to the right (Fig. 10.15), the left leading edge of the wing becomes more perpendicular to the slipstreams. This increases drag over the left wing and induces counterclockwise moments about the center of gravity in the yaw axis. This will tend to return the wing toward its initial position until the drag forces on each wing are equal. Again, because the wing tends to initially return towards its

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equilibrium position after disturbance, this increases the static stability of the wing. The contribution of this wing configuration to directional stability may be minor however. Perkins and Hage (1949, p. 318) note that the contribution of swept wings to directional stability can be estimated as $(C_{n\psi})_{\text{wing}}=-0.00006(\sqrt{\Lambda})$.

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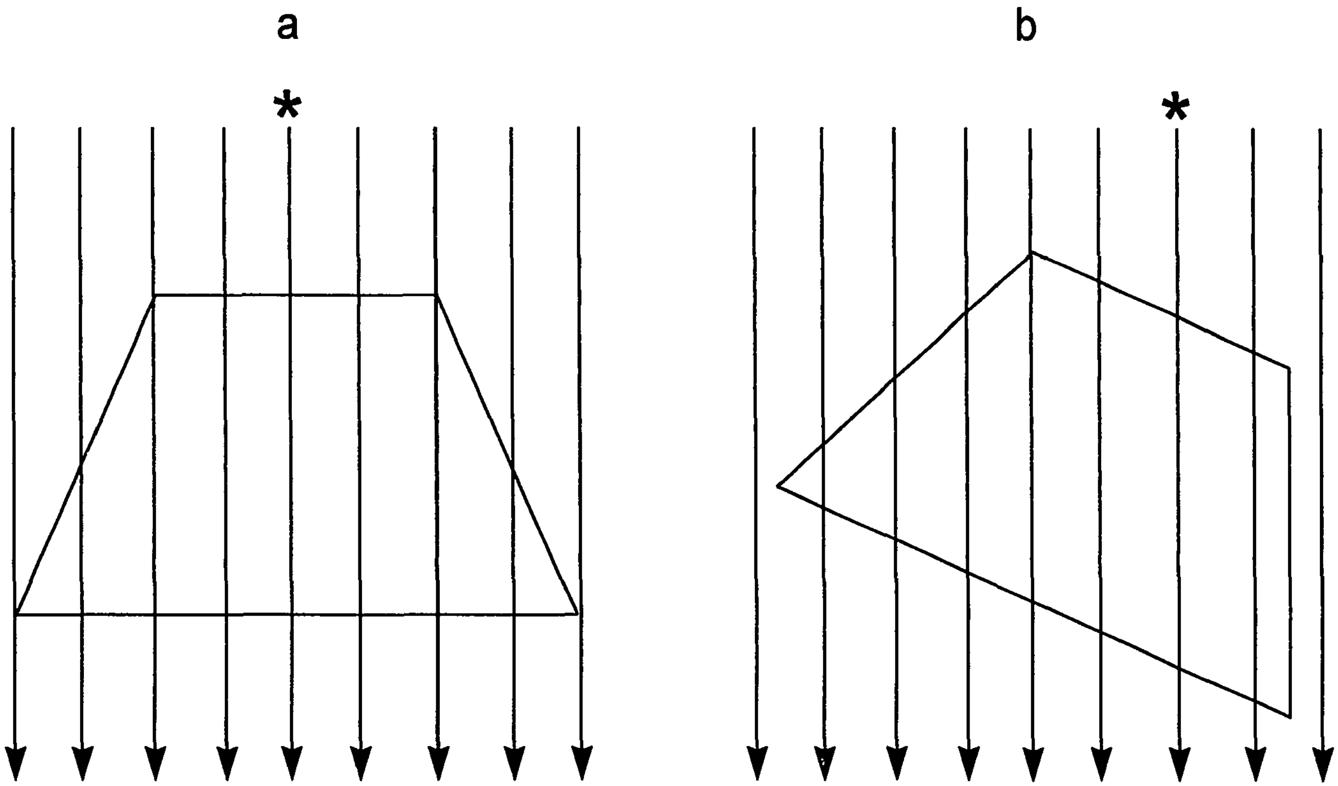

Figure 10.15: Yaw stability and swept wings. Swept wings are more stable about the yaw axis. A swept wing in straight and level flight experiences equal drag on each half of the wing (a). As the wing yaws to the right (b) there is greater drag over the left half of the wing and this tends to produce moments about the center of gravity that would return the wing to its initial position. Stars mark the slipstream (arrows) flowing over the midpoint of the leading edge of the wing.

CHAPTER 11: CARPAL CHARACTERS AND ARCHONTAN SYSTEMATICS

Dermopterans have traditionally been linked with the bats (Illiger, 1811; Leche, 1886; Shufeldt, 1911, Gregory, 1910; Pocock, 1926; Simpson, 1945) and some of the characters for such an association have been found in the hand and wrist (Novacek, 1980; Szalay and Lucas, 1993, 1996; Simmons, 1995). Stafford and Thorington (1998) provided a more detailed discussion of these issues, and they will not be restated here. However, a discussion of carpal morphology and development is offered as a test of certain hypotheses about archontan phylogeny.

Briefly, Stafford and Thorington (1998) showed that carpal morphology differs between megachiropterans and microchiropterans and these differences may be related to different aerodynamic constraints between the suborders. The carpal morphology of microchiropterans is diverse and may reflect a different set of functional constraints. The carpal morphology of the dermopterans shows both megachiropteran and microchiropteran characters. The function of these characters in dermopterans and bats (stabilization of the carpus in dorsiflexion) may be similar, but the locomotor roles may be quite different between these taxa.

Reduction in the number of proximal and intermediate carpal elements involving the scaphoid, lunate and centrale is a common condition among mammals. It occurs in marsupials, carnivores, rodents, insectivores, bats, tree shrews, and dermopterans to name a few. In the case of the scaphoid

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and lunate it is usually reported that the radial aspect of the lunate fuses to the ulnar aspect of the scaphoid. If the centrale is absent, it is usually stated to be either lost or fused to the distal aspect of the scaphoid (Leboueq, 1899; Steiner, 1922, 1942, 1965; Schmidt-Ehrenberg, 1942; Holmgren 1952; Altner, 1971). In archontans the composition and arrangement of elements making up the large proximal carpal element has been proposed as a synapomorphy of a chiropteran-dermopteran clade (the Volitantia Illiger, 1811, see Novacek, 1980; Szalay and Lucas, 1993; 1996; Simmons, 1995), or a dermopteran-paromomyid-primate clade (the Primatomorpha Beard, 1989, see also Beard 1993). Similarly, fusion of the scaphoid and lunate has been claimed as both a tuapiine and scandentian character Novacek, 1980, Novacek and Wyss, 1986). However, there has been some confusion over which scandentians possess which character state (Flower, 1870; Lyon, 1913; Clark, 1926; Davis, 1938; Grasse, 1955; Haines, 1955; Steiner, 1965; Verma, 1965; Novacek, 1980; Beard, 1993; Simmons, 1995), and adult morphologies have often been erroneously (Verma, 1965) or confusingly (Davis, 1938) described. There is no detailed description of carpal morphology in Urogale.

The Primatomorpha hypothesis of Beard, (1989, 1993) proposes that the lunate articulates with the distal aspect of the scaphoid in the paromomyiformes, a group of plesiadapiform primates, and that it has become fused to the distal scaphoid in dermopterans. Under this hypothesis the scaphoid has expanded ulnarly to articulate with the cuneiform, and the

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lunate has been displaced to articulate with the distal aspect of the scaphoid. These elements remain unfused in the paromomyiforms but are hypothesized to have fused into a single large element, the scaphocentralolunate, in dermopterans. However, fusion of the scaphoid, centrale, and lunate has also been proposed as a synapomorphy of the Volitantia (Novacek and Wyss, 1986; Szalay and Lucas, 1993, 1996; Simmons, 1994, 1995). Although the pattern of fusion is not specified in these hypotheses, it is testable. In tree shrews fusion of the scaphoid and lunate has also been used as a taxonomic character (Novacek, 1980; Beard, 1993; Simmons, 1994).

The literature on carpal development in archontans is extensive (Leboueq, 1899; Steiner, 1922, 1965; Schmidt-Ehrenberg, 1942; Holmgren, 1952; Altner, 1971) but lacks taxonomic breadth. Reduction of the scaphoid and lunate to a single element also occurs independently in murids and sciurids, as evidenced by the presence of a free lunate in Douglassia jeffersoni (Emry and Thorington, 1982, 1984).

The literature on tupaiine anatomy (Flower, 1870; Lyon, 1913; Davis, 1938; Holmgren, 1952; Haines, 1955; Verma, 1965; Altner, 1971) generally agrees that the Tupaiinae have a fused scaphoid and lunate. Steiner (1965) and Altner (1971) illustrate a separate lunate cartilage in fetal Tupaia glis, which coalesces into a single large proximal carpal prenatally. Holmgren (1952) agrees with this interpretation but shows the proximal half of magnum to be composed of centrale 3. This agrees with Steiner (1965) and Altner (1971) although these authors do not name this element. No

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evidence of a separate center of ossification for the lunate in Tupaia was seen, nor were there multiple centers of ossification in the magnum. This suggests that the loss of an ossification center is not evidence for the loss of a carpal element.

Verma (1965) reports that in Anathana wroughtoni not only are the scaphoid and lunate fused but so are the trapezium and trapezoid, the unciform and magnum, and that the centrale has been lost. This bizarre combination of fusion was not seen by Stafford and Thorington (1998). Their specimen showed the same carpal morphology as Tupaia and Urogale.

In spite of the general agreement on tupaiine carpal morphology Novacek (1980) claims the Tupaiidae retain an unfused lunate (pp. 78-79, fig. 23 & table 5, character #11 of his table). However, Simmons (1995) correctly codes this character as polymorphic for the family. There is no separate lunate in Tupaia, Urogale, or Anathana, but there is in Ptilocercus and Dendrogale. Therefore, scapholunate fusion is neither a tupaiid nor tupaiine character. Davis (1938, p. 386) does note a free lunate for Dendrogale but contradicts himself when he says "[t]he scaphoid and lunar are separate, instead of being fused into a single bone as they are in Tupaia", but adds later that "[i]n keeping with the fused condition of the scaphoid and lunar in Dendrogale the magnum articulates with the lunar, rather than with the cuneiform." Davis also claims that "[t]he carpus is strikingly similar to that of Ptilocercus." No special similarities between Dendrogale and Ptilocercus

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were noted here. With the exception of the free lunate, the carpus of Dendrogale is indistinguishable from that of Tupaia, Urogale, and Anathana.

Le Gros Clark (1926, p. 1207) noted none of the carpal characters subsequently recognized by Stafford and Thorington (1998) for Ptilocercus (Fig 11.1). Le Gros Clark says of the lunate that "On its distal aspect it has a narrow facet for articulation with the os magnum.", and that the magnum "...has an attenuated head, compressed laterally, which projects proximally to reach and articulate with the lunate." However, his figure 15 (p. 1207) shows extensive lunate-magnum contact, and no apparent attenuation of the magnum. He makes no special note of any unusual characteristics of the unciform, or of the cuneiform-pisiform-ulna complex. Characters which Stafford and Thorington (1998) found to be unique to Ptilocercus. In fact, the condition that Le Gros Clark figures for Ptilocercus is identical to Dendrogale (Fig. 11.2).

The articular patterns between the cuneiform, pisiform, and ulna in Ptilocercus are derived, as are the centrale, magnum, and unciform articulations. In Ptilocercus the centrale has expanded ulnarly, articulating with the lunate proximally and almost contacting the cuneiform. Also, the unciform has expanded radially to contact the ulnar aspect of the centrale. The combination of these conditions prevents the magnum from contacting the proximal carpal row in all but the most extreme positions. A similar condition has been noted in living strepsirhine primates (Godinot and Beard, 1993) and is also present in Tarsius bancanus. Here the centrale extends

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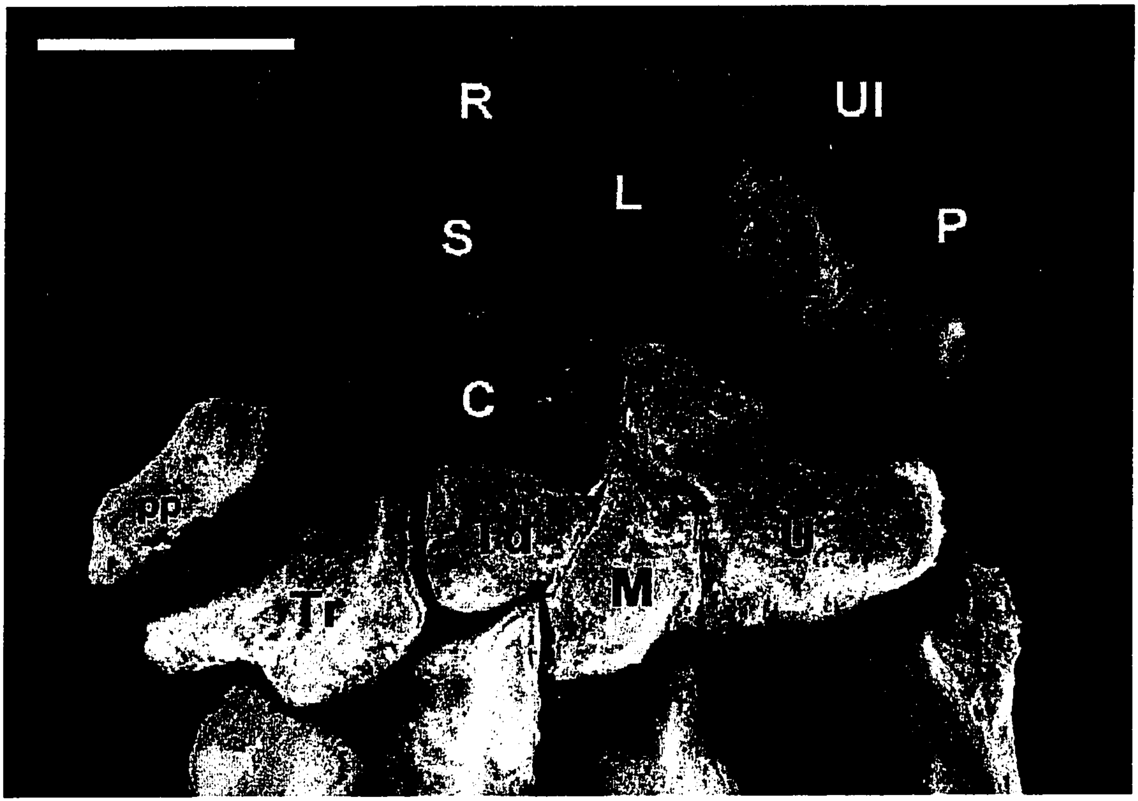

Figure 11.1: Scanning electron micrograph of the dorsal left carpus of USNM 121885 adult <u>Ptilocercus</u> <u>lowii</u>. Scale bar = 1 mm.

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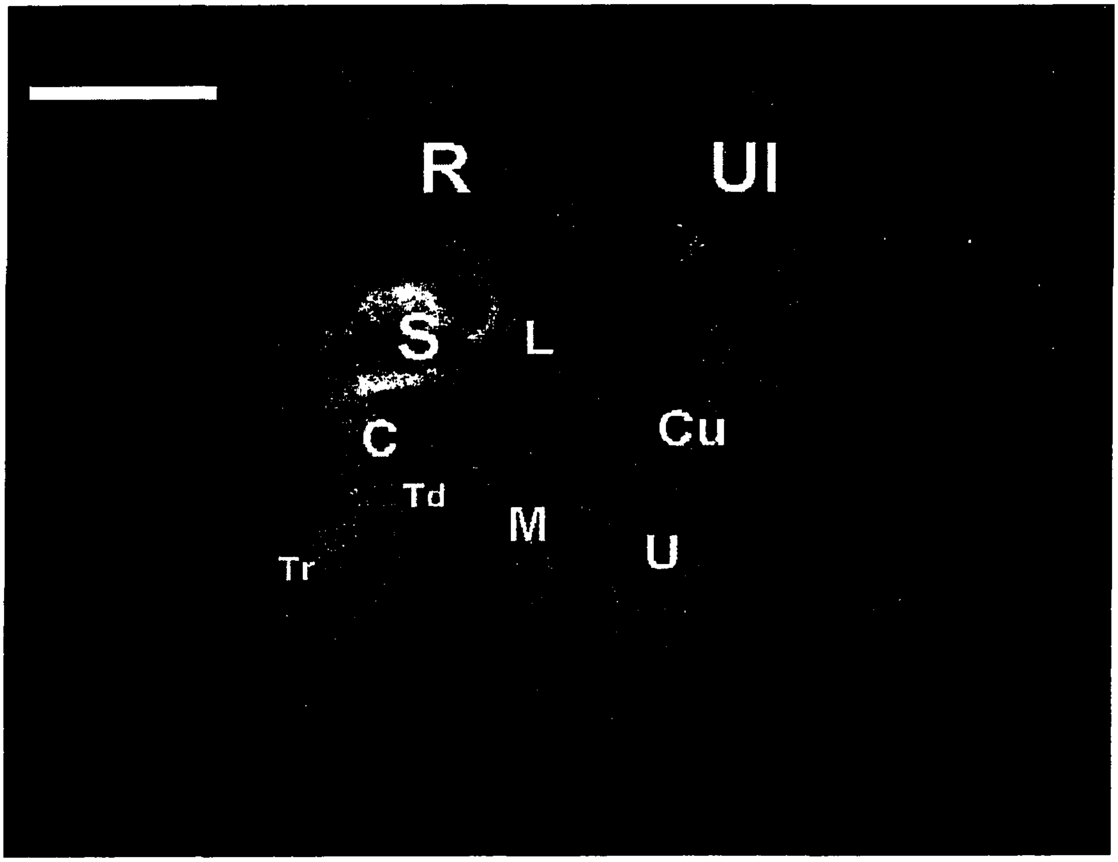

Figure 11.2: X-ray of the right carpus of USNM 256752 adult Dendrogale murina, image reversed. Scale bar = 1 mm. Abbreviations as in Figure 11.1.

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ulnarly to contact the unciform but this contact is restricted to the dorsal aspect of the carpus. Magnum-lunate contact is maintained palmarly through a distal extension of the lunate and the degree of contact probably varies with hand position. In Ptilocercus, however, it is the unciform that is expanded radially and contact between the magnum and the proximal carpal row is almost completely lost.

The differences in carpal morphology between Ptilocercus and the other tree shrews (Figs. 11.3-11.5) are difficult to interpret due to the lack of information on tree shrew locomotion. Most of what is available is very general in nature (see Banks, 1931; Wharton, 1950; Davis, 1962; Vandenbergh, 1963; Lim, 1967a; but also Bishop, 1964; and Jenkins, 1974 for more detailed treatments). The differences between Ptilocercus and the other tree shrews probably reflect the mechanical differences in degrees of ulnar deviation of the manus, indicate differences in digital abduction, and mirror the differences in the functional axes of the manus. Louise Emmons (personal communication) notes that Ptilocercus are more arboreal than other sympatric tree shrews in Borneo (see also Payne et al.,1985; Corbet and Hill, 1992) and that they spend relatively more time on large vertical supports. She has observed that when descending trunks head first Ptilocercus maximally abducts and pronates the upper extremities in order to grasp the trunk, forcing ulnar deviation of the manus. The derived nature of the cuneiform-pisiform-ulnar complex in Ptilocercus would resist dislocation of the carpus ulnarly in this position because the cuneiform and pisiform are

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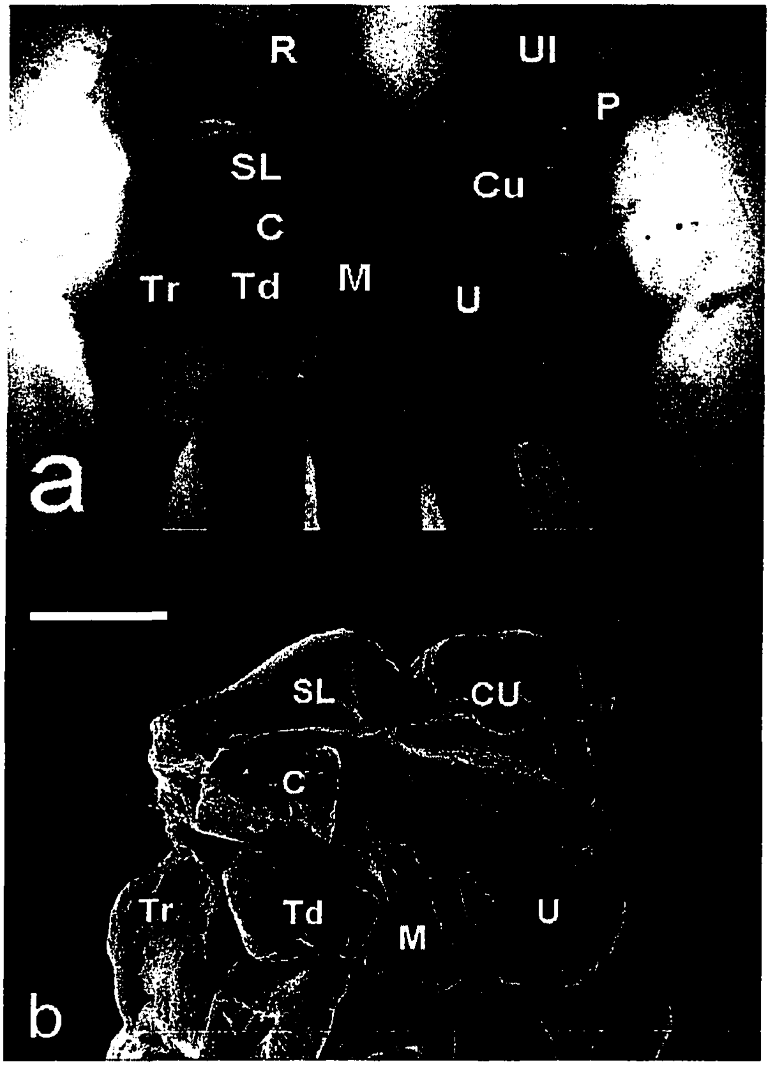

Figure 11.3: Postnatal carpal development and morphology in Tupaia. **a**, Dorsal left carpus of NZP 109835 4 day old Tupaia tana. **b**, Dorsal right carpus of USNM 396666 adult Tupaia minor, image reversed. Scale bars = 1 mm. SL = Scapholunate, Cu = Cuneiform, P = Pisiform, C = Centrale, Tr = Trapezium, Td = Trapezoid, M = Magnum, U = Unciform, pp = Prepollex, R = Radius, Ul = Ulna.

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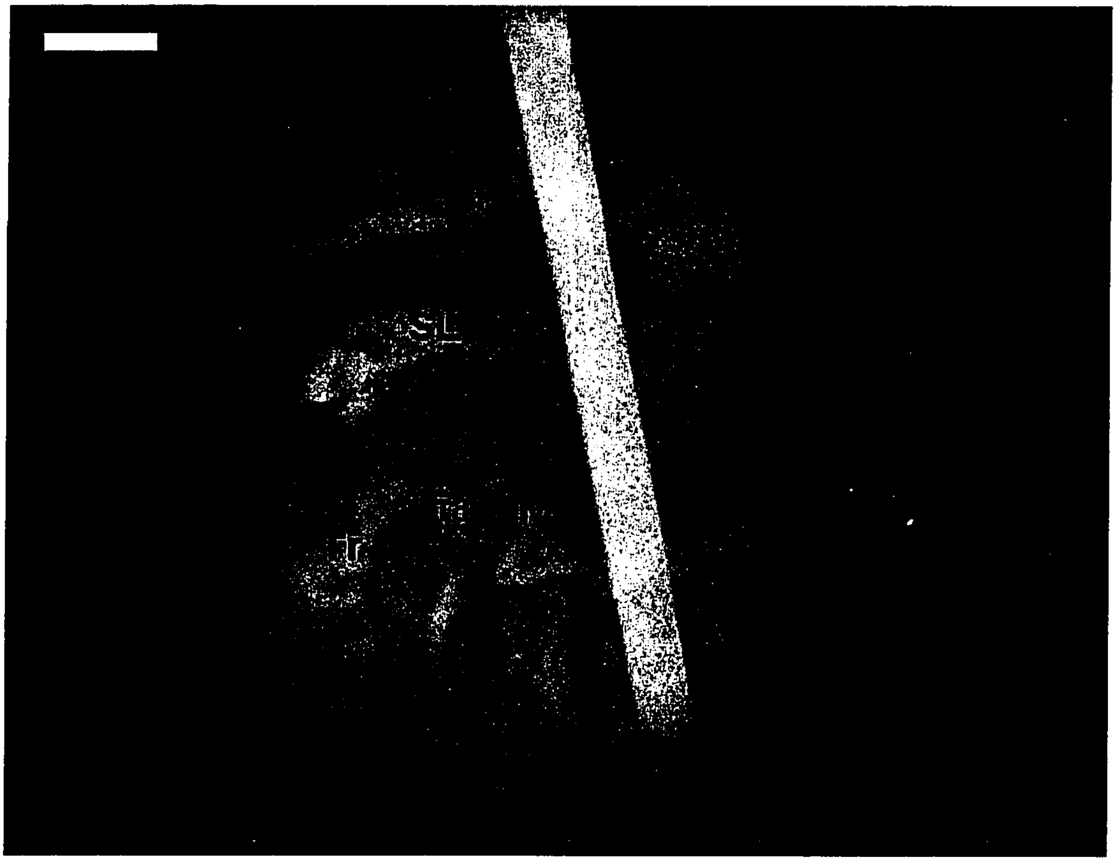

Figure 11.4: X-ray of the left carpus of USNM 292293 Urogale everetti.

Scale bar = 1 mm. Abbreviations as in Figure 11.3.

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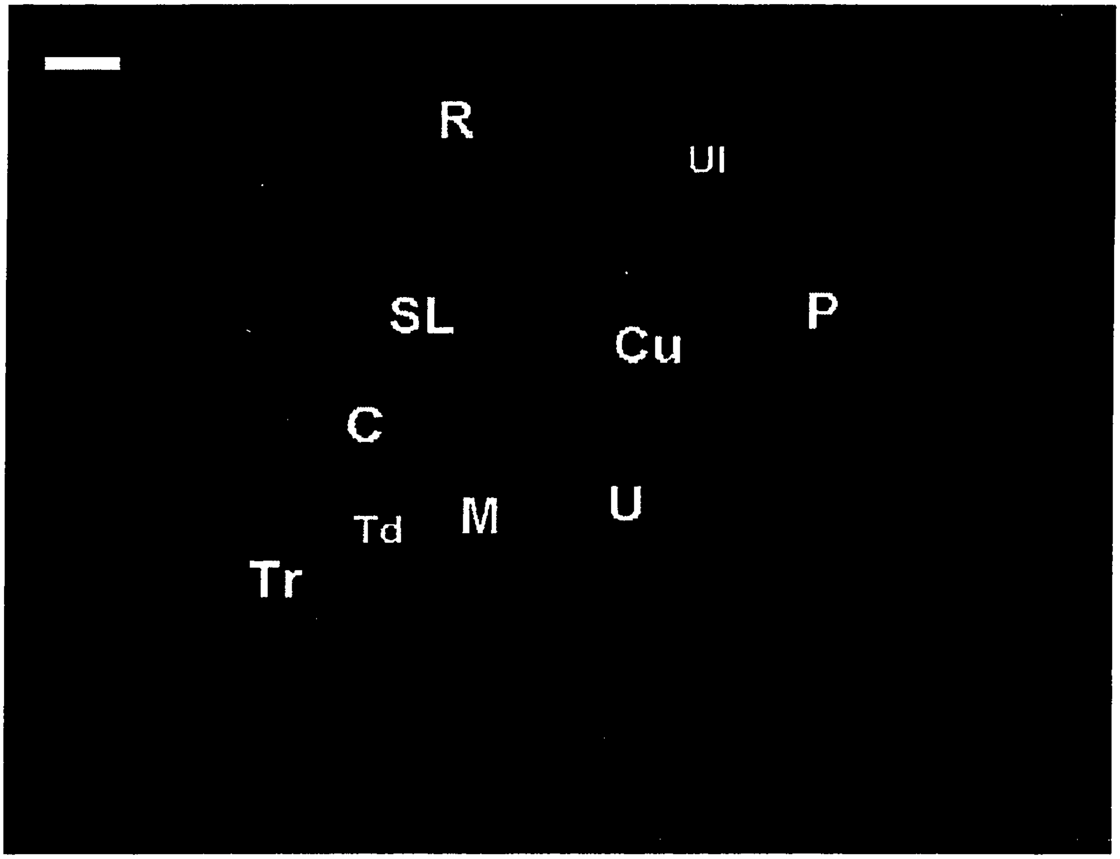

Figure 11.5: X-ray of the right carpus of FMNH 91265 Anathana ellioti, image reversed. Scale bars = 1 mm. Abbreviations as in Figure 11.3

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effectively wrapped around the ulnar styloid process. The interposition of the pisiform between cuneiform and the ulnar styloid process would also provide an effective stop to ulnar deviation of the manus. This arrangement would also stabilize the ulna as the antebrachium pivots over the manus. Ptilocercus appear to use a supinated and ulnarly deviated manus to grasp supports with highly abducted digits (see Figs. in Le Gros Clark, 1926; Napier and Napier, 1967; Nowak, 1988). The cuneiform-pisiform complex would therefore resist forces generated during plantar flexion of the manus (see Godinot and Beard, 1993; Preuschoft et al., 1993). Photographs also show that Ptilocercus spread their digits widely when grasping a branch. This would provide a fixed pivot point for the antebrachium. Photographs of tupaiine tree shrews do not show the same manual positioning as Ptilocercus (i.e. a supinated, ulnarly deviated manus, with splayed digits), although Jenkins (1974) notes that the deviation between digits I and V in Tupaia may be as large as 150^0, Bishop's (1964, Table 2, Fig. 12) data indicate much less digital divergence. In Tupaia, Urogale, and Anathana, fusion of the lunate would provide a more stable joint and prevent the concentration of stresses at the radiocarpal joint at the articulation between the scaphoid and lunate. This may be related to the different degrees of manual mobility in the more terrestrial Tupaia, Urogale, and Anathana compared to Ptilocercus. Similarly, the free lunate in Dendrogale may also reflect greater manual mobility. The radial expansion of the unciform in Ptilocercus also suggests a pattern of force transmission in which forces from digits IV and V are

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directed more radially as compared to other tree shrews. However, without detailed kinematic and behavioral data, these hypotheses are difficult to evaluate.

The Primatomorpha hypothesis proposes that the morphological details and how these relate to the mechanical positioning of carpal elements in colugos and paromomyiforms is homologous. This hypothesis would require that the large proximal carpal element of dermopterans be composed of fused scaphoid, centrale, and lunate (unless one or more of these elements were lost), **and** that the lunate be displaced distal to the scaphoid. In the dermopterans the cuneiform has developed two distinct articular facets on it's radial aspect and Beard (1989; 1993) proposes that the proximal facet articulates with the scaphoid portion and the distal one articulates with the lunate portion of this element. This parallels his interpretation of the carpals of the plesiadapid Nannodectes intermedius (USNM 442229). This specimen includes a scaphoid and a purported lunate, but not a cuneiform. The scaphoid has two distinct articular facets on its distal face. Beard (1989; 1993) also reports on Plesiadapis tricuspidens (MNHM R 5320) and Phenacolemur sp. (USGS 17847) which preserve the cuneiforms but lack both the scaphoid and lunate bones. The cuneiforms show two articular facets on their radial sides. Beard proposes that the more proximal facet is for the ulnarly expanded scaphoid and the more distal is for articulation with a distally displaced lunate. Combining these observations and interpretations, Beard proposes that a distally displaced lunate is present in

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Figure 11.6: Carpal development and morphology in microchiropterans (previous page). **A**: Dorsal left carpus of USNM 103405 juvenile Phyllonycteris poeyi. **B**: Dorsal left carpus of USNM 362098 adult Artibeus jamaicensis. **C**: Dorsal left carpus of USNM 549510 adult Furipterus horrens. **D**: Dorsal right carpus (reversed) of USNM 519701 adult Thyroptera tricolor. **E**: Dorsal right carpus (reversed) of USNM 577065 adult Myzopoda aurita. **F**: Dorsal right carpus (reversed) of USNM 437362 adult Otomops martiensseni. **G**: Dorsal left carpus of USNM 573474 adult Megaderma spasma. **H**: Dorsal right carpus (reversed) of USNM 548605 adult Rhinolophus inops. Scale bars = 1 mm.

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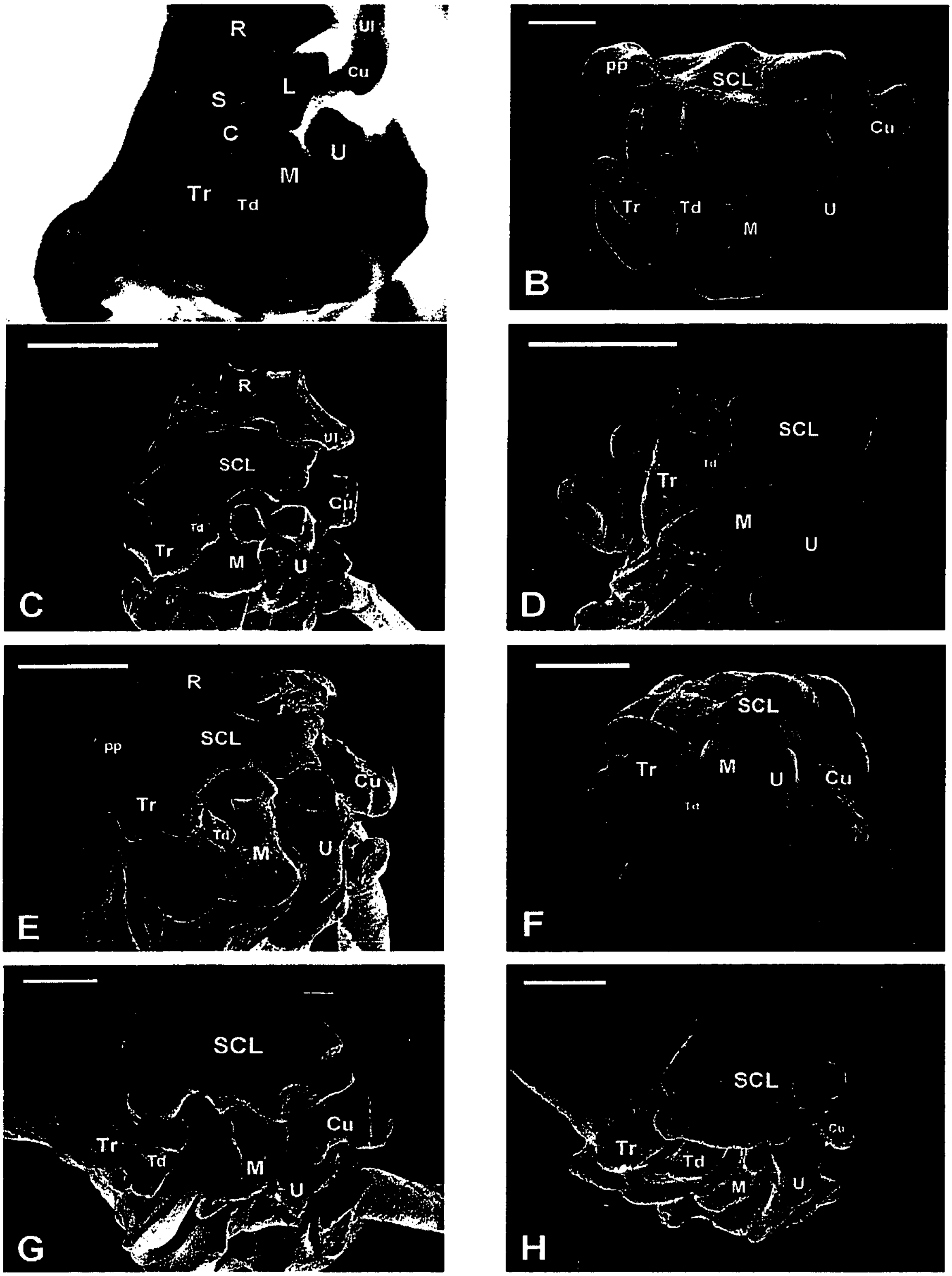

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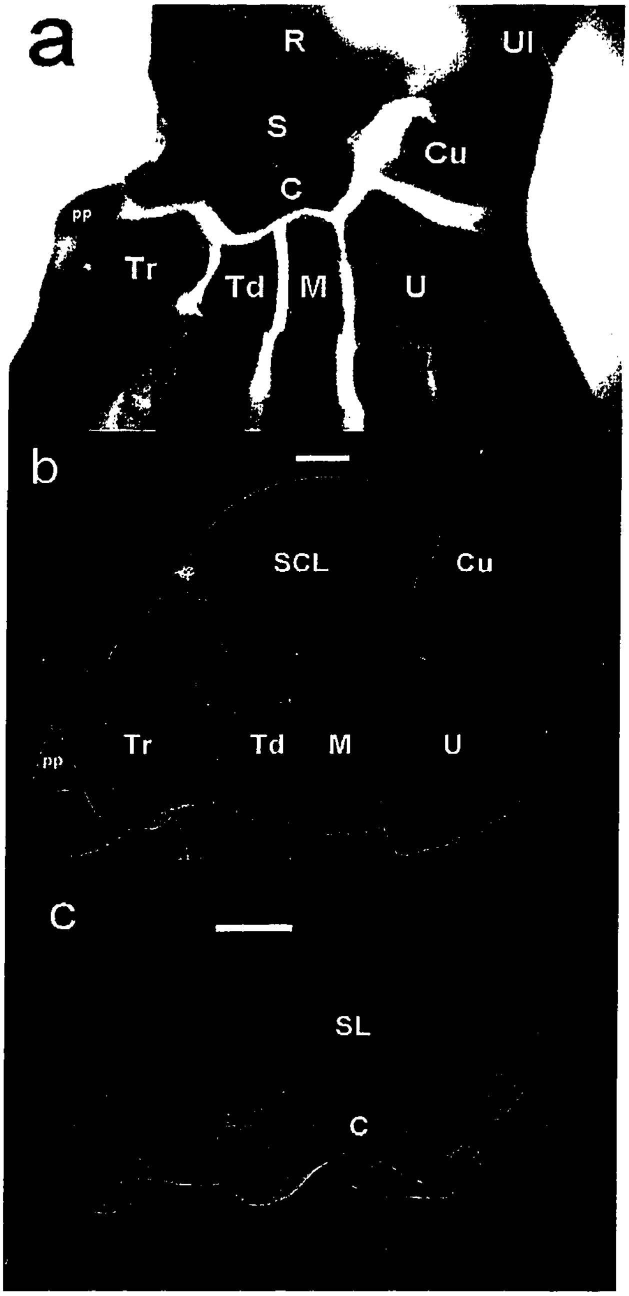

Figure 11.7: Carpal development and morphology in dermopterans. **a**, Dorsal left carpus of USNM 144374 fetal Galeopterus variegatus. **b**, Dorsal right carpus (reversed) of USNM 578084 adult Cynocephalus volans. **c**, Dorsal left scaphocentralolunate of USNM 317118 adult Galeopterus variegatus. Scale bars = 1 mm. Abbreviations as in Figure 11.6.

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all these taxa. It seems equally likely to me, however, that the proximal facet in these specimens could articulate with either the scaphoid or the lunate. Similarly, the distal facet could articulate with either the centrale, magnum, or unciform. Cuneiform-centrale contact occurs in Ptilocercus (Fig. 11.1), cuneiform-magnum contact in Dendrogale (Fig. 11.2) and Tupaia (Fig. 11.3), and cuneiform-unciform contact in the Microchiroptera (Fig. 11.6). Furthermore, the assignment of the above specimens has been seriously questioned (Krause, 1991). Regardless, the proposition that the Dermoptera have a distally displaced lunate, like that proposed for the fossils, is a testable hypothesis.

Prenatally dermopterans have a large proximal cartilage and a large intermediate cartilage (Stafford and Thorington, 1998). Postnatally (Fig. 11.7), fusion between these cartilages proceeds after the onset of ossification within the cartilages. There is no evidence for the existence of a separate lunate cartilage in colugos, but Tupaia at a comparable stage of development to the youngest colugo USNM 144374 still retain a distinct lunate cartilage (Steiner, 1965). However, Holmgren (1952, Fig. 33) shows a lunate cartilage fused to the ulnar side of the scaphoid cartilage. This element has already coalesced with a distal element composed of the cartilages of centralia 3 and 4. Unfortunately, Holmgren's Fig. 32 upon which this interpretation rests is difficult to interpret. This figure shows the lunate cartilage separated from the scaphoid cartilage along an oblique line.

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It also shows lunate-radius contact and extensive lunate-cuneiform contact. However, there is no cartilage for centralia 3 evident in this figure.

Obviously, the large proximal cartilage is the scapholunate and the large intermediate cartilage is the centrale. The developmental series presented by Stafford and Thorington (1998) shows that ossification is complete within the centrale and scapholunate cartilages while fusion between these elements is still incomplete. This is a combination of the processes seen in the bats and tree shrews. Interestingly, a cleared and stained colugo (USNM 144374, Stafford and Thorington, 1998) shows complete separation between the scapholunate and centrale cartilages even though it is significantly older than the specimen reported by Holmgren (1952). This may reflect a high degree of variability in the process of carpal fusion in colugos. Complete ossification within the scapholunate and centrale cartilages prior to ossification between these elements is documented in several of the colugo specimens, supporting this hypothesis. In any event, there is no evidence to support the homology of carpal elements as proposed by Beard (1989; 1993). However, the adult colugo USNM 317118 presents a defect in the distal face of the centrale. This specimen, although an adult based on complete fusion of all other cranial and postcranial sutures and epiphyses, shows incomplete fusion proximodistally between the centrale and scaphoid. Given that there is no separate lunate cartilage in the fetal colugo USNM 144374, that the juvenile colugos USNM 197203 and 143326 do not show a similar defect, and that this defect is not present in the right

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scaphocentrale of USNM 317118, it is best interpreted as a crack and not a suture.

Fusion of the scaphoid, centrale, and lunate has also been used as a taxonomic character of the Chiroptera (Flower, 1885; Grasse, 1955; Jepsen, 1966, 1970; Walton and Walton, 1970) and the Volitantia (Novacek, 1980; Szalay and Lucas, 1993, 1996; Simmons, 1994, 1995). Although the consensus now seems to be that the scaphoid, lunate, and centrale are fused in bats (Novacek, 1980; Beard, 1989; Szalay and Lucas, 1993, 1996; Simmons, 1994, 1995), the pattern of fusion in these hypotheses has not been specified. Most workers (Flower, 1885; Allen, 1893; Grasse, 1955; Jepsen, 1966, 1970; Walton and Walton, 1970; Szalay and Lucas, 1993, 1996; Simmons, 1994, 1995) only mention that the bones are fused and sometimes they either rely on previous studies for authority, or contradict previous statements that the centrale was "lost". For example, Flower (1885) and Grasse (1955) have been often cited as authority on the fusion of carpal elements in bats. However, Flower (1885, p. 290) only notes that "[i]n the carpus the scaphoid and lunar are united, and in some genera (as Pteropus) the cuneiform is joined with them, so that the proximal bone contains but a single bone. There is no centrale. The pisiform is very small."; and Grasse (1955, p. 1748) cites Leboucq "[d]'apres Leboucq (1899), le centrale au cours de la vie embryonnaire se fusionne rait avec le scapho-semilunaire." As far as can be determine, Leboucq (1899), Schmidt-Ehrenberg (1942), and Holmgren (1952) are the primary sources of data on

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carpal fusion in bats. They show that the scaphoid and lunate fuse mediolaterally while the centrale fuses to the distal aspect of the scaphoid. Stafford and Thorington (1998) confirmed that the patterns described by Leboueq (1899) for Vespertilio murinus, by Schmidt-Ehrenberg (1942) for Molossus , and by Holmgren (1952) for Pipistrellus ceylonicus and Hipposideros sp. are also found in five other genera of microchiropterans. I confirm here that fusion of the scaphoid, centrale, and lunate postnatally after intracartilage ossification has commenced is a valid chiropteran character. There is no evidence of postnatal scaphoid-lunate fusion in any other taxa examined, most notably in colugos. However, the dermopterans do show postnatal fusion between the centrale and scapholunate after intracartilage ossification is complete. The fact that only bats and dermopterans show coalescence of carpal elements after the ossification of those elements may indicate homology of the scaphocentralolunate in these taxa..

The patterns of carpal fusion and articulation between the two chiropteran suborders, however, are difficult to assess and require more detailed study. Different patterns of force transmission related to aerodynamic parameters, wing kinematics, or non-aerial locomotion may be factors in the differences between megachiropterans and microchiropterans. Likewise, the development of the trapezial-scaphoid locking mechanism in megachiropterans vs. a trapezoidal-centrale locking mechanism in most

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microchiropterans may reflect different functional requirements between the two suborders.

In the megachiropterans the trapezium possesses a large process which dorsally overrides the scaphoid and fits into a deep pit on the dorsal scaphocentralolunate, radial to the line of scaphoid-centrale fusion (Fig. 11.8). This trapezial process is bound to the scaphocentrale pit by a strong ligament. Engagement of the process and pit would stabilize and lock these carpals during dorsiflexion. In megachiropterans the second metacarpal has a large area of articulation with the trapezium, and this would provide support to the leading edge to the wing in flight by resisting dorsiflexion of the second metacarpal. The benefits of such leading edge rigidity are discussed in detail by Norberg (1970, 1972). Megachiropterans also use the pollex in suspensory positional behaviors associated with feeding and roosting. The locking mechanism and its strong ligamentous connection may serve to anchor the trapezium during positional behaviors where the pollex is hyperdorsiflexed. The locking mechanism would probably not be completely engaged during these behaviors because digits II-V are flexed against the forearm, but the high radial border of the pit would prevent the process from dislocating radially under tension (see Figs. 5 and 7 in Jenkins, 1981 which show the separation of carpal elements during suspensory locomotion in spider monkeys and gibbons).

In most microchiropterans the locking mechanism is located between the trapezoid and the centrale portion of the scaphocentralolunate (Fig. 11.6).

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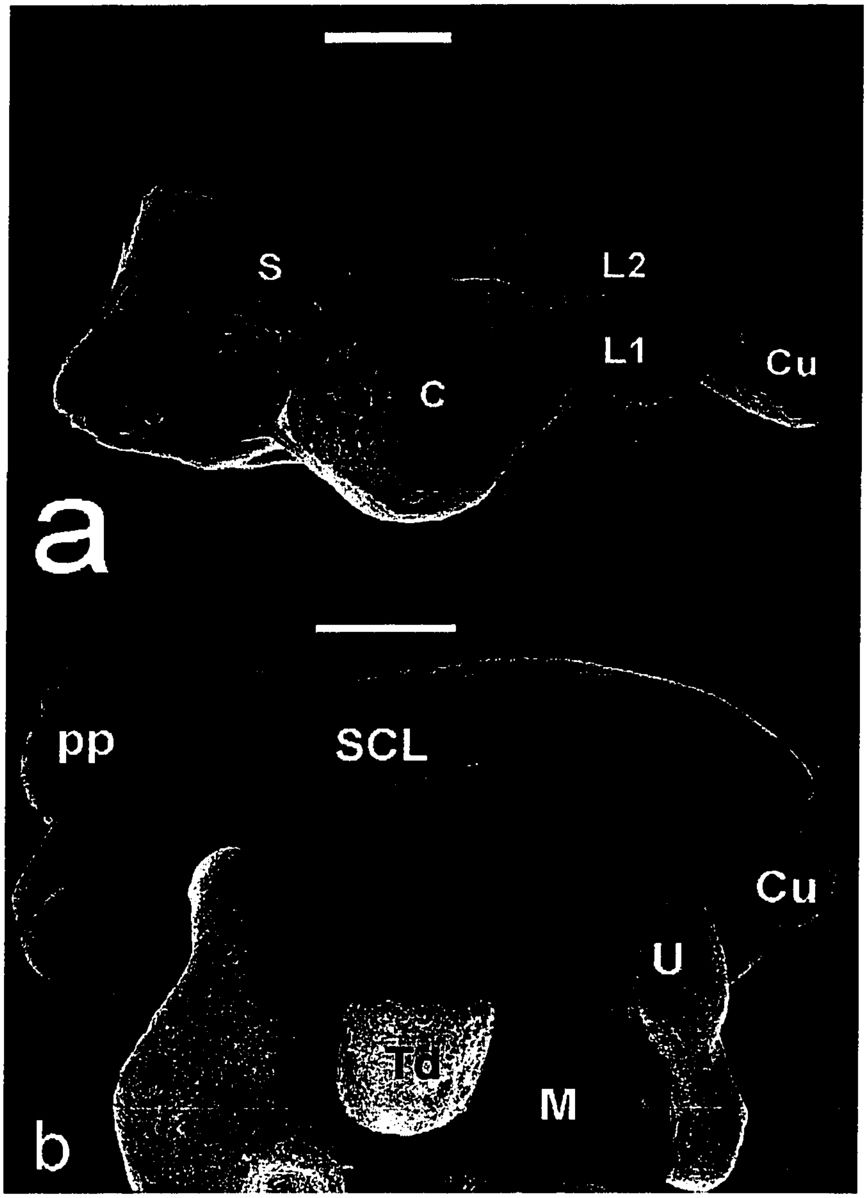

Figure 11.8: Carpal development and morphology in megachiropterans. **a**, Dorsal right scaphocentralolunate (reversed) of USNM 448865 juvenile Hypsignathus monstrosus. **b**, Dorsal right carpus (reversed) of USNM 543166 adult Hypsignathus monstrosus. Scale bars = 1 mm. L1 = dorsal component of lunate (centralia 3 of Holmgren, '52), L2 = palmar component of lunate (lunate of Holmgren, '52), other abbreviations as in Figure 11.6.

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This may reflect differential mobility of the pollex and thereby the leading edge of the wing between megachiropterans and microchiropterans. The differences in carpal-metacarpal II articulations may also reflect these factors and be functionally linked to the repositioned locking mechanisms. In microchiropterans the second metacarpal is wedged between the trapezoid and magnum and has less contact with the trapezium. This would still provide a rigid leading edge to the distal wing by stabilizing the second digit. At the same time it may provide greater mobility of trapezium and metacarpal I which would provide greater mobility of the propatagium. This could affect control and maneuverability in microchiropterans and be related to the more acrobatic nature of microchiropteran flight (i.e. somersaulting during landing, catching insects "on the wing", etc.).

Most microchiropteran families possess the locking mechanism illustrated by P. poeyi and A. jamaicensis (Figs. 11.6a,b). This mechanism is characterized by both the trapezium and trapezoid dorsally overriding the scaphocentralolunate. The trapezium dorsally overrides the trapezium and articulates with the radial lip of the centrale groove and with the scaphoid portion of the scaphocentralolunate when dorsiflexed. However, it is the proximal process of the trapezoid that articulates with the centrale groove and provides stabilization during dorsiflexion. The radial lip of the groove is variably developed between families, usually being high and sharp but can also be low and rounded and more closely resemble the tubercle seen in other families.

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The Molossidae are characterized by such low and rounded centrale borders. In this family the trapezium has expanded ulnarly to reduce centrale contact with the centrale portion of the scaphocentralolunate (Molossus and Tadarida for example). In other genera (Otomops) the trapezoid is completely cut off from contact with the scaphocentralolunate.

The Myzopodidae show a similar condition. Here the trapezoid still maintains contact with the dorsal centrale, but the trapezium also has a large degree of articulation here. In this condition there is no apparent radial lip to the centrale groove. The Furipteridae show still a different condition. Here the carpus shows both trapezial-scaphoid and trapezoidal-centrale locking mechanisms.

The Rhinopomatidae and Rhinolophidae also have low rounded centrale tubercles but are characterized by having no dorsal overlap of the scaphocentralolunate by any of the distal carpals. These families also lack the centrale groove and instead have a transverse (radio-ulnar) ridge across the distal surface of the scaphocentralolunate. These two families do not show any obvious dorsal locking mechanism.

The Megadermatidae show a condition similar to the rhinopomatids and rhinolophids. Megadermatids also show no dorsal overlap of the scaphocentralolunate by the distal carpals, but there is a large centrale tubercle that projects into the distal carpal row dorsally. This distal projection is tightly cupped between the trapezium and trapezoid radio-ulnarly

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and palmarly. Although very different from any other chiropteran pattern, this pattern would also provide a dorsal locking mechanism.

The conditions seen in the Furipteridae, Thyropteridae, Myzopodidae, and Molossidae may be modifications of the pattern seen in A. jamaicensis and most other microchiropterans. Because a portion of the centrale is wedged between the trapezium and trapezoid, the megadermatid condition is most similar to the common microchiropteran condition. The condition seen in the rhinolophids and rhinopomatids seems more divergent. Although the *development* of these locking mechanism could be related to body size in microchiropterans, there is no reason to believe that the *repositioning* of the locking mechanism between megachiropterans and microchiropterans is size related. Small Megachiroptera (i.e. Micropterus pusillus) have well developed trapezial-scaphoid mechanisms. The vampire bat Desmodus rotundus uses the pollex extensively in locomotion (Altenbach, 1979), as do many microchiropterans, but only the Furipteridae possess a trapezial locking mechanism. Norberg (1970) describes a proximal process of the trapezoid in Plecotus auritus as being "...wedged between the lunar, the trapezium, and the magnum..." (lunar=scaphocentralolunate). This process may be the same one that articulates with the centrale groove. However, Norberg believes that this arrangement acts to prevent radio-ulnar movements of the carpus rather than restrict dorsiflexion. She describes no locking mechanism for megachiropterans (Norberg, 1972).

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Detailed comparative studies of the kinematics of the chiropteran carpus are needed to fully understand the function and role of the morphological differences between the two chiropteran suborders. Similar studies on bat and colugo kinematics are also required to evaluate the striking similarity between the scaphocentralolunates in these taxa. Nevertheless, it is possible to generate some hypotheses about the function of the volitantian carpus.

Fusion of the scaphoid, centrale, and lunate obviously reduces mobility in the proximal carpal row, but it does this in specific ways. Flexion and extension of the carpus are not affected by scaphocentralolunate fusion in volitantians, but pronation-supination, and radial and ulnar deviation are. These movements are more restricted in the chiropterans than in the dermopterans, largely due to the shape of the distal radial articular surface in bats (Figs. 11.6, 11.7, 11.8). In bats the radio-carpal articular surface is highly angled and V shaped. In dermopterans, and all other taxa studied here this articular surface is much more hemispherical or ovoid in shape. In the non-chiropteran taxa there is also extensive contact between the distal radial articular surface and the carpals. In bats the two surfaces seem to be much less congruent. Here the scaphocentralolunate articulates with the radius mostly at the apex of the scaphocentralolunate, and that the dorsal and palmar articular surfaces mostly act as stops to dorsoflexion and palmar flexion. Similarly, because the proximal planform of the scaphocentralolunate is very strait in bats the ability to radially or ulnarly deviate the manus is restricted.

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This is not the case in dermopterans. Certainly, radio and ulnar deviation are limited compared to taxa with unfused scaphoid-centrale-lunate complexes, but the rounded planform of the dermopteran scaphocentralolunate (Fig. 11.7) would still allow some radial and ulnar deviation. In fact, the ability to ulnarly deviate the manus at the radio-carpal joint appears quite marked in dermopterans. Because the ulnar styloid process passes distal and ulnar to the cuneiform, and because the pisiform only has limited contact with the ulnar styloid process, it does not act as a stop against either of these carpal bones.

Because little is known about the kinematics of the carpus and non-aerial locomotion in bats, functional hypotheses are difficult to evaluate. Altringham (1996 p. 17, citing Pettigrew et al., 1989) claims that in microchiropterans the "...thumb and forefinger have minimal independent mobility..." while the megachiropterans have an "...opposable thumb and mobile forefinger..." However, Pettigrew et al. (1989 p. 492) cite Leen and Novick (1969) as the source of this observation. Leen and Novick (1969 p. 34) simply state that in "All living bats.... The thumb bears a claw and is not much modified from the typical mammalian form though it may, as in flying foxes, be rather elongate. The thumb, like that of primates, is also exceptionally mobile." This does not contradict the morphological evidence presented by Stafford and Thorington (1998), and discussed above, which suggests that the microchiropterans have a more mobile pollex, neither does is supply any special similarity between megabats and primates.

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Like the megachiropterans, the colugos also possess a definite trapezial-scaphoid locking mechanism, although it is not as well developed. Similarly, the trapezoid articulation with the centrale portion of the scaphocentralolunate is dorsally orientated as in microbats, although there is no hint of a centrale groove. Of all the taxa examined here only the Dermoptera and Chiroptera appear to have dorsally orientated centrale-trapezoid articular surfaces. These characters provide a close packed and stable articulation for the trapezium and trapezoid (and thereby for metacarpals I and II) in dorsiflexion. The significance of this complex may be related to the reduction in induced drag imparted by a dorsiflexed wingtip (Whitcomb, 1976; Thorington et al., 1998). Alternately, a dorsiflexed wingtip also reorients a portion of the lift force medially. This provides a more stable configuration to the wing and in some instances provides a self righting mechanism and thereby enhances static stability. Either of these hypotheses are conceptually easier to apply to a static airfoil model like that represented by the dermopterans. The implications of wingtip canards for unstable/dynamic systems has not been considered, and in bats these characters may simply be related to preventing hyperdorsiflexion of the wingtip during the downward stroke of the wing.

In any case, the colugo morphology represents a reasonable stage for a chiropteran ancestor. The similarity in the function of these characters (i.e. to stabilize the carpus in dorsiflexion) is significant, but whether or not the biological role (sensu Bock and von Wahlert, 1965) of the colugo carpus

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represents a reasonable functional precondition for a pre-flapping bat is difficult to evaluate. Certainly the dorsiflexed close packed position of the carpus in colugos would aid in increasing lift to drag ratios, and as bats developed flapping flight these characters may have been co-opted for other biological roles (i.e. the production of thrust). It has been suggested (Chapter 10) that ventral pronation of the forearm by dermopterans in the terminal phase of the glide reorients the propatagium and the wing tip canards in order to maintain their function at high angles of attack. Unfortunately, it is not currently known that dermopterans, or other gliding mammals, actually do this. However, such movement of the forelimb is not dissimilar to the flick phase of bat flight. In this phase of the wingbeat cycle the wing is transitioning from the upstroke to the downstroke. At this time the manus becomes strongly dorsiflexed, and the forelimb is pronated.

The comparative morphology and developmental history of the carpal complex of the Dermoptera has proved to be a valuable area for the evaluation of proposed phylogenetic affinities. Ptilocercus and Dendrogale retain a free lunate while in Tupaia the scaphoid and lunate cartilages coalesce prenatally and ossify from a single center. The process of carpal element reduction is assumed to be the same in Urogale and Anathana. The unique arrangement of the carpals in Ptilocercus may relate to a greater reliance on abducted digits and ulnarly deviated hand postures as compared to Tupaia, Urogale, and Anathana. The carpal morphology of Dendrogale probably best represents the ancestral scandentian condition.

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The large proximal carpal element in colugos and bats is a scaphocentralolunate. Both colugos and bats show postnatal ossification between discrete carpal elements. However, colugos but not bats show the prenatal coalescence of the scaphoid and lunate cartilages seen in most other mammals. Therefore, no evidence was found to support the homology of carpal elements as proposed by Beard (1989, 1993), namely that the dermopterans have displaced the lunate distal to the scaphoid and that such a repositioning is a synapomorphy of a cynocephalid - paromomyid clade.

The large proximal carpal element in Chiroptera is a scaphocentralolunate the discrete elements of which fuse postnatally after the onset of ossification. This character is homologous between the megachiropterans and microchiropterans but the unique articular relationships of the carpals in each suborder may reflect different functional-adaptive regimes. Because of the different processes producing scaphocentralolunate fusion in dermopterans and bats the hypothesis of scaphocentralolunate homology between colugos and bats can not be unequivocally supported. Nevertheless, the fact that these three elements do fuse, that only bats and dermopterans show ossification between already ossified carpal elements, similarities in the articular relationships of the carpus and in proposed and so far corroborated functional-adaptive explanations, suggest a common evolutionary origin of this character complex in dermopterans and bats.

The processes of carpal fusion and development in archontans require further study. Prenatal coalescence of cartilages concomitant with the loss

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or incorporation of a center of ossification appears to be the common pattern of carpal reduction in mammals. Why the bats and dermopterans deviate from this pattern is a question that cannot be answered here. However, that fact that volitantians do differ helps in the rejection of some phylogenetic hypotheses and may also help to resolve the relationships of these taxa. Similarly, more detailed studies on colugo and chiropteran functional morphology are needed, in conjunction with those of the relevant fossils. Studies on colugos are already underway, but the small size of most chiropterans coupled with rapid wing beat cycles makes the study of bat flight challenging to say the least. Studies of non-aerial chiropteran positional behavior would be easier to conduct, and may be more relevant in any case. Nevertheless, a detailed description of the kinematics of the bat carpus during aerial and arboreal locomotion is needed.

Of the three mammalian gliders known to glide with dorsiflexed wing-tips, all three show adaptations for maintaining the dorsiflexed position of the wing-tip, and all show adaptations for stabilizing the wing-tip in this orientation. This indicates that the selective pressures for maintaining a stable dorsiflexed wing tip may be great, and that such features may be prone to convergence. Still, the striking similarity of the morphology of the locking mechanism in dermopterans and megachiropterans makes this character difficult to dismiss a homoplasy. Even the similarities between the dermopteran and microchiropteran trapezoid-centrale complexes suggest a common origin. In fact, the morphology of the dermopteran carpus does

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make a reasonable functional antecedent stage for the evolution of the chiropteran carpus.

Two features are especially important here; 1) the dorsal locking mechanisms in these taxa, and 2) the degree of ulnar deviation in the manus of each taxon. Granted, the "ulnar deviation" of the chiropteran manus is accomplished through modifications of the carpo-metacarpal articulations and not the radio-carpal articulations as in dermopterans. However, selective forces related to positional behaviors (aerodynamic or not) that have produced this ability for extreme ulnar deviation in dermopterans may have later been built on by chiropterans and produced the highly abducted hand that the bats possess today. A more detailed study of tree shrews is also needed in this context, focusing on the ability of these taxa to splay the digits. As noted above, Ptilocercus seems to use a highly abducted hand grip, and the degree of digital splaying even in Tupaia can be great. Consequently, highly abducted finger positions may in fact be ancestral for archontans, although not to the striking degree seen in bats and dermopterans.

Similarly, the dorsal locking mechanism that began as a means of stabilizing the carpus during flight to reduce induced drag could have become co-opted to resist extreme dorsiflexion of the carpus during the flick phase of flight and during the downstroke. In any event, the evidence from the wrist seems to strongly support a hypothesis of dermopteran-bat holophyly.

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CHAPTER 12: CONCLUSIONS

It is clear that contrary to most past treatments of the living dermopterans the two morphologically and ecologically distinct extant species of dermopterans represent two genera, and that the differences between them are striking and consistent (Stafford and Szalay, in press). The appropriate names for these two taxa are Cynocephalus volans (Linnaeus, 1758) for the Philippine flying lemur, and Galeopterus variegatus (Geoffroy, 1796) for populations from the Sunda Shelf area and the Southeast Asian mainland. This interpretation generally conforms to the conclusions reached by Thomas (1908) and later confirmed by Szalay (1969) and Szalay and Lucas (1993, 1996). However, it contradicts commonly accepted classifications which recognized only one genus with two species (Corbet and Hill, 1992; DeBlase and Martin, 1981; Lawlor, 1979; Nowak, 1991; Simpson, 1945; Vaughan, 1986; Wilson and Reeder, 1993; Yates, 1984, McKenna and Bell, 1997), and also earlier workers (Cabrera, 1925; Chasen and Boden Kloss, 1929; Lyon, 1908, 1909, 1911; Miller, 1900, 1903, 1906), some of whom have recognized as many as 18 species. Such classifications were the result of assigning species status to every isolated island population of dwarfed G. variegatus. These dwarfed forms are not morphologically distinguishable from larger morphs of this species, other than in size, and do not warrant specific distinction. The distribution of the dwarfed forms suggests that body size reduction in colugos is associated

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with independent events of isolation on small islands (Case, 1978; Foster, 1964; Heaney, 1978; Krazanowski, 1967; McNab, 1994; Vartanyan et al., 1993) resulting from drops in sea level associated with periodic glaciation (Flenley, 1985; Groves, 1985; Heaney, 1985, 1986, 1991; Michaux, 1994; Ollier, 1985; Ruedi, 1996). The recent discovery of a dwarfed G. variegatus in northern Laos (Ruggeri and Etterson, 1998; Fig. 4.1) may highlight the importance of isolation of small populations in the dwarfing process if this population proves to be isolated from other mainland G. variegatus.

However, it may be useful to designate four subspecies of G. variegatus; G. v. variegatus Chasen and Boden Kloss, 1929 from Java and its surrounding islands, G. v. temminckii Chasen and Boden Kloss, 1929 from Sumatra and its surrounding islands; G. v. borneanus Chasen and Boden Kloss, 1929 from Borneo and its surrounding islands, and G. v. peninsulae Chasen and Boden Kloss, 1929 from the Malay Peninsula, mainland Southeast Asia, and associated islands. It may become useful to eventually designate separate subspecies for each of the dwarfed populations, and for other morphological variants from now isolated islands (i.e., the Batu Islands), but such action requires a more complete analysis of variability (morphological and genetic) within G. variegatus. This analysis is not yet complete.

Statements regarding morphological and ecological distinctness raise an important question, namely what are generic limits when phylogenetic relationships cannot be made an issue? Much effort has been expended

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discussing and debating species concepts and the recognition of species taxa (for a variety of perspectives and literature references see Claridge et al., 1997; Kimbel and Martin, 1993; Lambert and Spencer, 1995; Mayr and Ashlock, 1991). Nevertheless, little effort has been directed at definition and recognition of genera (Mayr, 1963; Simpson, 1945, 1961). Lemen and Freeman (1984) are particularly relevant for their discussion of problems regarding criteria for assessing whether speciose genera are paraphyletic or holophyletic. In the general practice of taxonomy, closely allied species that show morphologically distinct attributes which appear to correlate with different ecological conditions generally qualify as distinct genera. For example, among Primates the genera Leontopithecus, the lion tamarins, and Callithrix, the marmosets, can be distinguished based on their morphological adaptations for extractive foraging and exudate feeding, respectively (Hershkovitz, 1977; Rosenberger, 1992). Similarly, the genera Ateles, the spider monkeys, and Brachyteles, the woolly spider monkey, can be distinguished based on cranial and dental adaptations for frugivory and folivory respectively. Likewise, the extant baboons Papio and Theropithecus are clearly distinguishable in their hard parts based on diet-related adaptations. The results presented here parallel those of Lemen and Freeman (1984) who found few differences in shape within speciose bat genera, although significant differences in size within species of genera were common. Freeman (1981, 1982, 1988) also has documented similar patterns among genera of bats, and Emmons and Vucetich (1998) note the

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same kind of differences among genera of spiny rats (Echimyidae). Cynocephalus and Galeopterus show the same kind of striking cranial, dental, and postcranial differences encountered in other closely related mammals that have shown morphological evidence for adaptive divergence.

Cynocephalus and Galeopterus represent two such morphologically and ecologically distinct units. Cynocephalus has a more robust masticatory apparatus that Stafford and Szalay (in press) suggest to be adaptations to shearing, emphasizing the anterior (premolar and canine) dentition and vigorous molariform chewing. Galeopterus has a more gracile masticatory system and appears adapted to shredding or puncturing with the anterior dentition and protocone-talonid crushing with the molariform dentition. Such differences may be related to differences in quality or structure of food between the Sundaic and Philippine subregions. Similarly, differences in facial morphology may be related to these factors, or they possibly may be related to different mating or foraging strategies, or to different mechanisms of social control. Populations of dwarfed Galeopterus do not differ in their morphological attributes from their larger conspecifics in these respects.

In terms of the postcranial characters studied here, it is obvious that dermopterans stand out as different from other gliding mammals. It is also true that when dermopterans differ from other gliding mammals, that they tend to differ in the same way as the bats (see also Szalay and Lucas, 1993, 1996). For example, dermopterans and bats have relatively longer forelimbs than other mammals. The problem is that in many of the cases where bats

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and dermopterans differ from other mammals in similar ways, suspensory and slow climbing taxa also differ in the same ways. For example, bats and dermopterans tend to have relatively long humeri and radii, but so do Bradypus. Nevertheless, the temptation to ascribe characters that show such a taxonomic pattern to suspension is strong, and should be resisted. The relative lengths of the humeri and radii (and thereby the forelimb) are also long in other gliding mammals in comparison to their non-gliding relatives. This makes the distinctness of dermopterans in relation to other gliding mammals in many cases one of degree rather than one of kind. Also, not all suspensory taxa are similar to the dermopterans. Bradypus usually shows close similarity to the dermopterans, but Choloepus rarely does.

Bats, dermopterans and Bradypus all have relatively long necks. However, bats and dermopterans have a relatively longer axis than the other mammals studied here. The atlas is also relatively longer in dermopterans and megachiropterans than all other taxa studied here. For C3, C4, C6, and C7 Bradypus joins the volitantians in having relatively long vertebrae. The mechanics of neck elongation is obviously not related to gliding or flight (i.e. giraffes) alone, but the similar lengths of the first and second vertebrae in bats and dermopterans may indicate homology here. Neck elongation may be linked to feeding behaviors rather than extreme head positions. The majority of flexion and extension occurs at the atlanto-occipital joint, and not at any intervertebral joints. Similarly, the majority of head rotation takes place at the atlanto-axial joint.

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In spite of this, the characters used by Fenton and Crerar (1984) in their detailed study of chiropteran necks, and the conclusions reached by those authors are not contradicted here. It does, however, place these characters in an interesting evolutionary context. Most importantly, the characters used by these authors appear to be highly variable among microchiropterans, and many of these same characters are not restricted to the Chiroptera. Still, the differences in cervical morphology seen in megachiropterans and microchiropterans may reflect the functional considerations noted by Fenton and Crerar (1984). These same functional hypotheses may also apply to the dermopterans and Bradypus who, like the megachiropterans also utilize a ventrally flexed roosting posture when suspended from the substrate. Likewise, sciurids commonly cling to large vertical supports in a head-down orientation, with the cervical region strongly flexed. Whether or not tupaiids also use such a vertical clinging posture is uncertain although such postures have been observed in Ptilocercus lowii (Louise Emmons, pers. com.).

The elongation of the cervical region in volitantians, however, can not be unequivocally ascribed to flight and aerodynamic considerations. None of the non-dermopteran gliding mammals studied here have an elongated cervical region, and many of these animals do have an extensive propatagium. Similarly, the elongation of the neck in Bradypus obviously can not be ascribed to aerodynamic considerations. Also, in bats the propatagium extends only onto the shoulder at the gleno-humeral joint, and does not extend onto the cervical region. Of course, it is possible that a postulated

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volitantian morphotype included a propatagium and an elongate cervical region and that the demands of powered flight have necessitated the reduction of the propatagium in the Chiroptera. In such a case the elongate necks of the Chiroptera are simply retained ancestral characters. It is also possible that elongate necks are now subject to selective pressures associated with feeding in chiropterans. An elongate neck in insectivorous bats would increase the hemisphere within which the bat can capture prey. For nectarivorous species, along neck increases the distance away from obstacles that an animal may hover while probing flowers, reducing possible interference with the wings from obstacles. Elongate necks may also aid relatively large animals in foraging on relatively small terminal branches (see Grand, 1972).

The answer may also lie partly in the suspensory nature of the volitantian nonarial locomotion. Bradypus also have elongate necks, although the manner of this elongation is very different from that seen in volitantians. Volitantians have disproportionately elongated all of the cervical elements, Bradypus has not elongated the atlas or axis but has increased the number of cervical vertebrae, and elongated C3 to C9. Nevertheless, it is difficult to imagine how suspensory behavior alone influences neck length. Cyclopes (and Myrmecophaga to a much lesser extent) are also largely suspensory but do not show such cervical elongation. The hypotheses outlined above in regard to feeding may be more applicable in regard to cervical elongation, and it is likely that the interplay between suspensory locomotion and specific

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feeding strategies has produced the elongation of the volitantian neck and the convergent elongation of the neck of Bradypus.

Dermopterans are also different from other gliding mammals in attributes related to the strength of forelimb elements. Such attributes may in turn be related to dermopteran gliding. But dermopterans are also very different from bats. This is not entirely unexpected because flight must place a very different set of functional demands on the chiropteran skeleton. The animals that dermopterans seem the most similar to in attributes of forelimb element strength are either the sloths, or in some cases the strepsirhine lorises and pottos (Loridae). This strongly suggests that the differences between dermopterans and other gliding mammals are the result of the suspensory habitus of the former. The analysis also suggests that these differences may be the result of maintaining functional equivalence (i.e. shape changes required by changes in size; Biewener, 1989, 1990; Fleagle, 1985; Gould, 1975; Jungers, 1979; McMahon, 1975a,b; Alexander, 1977a,b) in taxa with relatively long limbs, be they dermopteran, xenarthran, or chiropteran.

This, in turn, suggests that neither gliding nor habitual underbranch suspension alone may be sufficient explanations for this forelimb elongation. Not all gliding mammals have long forelimbs, and not all underbranch suspensory taxa have long forelimbs. However, a particular mode of underbranch suspensory locomotion may exert selective forces for forelimb elongation. A comparative study of forelimb function and positional behaviors in Bradypus, Choloepus, Cyclopes, Cynocephalus, and Galeopterus

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may shed light on such selective forces. This model of a quadrumanous underbranch suspensory animal with greatly elongate forelimbs may well be the ancestral condition from which the living volitantians evolved, first into gliders and then from one of these lineages, into bats.

Elongation of the clavicle seems to be related to flight, but not to gliding or suspension. The later point is particularly well borne out by the fact that the living sloths have very reduced clavicles. However, there is a high degree of variability in the degree of clavicle reduction in sloths. Some individuals have clavicles represented by only a sliver of bone, while others have a more substantial shaft of bone. The relative cross sectional area of the clavicle, its polar moments, and second moments of area may reflect stresses placed on this element. Increase in $\mathbf{TCSA}_{\mathrm{Clavicle(STL)}}$ seems to be a character that separates the bats from all other mammals, and that separates the dermopterans from other gliding mammals. However, this need not indicate any particular functional link between bats and dermopterans. Dermopterans, although largely suspensory, are also slow climbers and increased resistance to torsional stress in the clavicle may be related to pivoting the body over/under the forelimb where the forelimb remains fixed for a relatively long period of time. Neither the lorids nor Cyclopes can really be classified as fully underbranch suspensors, but they are slow climbers with occasional underbranch hanging. Slow climbing may therefore explain the similarity in $\mathbf{J}_{\mathrm{Clavicle(STL)}}$ values among dermopterans, lorids, and Cyclopes. $\mathbf{I}_{\mathrm{ML,Clavicle(STL)}}$ seems to separate bats, with high values, from all other taxa

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studied here. It also separates dermopterans and Acrobates, again with high values, from all other gliding mammals. It is easy to hypothesize that forces acting on the dactylopatagium, or even plagiopatagium, in volitantians are producing these results, but it is difficult to see why Acrobates, with it's greatly restricted patagium, should differ in the same way. Similarly, little can be said regarding $\mathbf{I}_{\mathrm{AP,Clavicle(STL)}}$.

Dermopterans have unusually long humeri in relation to skeletal trunk length for a gliding mammal, but not nearly as elongate humeri as the bats. These results contradict Runestad and Ruff (1994) because their study indicated that dermopterans have humeri of comparable relative length in relation to other gliding mammals. The most comparable taxon in relative humerus length to the dermopterans is Bradypus, again indicating that a specific mode of underbranch quadrupedal suspension may be the causal factor here. When looking at $\mathbf{TCSA}_{\mathrm{Humerus(STL)}}$ we are also presented with a situation where dermopterans are different from all other gliding mammals in the same way as the bats are different from all other mammals (they both have relatively higher values). Again the dermopterans also have values similar to other quadrupedal suspensory taxa.

There are a number of reasons to expect why gliding mammals would be under pressure to reduce **TCSA** of the limb bones. Reduced **TCSA** may produce lighter bones. Any reduction in weight is beneficial in an aerodynamic sense because it may increase performance (see Chapter 10).

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Also, the earlier that an animal can deploy the wing after launching, the sooner it begins creating lift. After the animal launches from its support, and before it has deployed the gliding membrane it is subject to ballistic forces. During this time the animal will be losing altitude. Thin, light limb bones would have reduced mass moments of inertia and, along with proximal muscle packing, allow the wing to be deployed very rapidly. Again, the end result for an animal that can quickly deploy the wing is an increase in gliding distances. McArdle (1981), however, has also discussed the benefits of reduced mass moments of inertia and proximal muscle packing in lorises. This makes it difficult to ascribe the gracile limbs of dermopterans to uniquely aerodynamic factors.

There are some indications that reduction in limb bone **TCSA** does occur in gliding mammals, although not among the marsupials. However, it is again evident that dermopterans are different from other gliding mammals and quite similar to suspensory or climbing mammals. Also, $\mathbf{J}_{\mathrm{Humerus(STL)}}$ (polar moment of the humerus in relation to body size) in dermopterans seems to show more of a link with quadrupedal underbranch suspension than with gliding or the bats, although dermopterans do have high values for $\mathbf{J}_{\mathrm{Humerus(STL)}}$. The same is true for both $\mathbf{I}_{\mathrm{ML,Humerus(STL)}}$ and $\mathbf{I}_{\mathrm{AP,Humerus(STL)}}$ (the medio-lateral and anterior-posterior resistance to bending stress in the humerus in relation to body size.

The extreme elongation of the radius (Fig. 6.4) in dermopterans also seems to be most like the sloths and Acrobates. Such elongation is not

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common among other gliding mammals. A similar situation is seen regarding $\mathbf{TCSA}_{\mathrm{Radius(STL)}}$, and $\mathbf{J}_{\mathrm{radius(STL)}}$. With regard to these measures, bats generally stand out from all other mammals. Dermopterans also tend to stand out from all other gliding mammals, having higher values, but their values are not different enough to separate them from suspensory or climbing taxa. Probably the most surprising result here is the failure of $\mathbf{J}_{\mathrm{radius(STL)}}$ to clearly distinguish all of the bats from all other mammals. Such a separation was expected given the great range of pronation and supination that occurs in the chiropteran manus during the wing beat cycle. The wrists of bats and dermopterans have features that should resist hyperdorsiflexion (see Chapter 7, Stafford and Thorington, 1998), and that resist medio-lateral forces (Norberg, 1972). Chapter 7 also describes features in bat and dermopteran wrists that appear to restrict pronation and supination. It was therefore expected that the torsional forces generated by the chiropatagium in bats would be transmitted to the antebrachium, and that the radius would show adaptations to resisting such forces. Since dermopterans also have interdigital webbing it was expected that the radii of volitantians would show greater resistance to torsion than other gliding mammals. That they do not is surprising. However, volitantians do show adaptations to reduce pronation and supination at the elbow (Szalay and Lucas, 1993, 1996) and this may reduce the need for torsional resistance in the diaphysis.

However, bending moments of the radius in relation to body size (Figs. 6.15, 6.16) do distinguish the bats from all other taxa. Dermopterans again

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appear closest to suspensory or climbing taxa in these measures. It is interesting that the dermopterans differ from other gliding mammals in $I_{ML,Radius(STL)}$. Because of the orientation of the forelimb during gliding, the medio-lateral direction in which radial cross sectional diameters were measured generally correspond to the direction of the lift force. Consequently, it is possible that the forelimb of dermopterans is experiencing greater forces, in the direction of the lift force, than other gliding mammals. In fact, $I_{ML,Radius(STL)}$ is highest in dermopterans, intermediate in Petaurus, and lowest in the Pteromyinae (Fig. 6. 15). This progression also correlates well with the distal extent of the patagium.

The lorids require a brief discussion. A quick perusal of the lorid values presented in the previous chapters shows a high degree of variability in the data set. This variability generally reflects a dichotomy between the large bodied canopy dwelling taxa (Perodicticus and Nycticebus) and the smaller bodied subcanopy taxa (Arctocebus and Loris). Paradoxically, it is generally the larger bodied taxa that have values similar to the dermopterans. This is exactly the opposite of the expected results. The smaller bodied and more gracile Arctocebus and Loris are visually much more similar to the dermopteran phenotype.

The above discussions consider aspects of relative limb element length and cross sectional properties in relation to an estimator of body size (skeletal trunk length). These data suggest that gliding mammals do have significantly different values for many of these parameters as compared to

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their non-gliding relatives and bats. Dermopterans also tend to have significantly different values as compared to other gliding mammals. In may of these cases, the dermopterans are very similar to suspensory or climbing mammals. The following discussion considers the above data in relation to limb element length instead of skeletal trunk length. Such a treatment is necessary to evaluate whether or not the differences in the above mentioned parameters are related to the maintenance of functional equivalence. In other words, are the relatively thicker limbs of dermopterans, bats, and some suspensory taxa in relation to body size a result of the fact that these animals have also greatly elongated the limbs? In such a case, disproportionate thickening of the limb elements may be required in order to maintain optimal or maximum levels of bone strength, or to resist optimal or maximum levels stresses. In the following discussions, the length of the limb element is taken as an *estimator* of the moment arm of the forces acting on the specific limb element (Alexander, 1968; Wainwright et al., 1976). In this *model* the limb elements are treated as cantilevered beams fixed at one end, an admitted oversimplification. This facilitates the evaluation of the stresses acting on each limb element.

The data on clavicular robusticity (Fig. 6.17) presents a startling contradiction to the results based on $\textbf{TCSA}_{\text{Clavicle(STL)}}$ which showed that bats had relatively greater $\textbf{TCSA}_{\text{Clavicle}}$ than all other mammals. Also, when $\textbf{TCSA}_{\text{Clavicle}}$ is corrected for clavicular length, the dermopterans are no longer significantly different from other gliding mammals. Now, instead of seeming

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anomalous with respect to gliding mammals dermopterans seem to fall right where a gliding mammal should fall, with a relatively gracile clavicle. However, perhaps the most surprising change in interpretation is that now the bats are no different from the other mammals either. This may indicate that the relative increase in cross sectional area of the clavicle that was apparent in bats and dermopterans when corrected for body size may be an adaptation to retaining the strength of the clavicle as the clavicle elongates. In other words, the clavicle may need to maintain some particular resistance to medio-lateral or anterior-posterior bending, or to torsion in the clavicle. However, the results also suggest that the bending and torsional forces acting on the clavicle in bats, although greater than those indicated in gliding mammals, are not greatly different from those in arboreal, climbing, or even suspensory taxa. Given the high degree of variability in the microchiropteran taxa, however, it is best to reserve such speculation until such a time as a full study of the Microchiroptera can be made.

In general, once **TCSA, J**, and **I** are corrected for limb element length the distinctness of dermopterans from other gliding mammals, and the distinctness of bats from all other mammals seems to disappear (Figs 6.17 - 6.28). This suggests that the relative increase in cross sectional properties (**TCSA, J**, $\mathbf{I_{ML}}$, and $\mathbf{I_{AP}}$) in bats and dermopterans in relation to their body size may be a result of their having greatly elongate limb bones.

Scapular characters seem to further link taxa with large amounts of underbranch suspension in their locomotor repertoires. It is not the relative

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length of the dorsal scapular spine that is most important here, but the relative length of the vertebral border of the scapula (Fig. 6.30). It seems that the bats, dermopterans, Bradypus and Cyclopes all have longer vertebral borders of the scapula. In the bats this is probably associated with the flight stroke since the muscles that attach here (Altenbach, 1979; Vaughan, 1959, 1970) aid in and stabilizing the scapula during the flight stroke (Altenbach, 1979). In the other taxa mentioned above the lengthening of the vertebral border of the scapula may also be associated with the enhancement of the muscles that attach here (M. levator scapulae, M. rhomboides, M. serratus anterior, M. supraspinatus, M. infraspinatus, and M. spinodeltoides). However, in underbranch suspensory taxa the enhancement of these muscles may be related to supporting the animal. If the pectoralis muscles and serratus anterior cradle the thorax in quadrupedal mammals, then the muscles mentioned above may perform the same role in underbranch suspensory taxa. The fact that Choloepus does not show such elongation is problematic, but may reflect its ancestry from megalonychid ground sloths.

Bats have relatively long first digits (**RD1** = (Length of digit 1 / STL)*100) and so do dermopterans. The extreme elongation in **RD1** in megachiropterans may reflect the attachment of the propatagium further distally on this digit than in microchiropterans. Stafford and Thorington (1998) (see also Chapter 7) suggested that microchiropterans have a more mobile first digit than megachiropterans, based on the morphology of the carpals, and that the trapezium-scaphocentralolunate locking mechanism was

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related to stabilizing the first digit during underbranch suspension. Alternately it was suggested that this locking mechanism stabilized the second digit during flight. The higher **RD1** values in megachiropterans, coupled with the more distal extent of the propatagium on this digit, tend to support the first hypothesis. The less extensive elongation of the first digit in microchiropterans may be related to the compressive loading of this digit during quadrupedal locomotion. Contrary to popular opinion, some microchiropterans use quadrupedal locomotion quite extensively. Dermopteran **RD1** values are not nearly as high as those of the bats, but they are higher than most other nonchiropteran mammals. The dermopteran propatagium extends to the distal interphalangeal joint and this may explain the elongation of the thumb in dermopterans. However, the lorises also have relatively long thumbs, but do not possess a patagium. First digit elongation in lorises is clearly related to their unique mode of power grasping (Cartmill and Milton, 1977; Ishida et al., 1992). Although it seems unlikely that dermopterans engage in any power grasping, the extreme elongation of the first digit seen in bats may have resulted from releasing the first digit from the constraints imposed by use in non-aerial positional behaviors other than suspension. Dermopterans do engage the claw of the first digit when they are clinging to vertical supports (pers. obs.).

Relative length of the second digit (**RD2** = (Length of Digit 2 / STL)*100) shows a different pattern from the pattern that is common to digits three through five (**RD3, RD4, RD5**). For **RD3-RD5** bats cluster well above all

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other mammals, while sloths and dermopterans cluster above all non-chiropteran taxa. The differences in relative digit length among bats are intriguing and may be aerodynamically significant. Megachiropterans have a short **RD2** and long **RD3-RD5** while microchiropterans have long **RD2**s and short **RD3-RD5**s. Norberg (1969, 1970, 1972a, 1972b) discussed the importance of rigidity in the leading edge of the wing to chiropterans, but did not investigate inter-subordinal differences. It has been suggested (Stafford and Thorington, 1998; Chapter 7) that the trapezium-scaphocentralolunate locking mechanism of megachiropterans lends greater rigidity to the leading edge of the wing of megachiropterans and that this may be related to soaring behavior in megachiropterans. A shorter **RD2** fits well with this hypothesis. The lack of this locking mechanism in microchiropterans was suggested to be associated with more acrobatic flight in microchiropterans, but it is difficult to see how relatively longer **RD2** and shorter **RD3**s relate to maneuverability. However, others (Norberg, 1985, 1990; Norberg and Rayner, 1987, Vaughan, 1959) have noted the importance of high aspect ratio wings for many microchiropterans. Increasing **RD2** would increase the wing-span while reducing **RD3-RD5** would reduce the cord of the wing, thus producing high aspect ratio wings (see Chapter 10). A much larger study of chiropterans is needed to test this hypothesis.

Surprisingly, the dermopterans consistently have higher values for **RD2-RD4** than do the sloths (**RD2**, $t = 6.436$, $df = 9$, $p < 0.001$; **RD3**, $t = 8.651$, $df = 9$, $p < 0.001$; **RD4**, $t = 6.075$, $df = 7$, $p = 0.001$). It is

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tempting to ascribe the elongation of the dermopteran digits over the sloths to aerodynamic selective forces. However, dermopterans have adaptations for locking the phalanges in a flexed position (Simmons and Quinn, 1994),as do bats (Quinn and Baumel, 1993), and appear to use a means of suspension similar to that described as hook-hanging for the sloths (Mendel, 1985; Miller 1935). These factors suggest that aerodynamic factors can not be the only relevant considerations when evaluating dermopteran phalangeal morphology. The mechanical advantage offered to M. flexor digitorum profundus through an increase in the lever arm of the locking mechanism may be an important factor in digital elongation. Again we see that aerodynamic adaptations co-opt and are written over what appears to be suspensory adaptations.

The patterns of metacarpal elongation generally follow those of relative digit length. There are two exceptions however. Acrobates and Tupaia join the sloths, dermopterans, and lorids in having relatively long first metacarpals as compared to all other non-chiropteran mammals. Were it not for the inclusion of the dermopterans in this group it would be tempting to ascribe elongation of the first metacarpal to grasping relatively large supports with highly abducted digits. Certainly, metacarpal elongation in general does not seem associated with suspensory behaviors because sloths do not seem to have relatively long metacarpals. The fact that Sciurus also joins the group of animals with long metacarpals for metacarpals 2-5, also seems to contradict any grasping associations.

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The relative length of the proximal phalanges ((Proximal phalanx length / STL)*100) was also evaluated as part of this study, but is not presented here in detail. The only result that this analysis produced was that the xenarthrans have relatively shorter proximal phalanges than any of the other taxa studied here. Interestingly, the same was true for the study of the relative lengths of the intermediate phalanges ((Intermediate phalanx length / STL)*100). Bats had very long intermediate phalanges. Dermopterans and sloths had intermediate phalanges of very similar relative lengths, but longer than non-chiropteran mammals. The most surprising point here was the fact that sloths did not show relatively elongate intermediate phalanges compared to the dermopterans.

Intermediate phalangeal indices ((intermediate phalanx length / proximal phalanx length)*100) show a different picture. In this analysis the xenarthrans, not the bats, ended up being removed from the analysis because they were always the group with the highest values, and these values were quite disproportionate to the other values in the study (Figs 8.11-8.14), creating a huge amount of variability in the data set. Here, dermopterans have consistently higher values than all non-xenarthran mammals. Bats often cluster with the dermopterans above all the other non-xenarthran mammals, but they never fall far above the dermopterans. Apparently, even though the bats have greatly elongated their fingers they have not disproportionately elongated the intermediate phalanges compared to dermopterans. The degree of intermediate phalanx elongation seen in

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dermopterans *and bats* is similar to that reported for Phenacolemur simonsi by Beard (1989, 1990) [i.e., (intermediate phalanx / proximal phalanx)*100 = 131-133). However, the values reported by Beard (1989, 1990) for Ignacius graybullianus (105) fall within the lower range of values for bats and are well outside the range for dermopterans.

It is difficult to say what this means with any degree of certainty. The reduction of the proximal phalanx in sloths gives them their extremely high interphalangeal indices, yet sloths do not have relatively longer intermediate phalanges, in relation to body size, than dermopterans. Bats, on the other hand, have relatively longer intermediate phalanges, in relation to body size, than dermopterans and sloths, but do not have higher intermediate phalangeal indices than dermopterans. It seems likely that metacarpal and phalangeal elongation may be related to suspensory slow climbing. The sloths likely derived from more terrestrial lineages that had already undergone proximal phalanx reduction as a digging adaptation. Constrained by this, extremely enlarged claws, and reduced medial and lateral digits, the sloth developed elongate intermediate phalanges. The fact that grasping may have never been a option in the sloth lineage may also have released the intermediate phalanges from constraints imposed by grasping. Similarly, the removal of the manus from the non-aerial locomotor system in bats may have released their metacarpals and phalanges from constraints that are still acting on dermopterans. If this is the case, and elongation of the intermediate phalanges in relation to body size to the degree seen in

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dermopterans and sloths is related to suspension, then there is little reason to use intermediate phalangeal elongation as a character that indicates either an interdigital patagium, or gliding.

That extreme digital and metacarpal elongation in bats is associated with the demands of powered flight is not debatable; it is as close as it comes to a proof-like corroboration of causal correlation in ecological morphology. The role of the chiropatagium in thrust production is well documented (Norberg, 1970, 1976, 1985, 1986, 1990; Norberg and Rayner, 1987; Rayner, 1988; Scholey, 1986). However, analysis of the attainment of this condition has been hampered by a lack of appropriate functional-adaptive hypotheses and their tests. From the data presented above it seems likely that metacarpal and phalangeal elongation in mammals may be related to underbranch suspension and slow climbing behavior. A gliding mammal with these manual components already elongated, due to the demands of such positional behaviors, may have an opportunity to incorporate the hands into the gliding system that is not available to taxa with much shorter hands. The role of such wing tip extensions in enhancing performance, and in maintaining stability and control is described in chapters 10 and 11. It is possible that the demands of underbranch quadrumanous suspension mediate against further manual elongation in dermopterans. However, if the forelimbs were released from their role in non-aerial positional behaviors this could allow for further elongation of the manus in response to aerodynamic forces.

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This leads to a hypothesis for the evolution of powered flight in chiropterans. It is obvious that the incorporation of the manus into the flight system, associated with performance, stability, and control (further discussed in chapters 10 and 11), was a key factor in the evolution of powered flight in bats. However, another key component in this hypothesis is the removal of the manus, by the lineage antecedent to bats, from the constraints of the non-aerial positional system in that evolutionary process. This would have allowed further elongation of the manus, and may partially explain the importance of hindlimb suspension in chiropterans. Of course, bats have not completely removed the manus from the non-aerial positional system, but they have greatly reduced the number of manual elements involved in it. In fact, among chiropterans it is generally only the pollex that is involved in non-aerial positional behaviors.

The extreme hindlimb elongation seen in microchiropterans and dermopterans may be related to the extensive uropatagia in these taxa. Megachiropterans generally have less extensive uropatagia that are often not continuous between the hindlimbs. However, non-dermopteran gliding taxa with uropatagia (i.e., anomalurids and Petaurista) do not have relatively longer hindlimbs than gliding taxa with restricted or no uropatagia. Similarly, gliding rodents with extensive uropatagia that reach close to the knee (Anomalurus, Petaurista, Aeromys) do not have relatively longer femora than the pteromyines without such uropatagia. Also, Acrobates with a very restricted gliding membrane has very long legs. However, limb elongation in

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Acrobates in general may have less to do with its patagium than with its small size (see Cartmill, 1985; Thorington and Thorington, 1989). It seems more likely that longer hindlimbs in gliding taxa in general is related to increasing overall patagial surface area or to increasing aspect ratios (see Chapter 10). A third possibility is that elongate hindlimbs in gliding taxa relate to the need to achieve the highest launching velocities possible. This would allow animals to decrease their gliding angles and thereby increase gliding distances (again see Chapter 10). A comparison of leaping velocities in gliding and non-gliding taxa would serve to clarify the situation here.

The three taxa that appear to have relatively long femora are Acrobates, the dermopterans, and the microchiropterans. The long femora of Acrobates may be related to it's relatively small size and the use of relatively large supports. Alternately, the long femora in all three taxa could be related to the extent of their patagia. Dermopterans and microchiropterans have extensive uropatagia. In dermopterans the uropatagia extends to the tip of the tail and this is often also the case in microchiropterans. In Acrobates the patagium appears to extend only into the area of the knee and elongation of the femur may be the only means of increasing patagial surface area for this animal. Again, however, support for this hypothesis is not found among the flying squirrels. Although Petaurista does have the relatively longest femora of all the flying squirrels, and an extensive uropatagium, these differences are not significant.

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Interesting exceptions to the relative constancy of the femoral and tibial data are *Mysticina tuberculata* the New Zealand short-tailed bat and *Desmodus rotundus* the vampire bat. In bivariate plots of femoral cross-sectional area, polar moment, and second moments of area (Figs 12.1 - 12.4) these taxa consistently fall above the cluster of points for all other mammals. Both of these taxa, especially *Mysticina*, may be more extensively terrestrial than other chiropterans. The highly specialized chiropteran hindlimb may be subjected very different loading and stresses when moving terrestrially and this may explain the position of these taxa.

The patterns for $\mathbf{I}_{\mathrm{AP,Femur(STL)}}$, and $\mathbf{I}_{\mathrm{AP,Tibia(STL)}}$ are interesting. In both cases the arboreal taxa have significantly higher values than do the gliding taxa ($\mathbf{I}_{\mathrm{AP,Femur(STL)}}$: rodents, $t=13.74$, $df = 53$, $p<0.0005$; marsupials, $t=11.69$, $df=19$, $p < 0.0005$. $\mathbf{I}_{\mathrm{AP,Tibia(STL)}}$: rodents, $t = 9.33$, $df = 52$, $p < 0.0005$; marsupials, $t=17.85$, $df=20$, $p<0.0005$). There are no significant differences among dermopterans ($t=3.25$, $df=15$, $p=0.0054$). These data may indicate that higher stresses are not generated in the hindlimb of gliding mammals during launching. This may be compensated for by the relatively long hindlimbs of the gliders since you can reach high velocity by applying acceleration over a longer distance. So gliding mammals may not be able to leap stronger, but they may still be able to achieve relatively high launching velocities as a result of their elongate hindlimbs.

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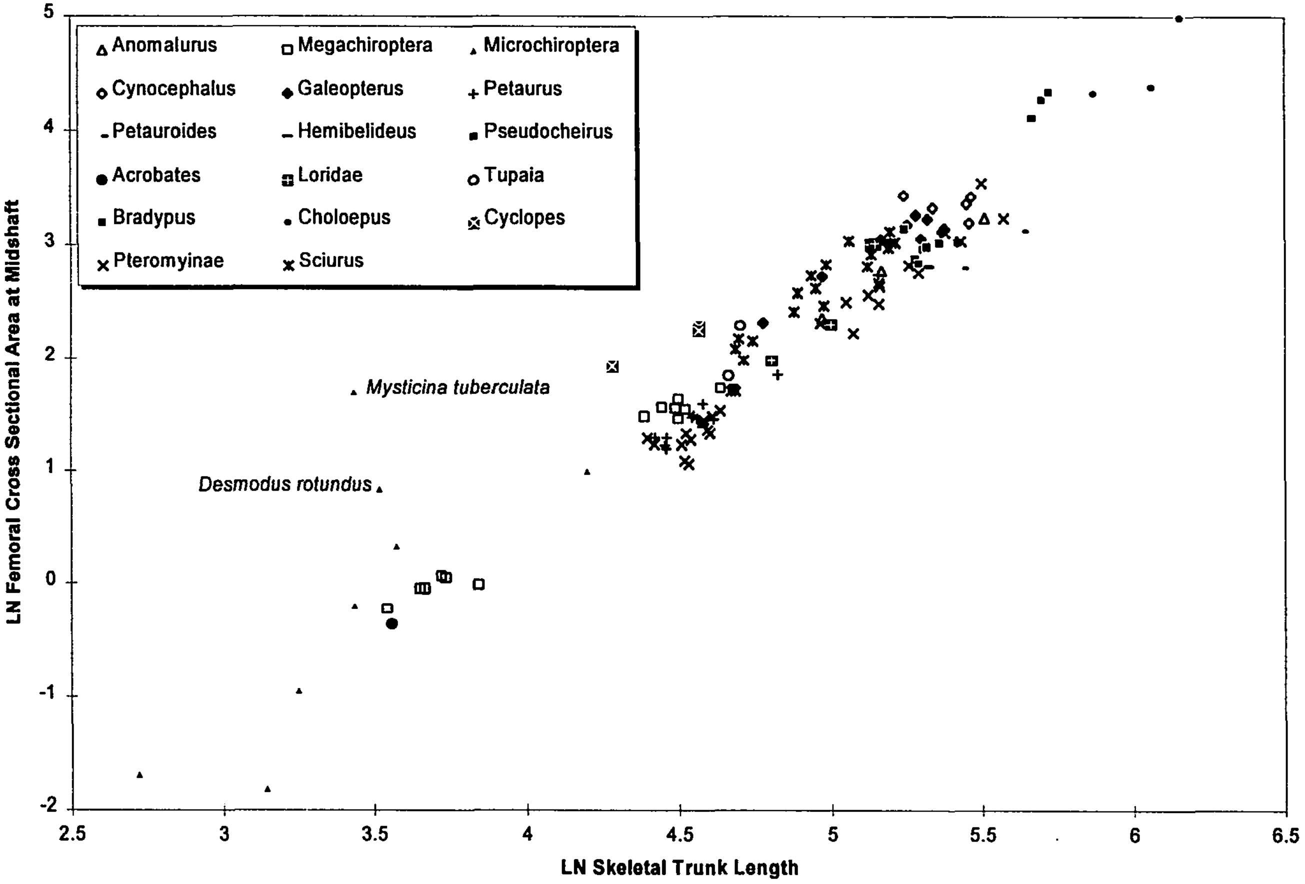

Figure 12.1: Femoral cross-sectional area in some mammals. Note the positions of D. rotundus and M. tuberculata.

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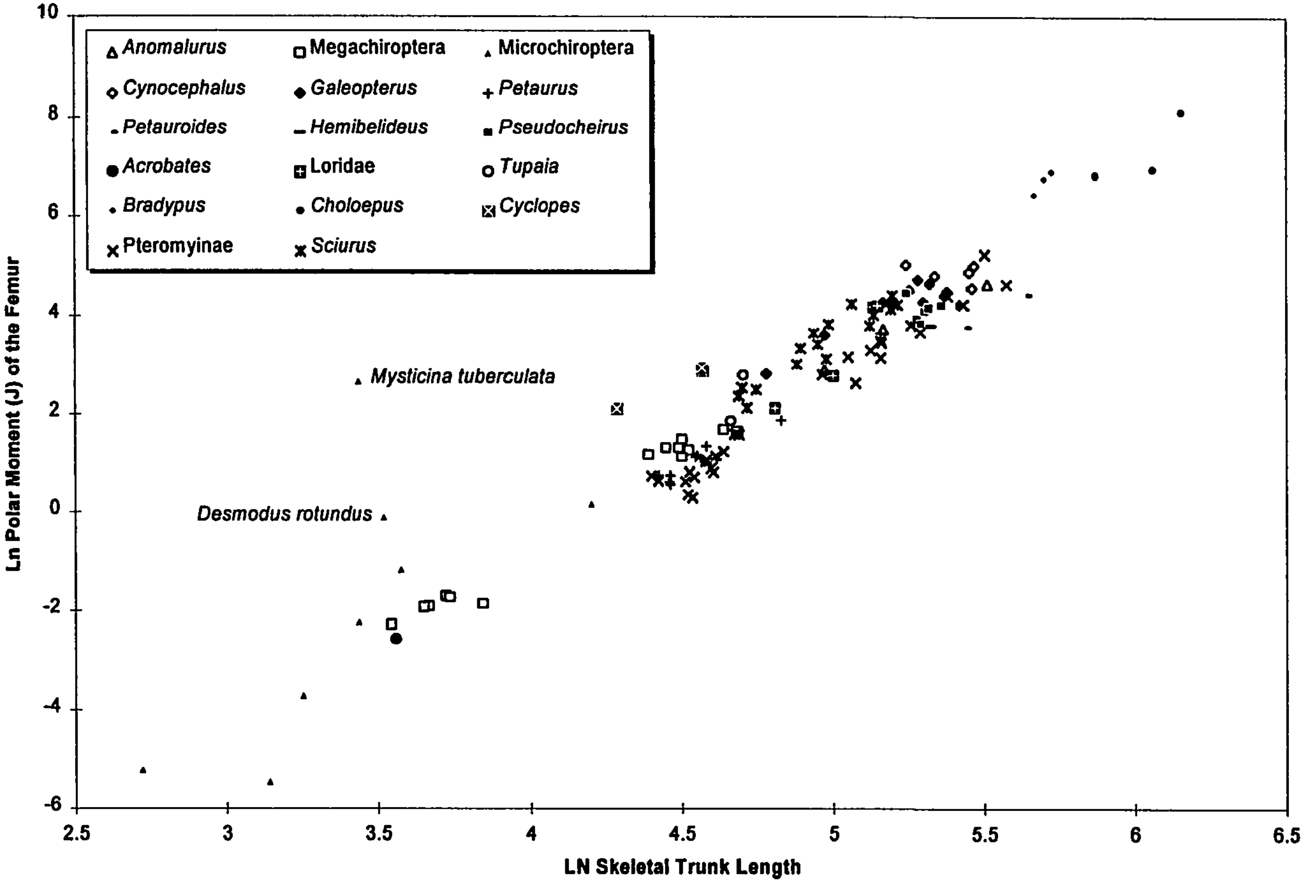

Figure 12.2: Polar moments of the femur in some mammals. Note the positions of D. rotundus and M. tuberculata.

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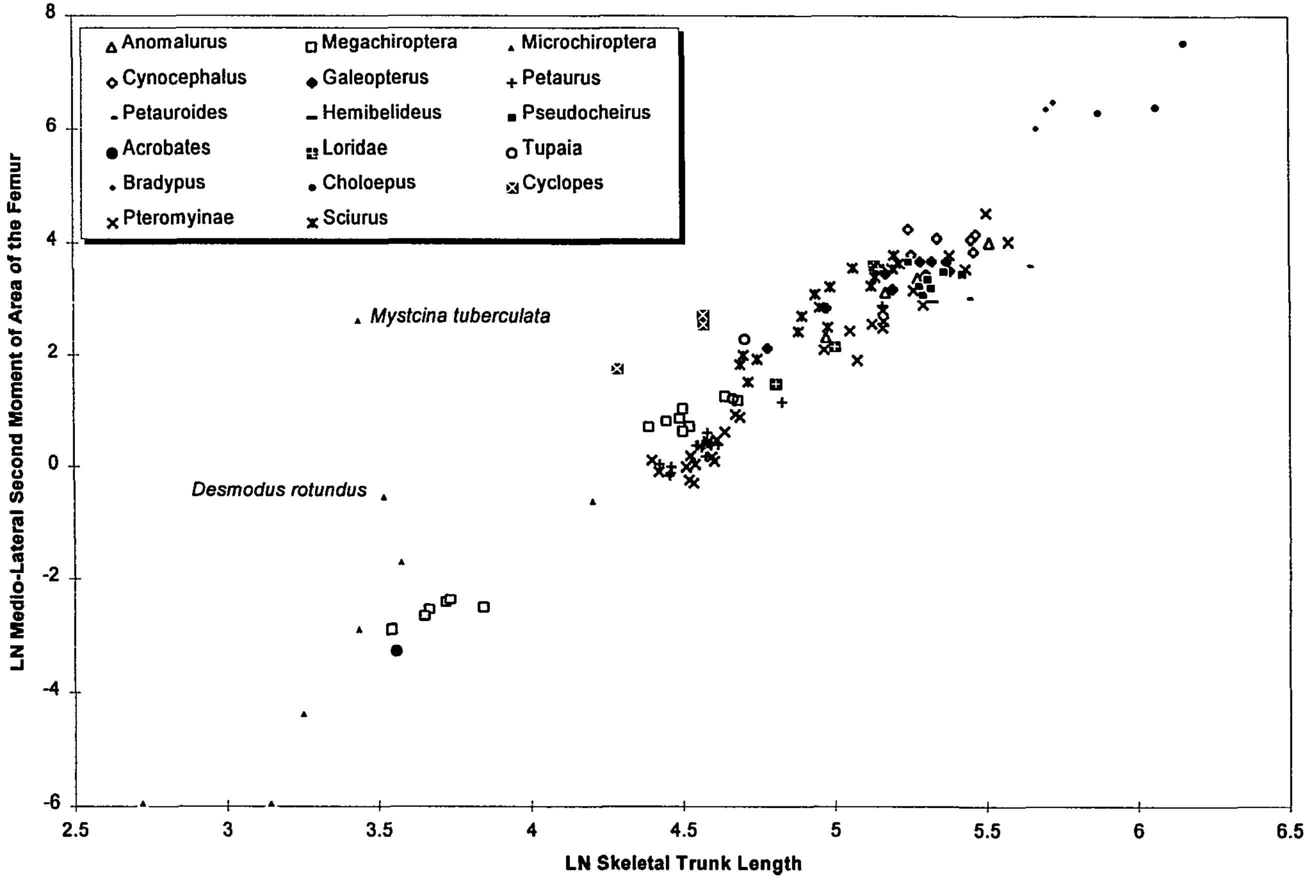

Figure 12.3: Medio-lateral bending moments of the femur in some mammals. Note the positions of D. rotundus and M. tuberculata.

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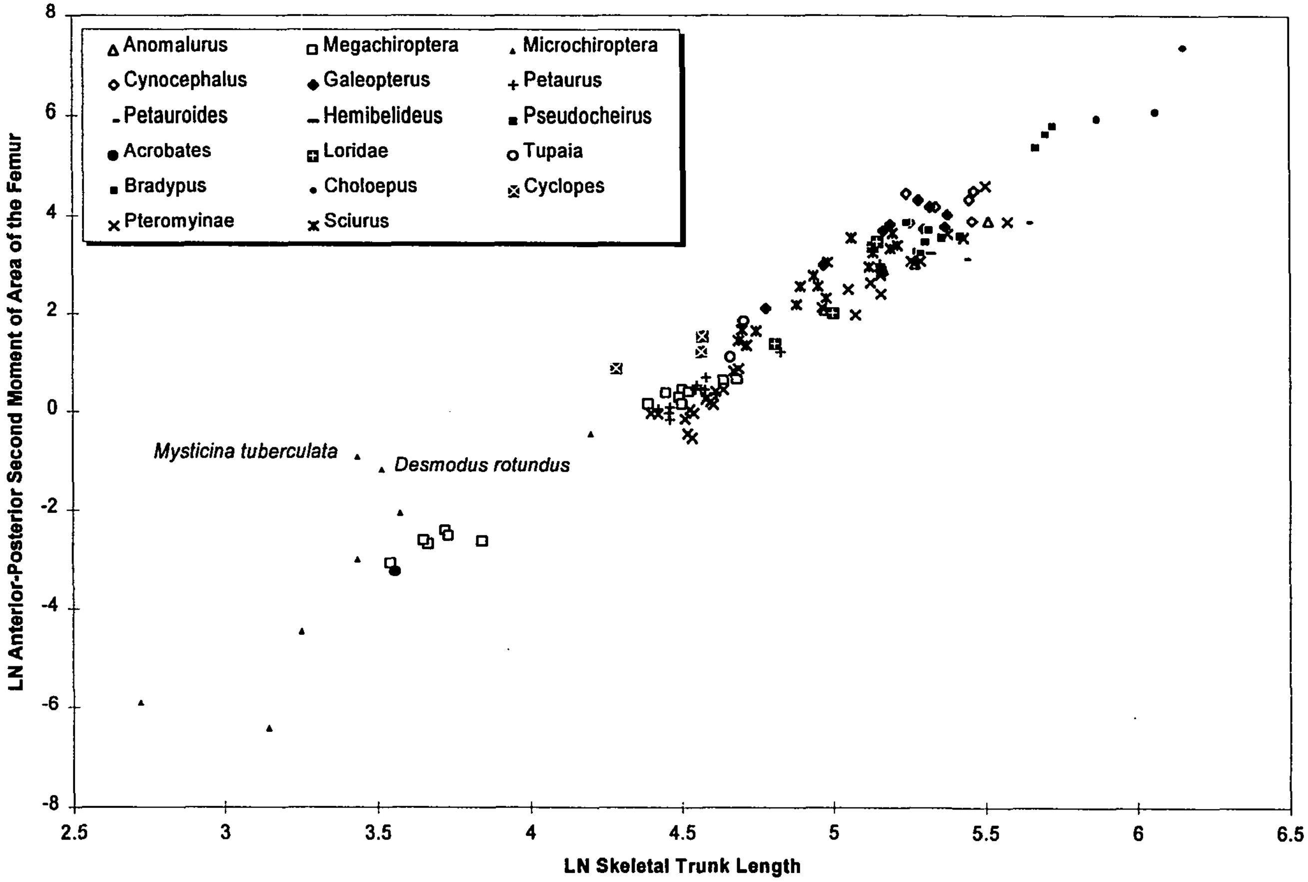

Figure 12.4: Anterior-posterior bending moments of the femur in some mammals. Note the positions of D. rotundus and M. tuberculata.

Many mammalian gliders show features that could function to reduce induced drag and enhance static stability. Reducing induced drag would increase gliding distance, increasing static stability would decrease the chances of a crash, and both of these factors have obvious benefits for gliding mammals. The selective pressures involved in the development of these mechanisms may have also included the benefits of reducing induced drag at high angles of attack. This last point supports the contention that what is happening in the terminal phase of the glide holds important information about the adaptations of gliding mammals. Mechanisms for reducing induced drag and enhancing static stability therefore seem to be common, although not universal, among gliding mammals. In the scaly-tailed "flying squirrels" the olecranon cartilages may function in the same manner as the wing tips of colugos, flying squirrels, and lesser gliding marsupials. However, it is unknown whether or not anomalurids glide with the olecranon cartilages dorsiflexed. Conversely, Acrobates appears to possess a very restricted gliding membrane and no structures that might reduce induced drag or enhance static stability in these animals.

In the dermopterans it is the dactylopatagium that is involved in the factors mentioned above. The dermopteran dactylopatagium is very similar to the chiropteran dactylopatagium and has long been seen as a character linking dermopterans and chiropterans. The transition from a gliding form with a dactylopatagium fulfilling the roles mentioned above to a bat-like animal where the chiropatagium produces thrust must have been a critical

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one in the acquisition of powered flight. Certainly the ventral rotation of the propatagium and manus during the flaring portion of the glide is similar to the ventral pronation of the forelimb that occurs during the down-beat of the chiropteran wing. The elbow features noted by Szalay and Lucas (1993, 1996) could certainly be adaptations to resisting torsional stresses at the elbow that are being incurred at the manus. In such a light, the dorsal locking mechanisms in the dermopteran and chiropteran manus (Chapter 7), fusion of the scaphoid, centrale, and lunate, and fusion of the radius and ulna distally all indicate resistance to high torsional forces in the antebrachium of dermopterans and chiropterans.

Hypotheses about the evolution of gliding in dermopterans.—Gliding flight would have led to some limited degree of limb elongation in a volitantian ancestor. However, adaptation to suspensory positional behaviors would have led along the same road. Which of these two steps preceded the other in the evolution of the volitantians is impossible to determine at present. What is plainly evident is that at some time the volitantians became largely suspensory taxa. This could have led to limb elongation that facilitated the development or the enhancement of gliding. Increases in limb length would lead to higher aspect ratios, higher lift to drag ratios, shallower gliding angles and increased gliding distances, lower wing loading, slower stalling speeds, and greater maneuverability. All of these factors would be beneficial to any gliding mammal.

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Given the similarities between dermopterans and Bradypus, and that both are arboreal quadrumanous suspensory folivores, one must contemplate the evolution of the Volitantia from such a form. This does not require the ancestral chiropteran to have been folivorous because such a hypothesis has extreme problems from a physiological and metabolic perspective. Such consideration also does not require that the extant dermopterans be "living fossils" or even very close morphologically to the volitantian ancestor. It simply requires that the ancestral volitantian possessed suspensory locomotion, a gliding membrane similar to the shared aspects of the living volitantians, and some degree of folivory in its diet. We know that Cynocephalus seems to prefer young leaves (Wischusen, 1992; pers. obs.) and that their dentition is not drastically altered from a basic tribosphenic plan (Chapter 4). The ancestral volitantian lineage likely already possessed a specialized shearing dentition and could easily have included a wide range of food items in its diet. The early split between dermopterans and chiropterans may have been the result of resource partitioning where the dermopteran lineage began to rely more and more on young leaves while the chiropteran lineage began to rely more and more on fruits and insects. Both dietary strategies would have selected for maintaining the enhanced ectolophs in dermopterans and microchiropterans, and the demands of insectivory may help explain the transition from gliding to powered flight (Hill and Smith, 1984, Smith, 1977). Subsequent competition among stem chiropterans could then have lead to further resource partitioning with the

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microchiropteran lineage continuing to specialize on insects while the megachiropteran lineage began to specialize on fruits. Such a historical-narrative explanation is capable of accounting for many of the similarities between dermopterans and bats, and is also able to account for differences among dermopterans.

One factor is certain, dermopterans appear to be very different from the other gliding mammals. Also, in many of the ways that dermopterans differ from other gliders, they seem similar to bats. These factors can be considered as gliding adaptations and do not necessarily falsify the hypothesis that that the similarities seen between bats and dermopterans are convergences. For example, all gliding mammals seem to have gracile and elongate limbs as compared to their closest non-gliding relatives. However, dermopteran limbs are very long, even for a gliding mammal, and in some of their aerodynamic properties dermopterans are similar to bats (Fig. 10.2).

The general picture of dermopteran gliding that can be inferred (pending corroborating field studies) is of an animal that is gliding slower than other gliding mammals of its size, and gliding at shallower glide angles. Yet it is also a picture of an animal that is more agile and maneuverable than other gliding mammals. In this sense, dermopterans are very like the models that some authors have proposed for a pre-flapping chiropteran.

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Appendix A: Craniodental Measurements

Genus	Species	Museum #	Sex	Age	Country
Cynocephalus	volans	USNM 536048	M	A	Philippines
Cynocephalus	volans	USNM 536049	F	A	Philippines
Cynocephalus	volans	USNM 123422	M	A	Philippines
Cynocephalus	volans	FMNH 56422	F	A	Philippines
Cynocephalus	volans	USNM 578084	F	A	Philippines
Cynocephalus	volans	USNM 462160	M	A	Philippines
Cynocephalus	volans	USNM 462158	M	A	Philippines
Cynocephalus	volans	USNM 144656	F	A	Philippines
Cynocephalus	volans	USNM 144658	M	A	Philippines
Cynocephalus	volans	FMNH 61032	M	A	Philippines
Cynocephalus	volans	FMNH 62067	M	A	Philippines
Cynocephalus	volans	USNM 536049	F	A	Philippines
Galeopterus	peninsulae	USNM 86786	F	A	Siam
Galeopterus	peninsulae	USNM 253412	F	A	Siam
Galeopterus	peninsulae	USNM 258872	M	A	Siam
Galeopterus	peninsulae	USNM 258874	M	A	Siam
Galeopterus	variegatus	USNM 311279	M	A	Malaysia
Galeopterus	aoris	USNM 122427	M	A	Malaysia
Galeopterus	temminckii	USNM 115605	F	A	Rhio Archipelago
Galeopterus	temminckii	USNM 49640	F	A	Rhio Archipelago
Galeopterus	chombolensis	USNM 144372	M	A	Rhio Archipelago
Galeopterus	chombolensis	USNM 144373	F	A	Rhio Archipelago
Galeopterus	temminckii	USNM 143325	F	A	Sumatra
Galeopterus	temminckii	USNM 49693	F	A	Sumatra
Galeopterus	saturatus	USNM 121747	M	A	Batu Islands
Galeopterus	saturatus	USNM 122766	?	A	Batu Islands
Galeopterus	gracilis	USNM 104600	M	A	Natuna Islands
Galeopterus	borneanus	USNM 176431	M	A	Borneo
Galeopterus	borneanus	USNM 197202	F	A	Borneo

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Site	Skull Length	Basal Length	Postorbital Constriction	Rostral Breadth	Palatal Length	Breadth of the Skull at the Glenoid Fossa
Mindanao	69.50	62.60	16.65	21.95	30.25	40.40
Mindanao	74.99	69.57	17.18	24.71	33.88	44.77
Mindanao	69.46	62.81	14.97	21.49	31.42	38.08
Mindanao	71.74	64.71	18.74	23.71	31.08	39.64
Leyte	66.80	60.57	15.03	20.24	29.56	36.69
Dinegat	68.56	62.13	18.16	23.34	32.43	40.28
Dinegat	67.04	60.07	16.51	21.69	29.49	36.16
Basilan	68.10	62.41	16.93	22.14	31.12	40.51
Basilan	66.90	60.63	15.14	21.73	30.94	40.20
Davao	72.59	66.32	17.60	24.52	32.22	39.41
Davao	70.14	64.16	18.02	21.64	31.25	39.84
Mindanao	74.41	69.24	17.61	24.78	33.89	44.41
Trong	71.11	65.44	22.13	21.72	33.16	39.06
Ban Kiriwong	72.73	67.28	21.13	23.11	34.66	38.28
Kao Chong Trang	71.23	65.54	22.45	21.62	33.94	39.26
Kao Chong Trang	69.91	63.86	23.23	20.58	33.54	40.11
Langkawi Island	58.14	53.00	20.67	17.31	27.64	31.07
Pulo Aor	59.10	53.54	19.52	16.65	27.17	32.72
Pulo Bintang	74.53	67.98	23.14	20.79	35.68	40.09
Pulo Bintang	72.78	67.27	21.34	20.28	34.25	40.50
Pulo Jombol	64.50	59.50	21.24	18.54	30.24	34.89
Pulo Jombol	67.34	62.11	20.39	20.37	31.39	34.41
Pulo Rupat	73.98	67.78	21.48	20.35	35.94	37.66
Pulo Kundur	71.20	65.17	20.77	20.57	34.92	38.07
Tana Bala	72.41	65.46	23.35	23.02	33.54	38.97
Pulo Pinie	70.77	65.31	22.61	20.49	33.26	37.33
Sirhassen	61.32	56.19	19.02	17.61	29.00	32.06
Talisan Mountain	67.87	62.62	21.24	18.53	32.44	35.89
Labuan Klambu	72.09	66.26	22.06	20.10	33.69	37.24

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Height of the Coronoid Process of the Mandible	Mesio-Distal Width of I2	Buccal-Lingual Height of I2	I2 Area	Mesio-Distal Width of I3	Buccal-Lingual Height of I3	I3 Area	Mesio-Distal Width of C1 at Base
5.67	1.59	2.20	3.49	-	-	-	6.93
7.25	2.06	2.21	4.54	6.49	6.31	40.95	6.10
4.67	1.67	1.82	3.04	5.41	6.11	33.02	6.02
5.75	1.61	1.79	2.88	6.10	6.22	37.94	6.34
4.86	1.45	1.62	2.34	5.48	5.64	30.88	6.26
5.26	1.60	1.67	2.66	5.72	6.07	34.66	6.23
4.73	1.41	1.43	2.02	5.83	5.64	32.85	6.26
4.70	1.62	1.69	2.73	5.86	6.33	37.06	6.68
5.66	1.34	1.98	2.65	5.69	5.47	31.10	6.17
4.76	2.12	2.28	4.81	5.53	6.32	34.92	6.47
6.23	1.61	2.10	3.37	5.49	5.97	32.72	5.85
7.36	1.96	2.24	4.40	6.33	6.00	37.96	7.22
4.71	2.86	1.84	5.25	5.39	3.31	17.81	6.24
4.19	3.10	2.10	6.50	5.98	4.00	23.89	6.49
3.76	2.66	1.82	4.83	5.45	3.31	18.04	5.43
3.78	2.47	1.71	4.21	6.09	2.96	18.00	7.12
2.48	2.33	1.62	3.76	3.95	2.82	11.14	4.67
2.84	2.21	2.09	4.62	-	-	-	6.39
4.03	2.80	2.10	5.88	5.39	3.49	18.81	6.30
3.86	2.68	2.00	5.35	4.89	3.30	16.12	6.28
4.49	2.65	1.85	4.90	4.46	3.42	15.23	5.88
4.26	2.58	1.60	4.13	4.94	3.04	15.02	5.67
4.06	2.88	1.84	5.28	5.25	3.39	17.75	6.14
2.78	2.78	2.08	5.78	4.94	3.22	15.93	6.33
3.84	3.18	2.37	7.54	5.67	3.76	21.30	6.61
4.24	2.70	1.73	4.66	4.74	3.19	15.10	5.67
2.15	2.73	2.00	5.47	4.94	3.02	14.92	5.88
4.96	2.69	2.29	6.16	5.43	3.22	17.50	6.65
4.47	2.51	1.76	4.41	6.49	2.92	18.94	6.94

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Height of C1	C1 Area	Number of Tines on C1	Length of Molar Toothrow (M1-M3)	Length of Molariform Toothrow (P4-M3)	Lever Arm of Masseter Muscle	Mesio-Distal Length of P3	Buccal-Lingual Width of P3
4.08	14.11	0	11.90	16.12	26.86	5.78	4.57
3.08	9.39	0	12.14	16.96	29.35	6.42	3.92
4.67	14.04	0	11.78	16.61	26.92	5.81	3.52
4.47	14.15	0	11.89	16.40	27.65	5.68	3.19
5.01	15.67	0	11.66	16.01	25.51	5.15	3.52
5.08	15.82	0	11.56	16.17	26.15	5.65	3.37
4.75	14.87	0	10.82	15.29	25.72	6.14	3.29
5.19	17.33	0	11.71	16.34	26.80	5.98	3.40
-	-	0	10.95	15.40	26.41	5.69	3.40
4.84	15.63	0	11.27	15.91	27.76	5.68	3.29
5.30	15.47	0	11.56	15.90	26.50	5.88	3.38
4.49	16.22	0	12.14	16.97	30.17	6.78	3.43
3.02	9.43	6.50	10.37	14.20	24.58	5.06	2.78
3.42	11.08	6.50	10.65	14.80	24.42	5.82	3.85
3.53	9.56	5.50	10.15	13.88	23.97	5.23	2.97
3.42	12.16	5.00	9.66	15.21	23.88	5.22	3.54
2.55	5.95	5.00	8.15	11.72	20.19	4.37	2.13
2.83	9.03	6.50	9.92	13.36	21.30	4.96	2.57
3.02	9.51	6.00	10.34	14.68	24.80	5.34	2.84
2.75	8.64	7.00	9.94	14.21	24.37	4.81	2.74
2.78	8.17	6.00	9.33	13.50	23.42	4.96	2.67
2.20	6.25	6.00	9.67	13.83	23.58	3.64	3.83
2.78	8.53	6.50	9.67	13.72	24.34	4.91	2.96
3.10	9.81	6.50	10.20	14.12	24.58	5.02	2.24
3.59	11.88	-	11.63	16.25	25.92	5.39	2.61
2.81	7.95	6.00	10.11	14.00	24.74	4.85	2.48
2.78	8.16	6.00	8.33	11.90	20.58	5.06	2.29
2.90	9.64	5.50	10.00	13.59	11.18	4.98	2.33
2.94	10.20	6.00	9.84	13.55	11.78	5.35	2.37

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P3 Basal Area	Mesio-Distal Length of P4	Buccal-Lingual Width of P4	P4 Basal Area	Mesio-Distal Length of M1	Buccal-Lingual Width of M1	M1 Basal Area	Mesio-Distal Length of M2
26.39	4.40	5.32	11.70	4.63	5.13	11.85	4.15
25.13	5.09	5.30	13.48	4.56	5.44	12.38	4.39
20.45	4.78	4.65	11.10	4.49	5.36	12.03	4.14
18.12	4.63	4.50	10.41	3.99	4.95	9.87	3.85
18.08	4.47	4.79	10.71	3.92	5.17	10.13	3.81
19.01	4.72	4.87	11.47	4.48	5.30	11.86	4.05
20.18	4.69	4.88	11.43	4.40	5.27	11.58	3.83
20.30	4.76	4.82	11.47	4.26	5.12	10.91	4.13
19.32	4.59	4.68	10.73	3.88	5.19	10.07	4.00
18.66	4.71	4.70	11.07	4.42	5.13	11.32	4.25
19.87	4.41	4.77	10.51	4.32	5.01	10.80	3.95
23.23	5.18	5.39	13.96	4.65	5.43	12.63	4.45
14.05	3.27	3.55	5.80	3.22	4.00	6.45	3.14
22.38	3.81	4.28	8.13	3.25	4.21	6.83	3.26
15.49	3.57	4.04	7.20	3.44	3.85	6.61	3.34
18.48	3.86	4.21	8.13	3.04	4.10	6.23	3.04
9.31	3.11	3.32	5.15	2.56	3.41	4.36	2.51
12.73	3.35	3.83	6.41	3.00	3.89	5.83	2.91
15.15	3.83	3.93	7.51	3.21	4.03	6.46	3.12
13.17	3.42	3.92	6.70	2.97	4.17	6.18	3.00
13.22	4.00	4.00	8.00	3.08	3.67	5.65	3.13
13.90	-	-	-	3.10	3.71	5.76	3.10
14.51	3.52	4.06	7.14	2.82	4.01	5.65	2.75
11.27	3.55	3.88	6.88	3.35	4.00	6.69	3.27
14.07	4.37	4.41	9.63	3.71	4.45	8.26	3.63
12.02	3.76	4.07	7.64	3.09	4.04	6.22	3.26
11.57	3.06	3.51	5.37	2.73	3.47	4.74	2.73
11.59	3.59	3.63	6.52	3.27	3.82	6.23	3.18
12.66	3.31	3.96	6.54	3.18	3.96	6.30	3.06

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Buccal-Lingual Width of M2	M2 Basal Area	Mesio-Distal Length of M3	Buccal-Lingual Width of M3	M3 Basal Area	Area of M1 Anterior Stylar Shelf	Area of M1 Posterior Stylar Shelf	Depth of the Mandible Below m1
5.27	10.94	3.43	4.99	8.54	3.18	3.96	7.73
5.65	12.39	3.43	5.28	9.03	3.11	4.02	8.10
5.50	11.37	3.15	5.14	8.09	3.43	4.08	7.95
5.43	10.45	3.26	4.73	7.70	2.47	2.98	8.86
5.29	10.07	3.41	4.67	7.95	3.03	3.42	7.79
5.48	11.07	3.11	5.10	7.93	3.30	3.55	8.71
5.60	10.72	2.71	5.09	6.90	3.10	3.35	8.52
5.21	10.75	3.56	5.14	9.15	3.50	3.19	8.75
5.52	11.03	3.05	4.90	7.45	-	-	8.54
5.15	10.92	3.40	4.94	8.38	2.53	3.16	8.87
5.16	10.18	2.94	4.93	7.23	2.76	2.99	8.55
5.67	12.62	3.39	5.47	9.26	2.91	3.77	8.10
4.33	6.80	2.86	4.53	6.47	1.70	2.27	7.76
4.74	7.71	3.59	4.84	8.67	2.02	2.25	8.47
4.19	6.99	3.08	4.11	6.31	1.32	1.90	8.48
4.34	6.59	3.04	4.27	6.48	1.72	1.66	7.55
3.63	4.55	2.51	3.65	4.57	1.20	1.25	6.08
4.18	6.08	3.01	4.24	6.37	1.68	1.59	7.03
4.37	6.81	3.42	4.42	7.55	2.09	1.63	7.60
4.31	6.47	3.18	4.46	7.09	1.80	1.83	8.14
3.83	5.99	3.25	4.00	6.50	0.79	0.75	6.70
3.84	5.95	3.02	4.08	6.16	1.30	1.57	7.46
4.36	5.98	3.09	4.28	6.60	-	-	7.09
4.29	7.00	3.06	4.29	6.56	1.60	2.10	8.15
5.06	9.19	3.43	4.98	8.54	2.25	2.05	7.65
4.26	6.93	3.02	4.26	6.43	1.30	1.55	7.61
3.76	5.13	2.49	3.71	4.62	1.24	1.29	6.61
4.04	6.43	2.69	3.92	5.28	1.74	2.05	7.75
4.12	6.31	3.02	4.24	6.41	1.80	1.78	6.92

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Depth of the Mandible Below c1	Height of the Ascending Ramus of the Mandible	Length of Molar Toothrow (m1-m3)	Length of Molariform Toothrow (p4-m3)	Number of tines on i1	Mesio-Distal Width of i1	Buccal-Lingual Height of i1	i1 Area
7.54	21.22	13.15	18.37	9.00	2.85	3.46	9.84
9.26	23.81	13.58	19.08	9.00	2.79	3.44	9.60
7.90	19.77	13.67	18.82	10.00	2.76	3.27	9.01
8.50	22.39	12.05	17.03	9.00	2.48	2.92	7.23
7.86	20.92	12.63	17.80	9.00	2.34	2.80	6.54
8.36	20.84	13.32	18.49	10.00	2.39	3.15	7.50
8.37	19.25	12.54	17.40	9.00	2.38	3.16	7.52
8.01	20.70	13.26	18.27	9.00	2.47	3.06	7.54
7.93	19.09	12.16	17.51	10.00	2.43	3.38	8.21
9.51	21.20	12.27	17.31	-	-	-	-
8.24	20.49	13.02	18.30	10.00	3.01	3.16	9.48
8.25	22.14	13.56	19.28	9.00	2.73	3.31	9.04
7.23	29.21	12.16	16.75	7.00	2.57	3.14	8.08
7.35	22.01	11.63	16.47	7.00	2.72	3.68	9.99
6.90	21.21	10.99	15.75	7.00	2.60	3.29	8.55
6.35	18.26	10.85	15.50	6.50	2.43	3.14	7.61
6.06	14.57	9.56	13.37	-	-	-	-
6.23	15.22	10.11	14.04	6.00	2.40	2.93	7.02
6.09	18.49	11.57	16.63	7.00	2.70	3.16	8.53
7.26	19.03	11.18	15.82	6.00	2.30	2.76	6.35
6.24	15.68	10.25	15.17	8.00	2.83	2.75	7.79
6.55	16.78	10.67	15.27	8.00	2.69	3.10	8.36
6.38	19.51	10.90	15.45	9.00	2.43	2.97	7.22
7.12	17.82	11.55	16.83	7.50	2.61	2.78	7.25
7.27	19.30	12.33	17.67	7.00	3.10	2.90	8.99
6.96	19.36	10.99	15.62	8.00	2.47	3.03	7.47
6.28	15.18	9.76	13.80	7.00	2.16	2.82	6.09
6.59	17.32	11.39	15.92	7.00	2.57	2.86	7.35
6.75	18.02	11.06	15.51	8.00	2.73	2.73	7.48

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Number of tines on i2	Mesio-Distal Width of i2	Buccal-Lingual Height of i2	i2 Area	Number of tines on i3	Mesio-Distal Width of i3	Buccal-Lingual Height of i3	i3 Area
12.00	4.04	3.20	6.45	4.50	4.51	2.39	5.37
11.00	4.01	3.41	6.83	3.00	4.45	2.28	5.06
12.50	3.95	3.37	6.66	4.00	4.02	2.18	4.37
11.50	3.77	2.76	5.19	4.00	4.18	2.13	4.44
11.00	3.46	2.95	5.10	4.00	4.02	2.17	4.35
13.00	3.99	3.04	6.06	5.00	4.18	2.29	4.77
11.00	3.44	3.10	5.32	4.00	4.49	2.13	4.78
12.00	3.85	3.11	5.98	5.00	4.15	2.38	4.93
13.00	3.82	3.38	6.45	4.00	3.96	2.29	4.52
13.00	3.79	3.47	6.58	4.00	4.19	2.26	4.72
12.00	4.43	3.08	6.81	4.00	4.06	2.60	5.26
11.00	3.76	3.43	6.44	3.00	4.61	2.65	6.12
9.00	3.76	3.27	6.13	7.00	4.53	1.71	3.88
8.50	4.13	3.57	7.36	4.50	4.69	1.82	4.26
9.00	4.01	3.37	6.76	6.00	4.17	1.23	2.56
9.00	4.04	3.23	6.52	5.00	3.88	1.42	2.74
-	-	-	-	5.00	3.61	1.31	2.36
7.00	3.22	3.22	5.18	4.00	3.63	1.66	3.00
9.00	4.24	3.40	7.20	5.00	4.10	1.45	2.96
8.00	3.65	2.99	5.46	5.00	4.11	1.73	3.55
9.00	4.08	2.96	6.04	5.50	3.88	1.17	2.26
9.50	4.04	3.06	6.18	5.00	3.80	1.39	2.63
10.00	3.60	3.01	5.40	5.00	3.98	1.42	2.82
9.00	3.96	2.98	5.90	6.00	4.33	1.55	3.36
8.00	4.29	2.98	6.38	-	-	-	-
9.50	3.62	3.01	5.44	5.50	3.96	1.21	2.39
8.00	2.98	3.02	4.50	4.00	3.35	1.39	2.32
9.50	3.96	2.90	5.74	5.00	3.84	1.75	3.36
10.00	3.90	2.98	5.81	6.00	4.24	1.55	3.29

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Number of tines on c1	Mesio-Distal Width of c1 at Base	Height of c1	c1 Area	Mesio-Distal Length of p3	Buccal-Lingual Width of p3	p3 Basal Area	Mesio-Distal Length of p4
0	6.49	3.37	10.94	6.56	3.23	21.16	5.33
0	5.97	4.72	14.06	6.82	3.39	23.07	5.59
0	5.30	4.78	12.64	6.21	2.94	18.21	5.33
0	5.51	4.39	12.08	5.88	2.69	15.80	4.98
0	5.43	4.66	12.65	6.02	2.97	17.83	5.14
0	5.47	4.92	13.44	6.39	3.09	19.75	5.24
0	5.43	4.03	10.94	6.68	3.11	20.76	5.26
0	5.51	5.38	14.82	5.86	3.24	18.96	4.80
0	5.88	4.00	11.76	6.09	3.02	18.36	5.48
0	5.65	5.06	14.27	5.88	3.36	19.76	5.17
0	5.21	4.96	12.91	6.69	2.96	19.80	5.57
0	6.20	4.78	14.81	6.65	3.35	22.27	5.71
5.50	5.96	2.82	8.39	6.69	2.08	13.93	4.69
7.00	6.50	3.30	10.73	6.35	2.76	17.51	4.70
5.50	5.90	2.78	8.20	6.15	2.52	15.49	4.76
3.50	6.95	2.82	9.78	6.73	2.53	16.98	4.80
5.00	4.83	2.56	6.18	5.09	1.78	9.03	3.86
5.50	5.33	2.69	7.16	6.04	1.78	10.74	3.83
5.00	6.26	3.05	9.54	6.48	2.31	14.96	4.49
7.00	6.10	3.17	9.66	5.84	2.18	12.70	4.29
6.50	6.04	2.69	8.14	6.33	1.58	10.03	4.04
5.00	6.12	2.50	7.63	5.92	2.09	12.33	4.61
4.00	5.65	2.43	6.84	6.00	2.25	13.50	4.43
6.50	6.41	2.61	8.36	6.61	1.92	12.68	4.86
-	6.20	2.86	8.86	6.57	2.98	19.58	4.98
4.00	5.88	2.85	8.36	5.90	2.58	15.19	4.28
5.00	6.04	2.41	7.27	5.76	2.08	11.98	3.92
6.00	6.37	2.78	8.84	6.45	2.16	13.95	4.57
6.00	7.02	2.61	9.17	7.06	1.92	13.55	4.57

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Buccal-Lingual Width of p4	p4 Basal Area	Mesio-Distal Length of m1	Buccal-Lingual Width of m1	m1 Basal Area	Area of m1 Trigonid	Area of m1 Talonid	Area of m1 Entoconid-Distocuspid Plateau
3.74	19.92	4.62	3.76	17.35	2.94	8.20	1.28
3.77	21.07	4.65	3.73	17.33	3.78	8.54	1.18
3.53	18.79	4.78	3.55	16.97	3.80	6.79	1.04
3.34	16.63	4.03	3.43	13.81	3.38	6.63	0.90
3.57	18.31	4.13	3.50	14.43	3.07	7.74	0.80
3.78	19.78	4.75	3.86	18.34	3.63	8.78	1.53
3.46	18.16	4.39	3.67	16.11	-	-	-
3.87	18.53	4.52	3.86	17.42	3.69	8.52	1.36
3.69	20.18	4.08	3.51	14.30	-	-	-
3.87	19.96	4.40	3.57	15.71	2.94	7.41	
3.59	19.98	4.42	3.60	15.91	3.67	7.30	1.03
3.88	22.16	4.69	3.80	17.82	4.25	6.30	1.10
3.06	14.37	3.96	3.18	12.60	2.42	5.26	0.93
3.21	15.05	3.97	3.24	12.85	2.14	6.46	0.97
3.27	15.55	4.02	3.11	12.49	2.24	6.83	0.79
3.16	15.17	3.56	3.04	10.79	1.64	4.61	0.92
2.65	10.20	3.07	2.65	8.12	1.77	4.06	0.61
2.81	10.76	3.26	2.87	9.34	1.79	4.76	0.83
2.87	12.87	3.39	3.08	10.44	1.60	6.11	-
3.13	13.39	3.54	2.98	10.52	1.58	5.04	0.80
3.10	12.53	3.39	2.49	8.43	1.26	4.02	0.72
3.06	14.12	3.59	3.18	11.44	1.91	4.66	0.70
3.28	14.51	3.57	3.09	11.02	-	-	-
3.10	15.07	3.59	3.14	11.29	1.78	4.55	0.68
3.51	17.48	3.51	3.35	11.75	-	-	-
3.26	13.92	3.38	3.20	10.80	1.99	5.30	0.56
2.69	10.56	3.22	2.73	8.82	0.86	3.85	0.54
3.06	13.99	3.43	3.14	10.78	1.74	4.19	0.59
3.02	13.81	3.47	2.78	9.63	1.52	4.08	0.80

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Mesio-Distal Length of m2	Buccal-Lingual Width of m2	m2 Basal Area	Mesio-Distal Length of m3	Buccal-Lingual Width of m3	m3 Basal Area
4.68	3.82	17.85	4.36	3.63	15.83
4.68	3.80	17.78	4.43	3.79	16.77
4.82	3.78	18.22	4.59	3.26	14.96
4.03	3.49	14.06	3.95	3.03	11.93
4.25	3.68	15.60	4.33	3.59	15.53
4.86	3.87	18.81	4.37	3.56	15.54
4.64	3.66	16.96	4.08	3.09	12.59
4.89	3.72	18.19	4.71	3.48	16.39
4.66	3.38	15.73	4.06	2.58	10.45
3.99	3.67	14.62	3.66	3.08	11.27
4.64	3.70	17.15	4.14	3.42	14.16
4.61	3.80	17.51	4.45	3.76	16.71
4.33	3.51	15.19	4.24	3.35	14.21
4.03	3.48	14.01	4.16	3.27	13.59
4.18	3.29	13.75	3.70	3.10	11.44
3.56	3.13	11.13	3.75	3.02	11.33
3.42	2.77	9.44	3.33	2.51	8.36
3.25	3.23	10.48	3.31	2.97	9.83
3.54	3.29	11.63	3.72	3.28	12.19
3.44	3.20	11.01	3.81	3.20	12.16
3.51	3.10	10.89	3.43	3.06	10.50
3.63	3.10	11.27	3.59	3.22	11.58
3.56	3.20	11.39	3.60	3.09	11.09
3.92	3.31	12.95	3.88	3.22	12.50
4.08	3.35	13.66	4.04	3.22	13.03
3.48	3.38	11.76	3.57	3.35	11.96
3.27	2.90	9.46	3.22	2.65	8.55
3.51	3.39	11.89	4.29	3.14	13.47
3.71	2.98	11.07	3.63	2.84	10.30

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Appendix B: Postcranial Measurements

Genus	Species	Museum #	Sex	Age	Country
Anomalurops	beecrofti	USNM 84546	F	A	W. Africa
Anomalurops	beecrofti	USNM 84547	?	A	W. Africa
Anomalurops	beecrofti	USNM 466118	F	J	Ivory Coast
Anomalurus	derbianus	USNM 466119	F	A	Ivory Coast
Anomalurus	derbianus	USNM 466120	M	A	Ivory Coast
Anomalurus	derbianus	USNM 466121	F	J	Ghana
Anomalurus	peli	USNM 429832	F	A	Ghana
Anomalurus	peli	USNM 466126	M	J	Ivory Coast
Anomalurus	peli	USNM 399470	?	A	?
Hypsignathus	monstrosus	USNM 396650	F	A	NZP
Hypsignathus	monstrosus	USNM 396640	F	A	NZP
Hypsignathus	monstrosus	USNM 396675	M	A	NZP
Hypsignathus	monstrosus	USNM 463935	F	A	NZP
Hypsignathus	monstrosus	USNM 464511	M	A	NZP
Hypsignathus	monstrosus	USNM 464514	M	A	NZP
Hypsignathus	monstrosus	USNM 464996	F	A	NZP
Hypsignathus	monstrosus	USNM 464998	F	A	NZP
Cynopterus	brachyotis	USNM 573383	M	A	Philippines
Cynopterus	brachyotis	USNM 573387	M	A	Philippines
Cynopterus	brachyotis	USNM 573400	M	A	Philippines
Cynopterus	brachyotis	USNM 573403	F	A	Philippines
Cynopterus	brachyotis	USNM 573409	F	A	Philippines
Cynopterus	brachyotis	USNM 573410	F	A	Philippines
Macroderma	gigas	USNM 396827	F	A	Australia
Myzopoda	aurita	USNM 577065	M	A	Madagascar
Artibeus	jamaicensis	USNM 362098	F	A	Dominica
Tadarida	condylura	USNM 365686	F	A	Mozamique
Desmodus	rotundus	USNM 523439	M	A	Mexico
Thyroptera	discifera	USNM 102922	?	A	Venezuela
Euripterus	horrens	USNM 549507	M	A	Brazil
Mystacina	tuberculata	USNM 120576	F	A	New Zealand
Cynocephalus	volans	FMNH 61032	M	A	Philippines
Cynocephalus	volans	FMNH 56442	F	A	Philippines
Cynocephalus	volans	FMNH 62067	M	A	Philippines
Cynocephalus	volans	FMNH 61030	F	A	Philippines
Cynocephalus	volans	FMNH 56441	F	A	Philippines
Cynocephalus	volans	USNM 144662	M	S	Philippines
Cynocephalus	volans	USNM 239191	F	A	Philippines
Cynocephalus	volans	USNM 578084	M	A	Philippines
Cynocephalus	volans	Uncatalogued	?	A	Philippines
Galeopterus	variegatus	USNM 155363	?	A	Indonesia
Galeopterus	variegatus	USNM 154600	F	S	Indonesia
Galeopterus	variegatus	USNM 49640	F	A	Indonesia
Galeopterus	variegatus	USNM 49693	F	A	Sumatra
Galeopterus	variegatus	USNM 198704	M	A	Borneo
Galeopterus	variegatus	USNM 197202	F	A	Borneo

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Genus	Species	Museum #	Sex	Age	Country
Galeopterus	variegatus	USNM 196905	M	A	Borneo
Galeopterus	variegatus	USNM 151887	M	A	Borneo
Galeopterus	variegatus	USNM 317118	?	A	Borneo
Galeopterus	variegatus	USNM 49470	?	A	Malaysia
Galeopterus	variegatus	USNM 197203	F	J	Borneo
Petaurus	australis	USNM 221150	F	A	NSW
Petaurus	breviceps	USNM 237728	M	A	NSW
Petaurus	breviceps	USNM 221215	M	A	NSW
Petaurus	breviceps	USNM 319791	?	A	NZP
Petaurus	breviceps	USNM 221218	M	A	NSW
Petaurus	breviceps	USNM 297823	?	A	NZP
Petaurus	breviceps	USNM 270812	M	A	NZP
Petaurus	breviceps	USNM 49937	M	A	NSW
Petaurus	breviceps	USNM 396817	F	A	NT
Petaurus	breviceps	USNM 543146	M	A	N. Moluccas
Petaurus	breviceps	USNM 534229	M	A	New Guinea
Petaurus	norfolcensis	USNM 293168	M	A	Australia
Petaurus	norfolcensis	USNM 362186	?	?	?
Schinobates	volans	USNM 221137	F	S	NSW
Schinobates	volans	USNM 238417	M	S	Queensland
Hemibelideus	lemuroides	USNM 238366	M	A	Queensland
Pseudocheirus	occidentalis	USNM 237653	M	A	W. Australia
Pseudocheirus	occidentalis	USNM 237694	F	S	W. Australia
Pseudocheirus	herbertensis	USNM 238391	F	A	Queensland
Pseudocheirus	herbertensis	USNM 238396	M	A	Queensland
Pseudocheirus	perigrinus	USNM 221155	F	A	NSW
Pseudocheirus	perigrinus	USNM 238377	M	A	Queensland
Pseudocheirus	perigrinus	USNM 277372	?	A	NSW
Acrobates	pygmaeus	USNM 582004	M	A	?
Perodicticus	potto	USNM 481774	F	A	Liberia
Arctocebus	calabarensis	USNM 511930	?	A	Cameroun
Loris	tardigradus	USNM 256737	F	A	Sri Lanka
Nycticebus	coucang	USNM 300000	M	A	Malaysia
Tupaia	glis	USNM 397984	?	A	?
Tupaia	glis	USNM 574901	M	A	?
Bradypus	variegatus	USNM 252306	M	A	Costa Rica
Bradypus	variegatus	USNM 252299	F	A	Costa Rica
Bradypus	tridactylus	USNM 256676	F	A	Guyana
Choloepus	didactylus	USNM 548401	M	A	?
Choloepus	hoffmanni	USNM 260868	F	A	?
Choloepus	didactylus	USNM 257009	?	A	British Guiana
Cyclopes	didactylus	USNM 200353	?	A	Brazil
Cyclopes	didactylus	USNM 283876	F	A	Panama
Cyclopes	didactylus	USNM 583067	F	A	Belize
Petaurista	petaurista	USNM 256914	?	A	China
Petaurista	philippensis	USNM 258016	F	A	China

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Genus	Species	Museum #	Sex	Age	Country
Petaurista	petaurista	USNM 174080	?	A	Kashmir
Petaurista	petaurista	USNM 174079	M	A	Kashmir
Petaurista	alborufus	USNM 332937	?	S	Taiwan
Petaurista	sp	USNM 267209	F	A	Siam
Petaurista	philippensis	USNM 258017	M	A	China
Petaurista	petaurista	USNM 197320	F	A	Borneo
Petaurista	petaurista	USNM 173374	F	A	Kashmir
Petaurista	leucogenys	USNM 20941	F	A	Japan
Petaurista	philippensis	USNM 257844	F	A	China
Petaurista	elegans	USNM 292647	M	A	Borneo
Petaurista	sp	USNM 254807	?	S	China
Petaurista	petaurista	USNM 49660	F	A	Batu Islands
Petaurista	philippensis	USNM 307073	M	S	NZP
Trogopterus	xanthipes	USNM 258520	F	S	China
Trogopterus	xanthipes	USNM 268872	?	A	China
Aeromys	tephromelas	USNM 196743	F	A	Borneo
Hylopetes	fimbriatus	USNM 173363	F	A	Kashmir
Hylopetes	fimbriatus	USNM 173365	F	A	Kashmir
Hylopetes	fimbriatus	USNM 353243	F	S	Pakistan
Hylopetes	fimbriatus	USNM 173361	F	S	Kashmir
Hylopetes	phayrei	USNM 267267	?	S	Thailand
Iomys	horsfieldi	USNM 292654	F	S	Borneo
Glaucomys	sabrinus	USNM 397068	M	A	Michigan
Glaucomys	sabrinus	USNM 551841	M	A	Michigan
Glaucomys	sabrinus	USNM 398288	F	A	California
Glaucomys	sabrinus	USNM 235940	M	A	Alberta
Glaucomys	sabrinus	USNM 332333	M	A	Tennessee
Glaucomys	sabrinus	USNM 267440	M	A	Tennessee
Glaucomys	sabrinus	USNM 524544	F	S	Michigan
Glaucomys	sabrinus	USNM 524543	F	S	Michigan
Glaucomys	sabrinus	USNM 397065	F	A	Michigan
Glaucomys	sabrinus	USNM 397040	F	A	Michigan
Glaucomys	sabrinus	USNM 397021	F	A	Wisconsin
Glaucomys	sabrinus	USNM 397022	F	A	MIchegan
Glaucomys	sabrinus	USNM 398287	F	A	Washington
Glaucomys	sabrinus	USNM 397017	F	A	Michegan
Sciurus	carolinensis	USNM 528045	M	A	North Carolina
Sciurus	carolinensis	USNM 500992	M	A	Massachusets
Sciurus	carolinensis	USNM 503982	M	A	Virginia
Sciurus	carolinensis	USNM 528175	M	A	W. Virginia
Sciurus	carolinensis	USNM 396202	?	A	Virginia
Sciurus	carolinensis	USNM 398003	F	A	Maryland
Sciurus	deppei	USNM 244953	M	A	Guatamala
Sciurus	deppei	USNM 244934	M	A	Guatamala
Sciurus	deppei	USNM 244938	M	A	Guatamala
Sciurus	deppei	USNM 244954	M	A	Guatamala

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Genus	Species	Museum #	Sex	Age	Country
Sciurus	deppei	USNM 244956	F	A	Guatamala
Sciurus	deppei	USNM 244958	F	A	Guatamala
Sciurus	niger	USNM 397160	F	A	Michigan
Sciurus	niger	USNM 270303	?	A	S. Carolina
Sciurus	niger	USNM 564075	F	A	Minnesota
Sciurus	niger	USNM 261765	M	A	Maryland
Sciurus	niger	USNM 257984	M	A	Florida
Sciurus	niger	USNM 548038	F	S	Illinois

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Museum #	Site	Mass in g.	Skeletal Trunk Length	Length of Cervical Vertebrae
USNM 84546	Benito River	-	-	-
USNM 84547		-	-	-
USNM 466118	Sienso	528.00	-	-
USNM 466119	Sassandra River	-	194.83	28.01
USNM 466120	Niebe	454.55	175.29	25.51
USNM 466121	Adamso	-	144.28	21.16
USNM 429832	Oda 5 deg 52 min N, 1 deg 0 min W	1,818.18	278.05	37.52
USNM 466126	Yabrasso	700.00	-	-
USNM 399470	?	-	247.61	-
USNM 396650		-	90.13	32.84
USNM 396640		-	92.07	31.41
USNM 396675		-	103.43	38.14
USNM 463935		-	85.41	26.56
USNM 464511		-	107.92	40.24
USNM 464514		-	80.49	29.40
USNM 464996		-	89.16	30.39
USNM 464998		-	90.06	32.35
USNM 573383	Luzon	-	39.10	12.82
USNM 573387	Luzon	-	34.57	11.43
USNM 573400	Luzon	-	38.49	13.92
USNM 573403	Luzon	-	46.67	13.88
USNM 573409	Luzon	-	41.36	13.92
USNM 573410	Luzon	-	41.83	13.17
USNM 396827	NT	-	66.67	26.12
USNM 577065	Toliara	-	25.80	9.52
USNM 362098	Clarke Hall	-	35.67	11.84
USNM 365686	Tete	-	31.02	9.47
USNM 523439	Las Piedras	33.00	33.67	15.33
USNM 102922	San Julian	-	23.15	6.52
USNM 549507	Para	-	15.18	6.03
USNM 120576		-	31.00	9.58
FMNH 61032	Mindanao	-	235.27	116.69
FMNH 56442	Mindanao	-	232.87	109.20
FMNH 62067	Mindanao	-	189.11	87.67
FMNH 61030	Mindanao	-	238.90	112.97
FMNH 56441	Mindanao	-	236.45	109.30
USNM 144662	Basilan	-	-	-
USNM 239191	Basilan	-	-	-
USNM 578084	Biliran	-	191.23	94.67
Uncatalogued	?	-	208.22	105.58
USNM 155363	East Java	-	175.66	99.56
USNM 154600	Mt. Salk	1,477.27	144.11	78.07
USNM 49640	Pulo Bintang	-	215.00	105.43
USNM 49693	Pulo Kundur	1,480.00	204.56	100.91
USNM 198704	Laham	-	175.30	92.19
USNM 197202	Labuan Klambu	-	216.68	106.17

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Museum #	Site	Mass in g.	Skeletal Trunk Length	Length of Cervical Vertebrae
USNM 196905	Mt. Talisaian	341.00	118.85	91.71
USNM 151887	Pulo sebuku	-	179.45	83.33
USNM 317118	Jesselton	-	168.97	99.34
USNM 49470	Peninsula	1,227.27	196.84	104.02
USNM 197203	Labuan Klambu	-	200.32	59.68
USNM 221150	Wandandian	-	173.54	26.89
USNM 237728	Ebor	-	95.83	14.01
USNM 221215	Wandandian	-	101.10	14.06
USNM 319791		-	97.21	16.26
USNM 221218	Wandandian	-	94.20	14.22
USNM 297823		-	97.66	14.51
USNM 270812		-	94.63	14.30
USNM 49937		-	86.64	13.24
USNM 396817	162 mi SE Darwin	-	86.61	12.69
USNM 543146	Halmahera Id	-	83.40	13.39
USNM 534229	Mt. Hageb	-	86.21	12.38
USNM 293168		-	-	-
USNM 362186		-	124.80	17.47
USNM 221137	Wandandian	-	281.61	32.54
USNM 238417	Atherton	-	230.36	24.21
USNM 238366	Atherton	-	205.04	23.82
USNM 237653	Busselton	-	189.39	-
USNM 237694	Busselton	-	196.06	28.63
USNM 238391	Atherton	-	225.87	29.27
USNM 238396	Atherton	-	212.58	26.51
USNM 221155	Wandandian	-	198.51	25.51
USNM 238377	Atherton	-	201.21	27.02
USNM 277372	Blue Mts	-	203.70	26.85
USNM 582004	San Diego Zoo	-	35.08	5.33
USNM 481774	Tars Town	-	169.27	32.27
USNM 511930	Kumba	-	148.40	26.67
USNM 256737	Northwest	-	122.32	17.29
USNM 300000	Kuala Lumpur	-	171.66	29.05
USNM 397984	?	-	106.02	17.75
USNM 574901	?	-	110.33	19.16
USNM 252306	NZP	3,950.00	299.02	86.08
USNM 252299	NZP	-	289.08	86.14
USNM 256676	NZP	-	306.19	87.85
USNM 548401	NZP	-	471.17	52.92
USNM 260868	NZP	-	354.82	48.95
USNM 257009	NZP	-	428.67	61.40
USNM 200353	Para	-	72.50	11.67
USNM 283876	NZP	-	96.38	15.33
USNM 583067	Toledo	-	96.24	16.02
USNM 256914	Cochin, Prang	-	-	-
USNM 258016	Cochin, Bienhoa	-	-	-

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Museum #	Site	Mass in g.	Skeletal Trunk Length	Length of Cervical Vertebrae
USNM 174080	Dachin, Khistwar	-	218.33	28.58
USNM 174079	Dachin, Khistwar	-	231.55	31.19
USNM 332937	Nan Tou Hsien	-	192.20	26.07
USNM 267209	Doi Chiengtao	-	-	-
USNM 258017	Cochin, Bienhoa	-	-	-
USNM 197320	Landas	-	245.10	37.42
USNM 173374	Kamri Nullah	-	237.86	29.40
USNM 20941	Tokyo Market	-	228.65	27.38
USNM 257844	Cochin, Bien Hoa	-	-	-
USNM 292647	Mt. Kinabalu	-	217.13	27.61
USNM 254807	Szechwan, Mupin	-	159.94	22.72
USNM 49660	Tana Bala	-	263.55	31.70
USNM 307073	NZP	-	156.08	21.96
USNM 258520	Szechwan, Wei Chow	-	143.24	19.45
USNM 268872	Szechwan	-	198.42	24.48
USNM 196743	Telok, Sombong	-	-	37.56
USNM 173363	Pelawar	-	173.71	23.51
USNM 173365	Kamri	-	174.24	26.70
USNM 353243	Hazara, Snogran	-	168.11	25.81
USNM 173361	Pelawar	-	173.93	23.32
USNM 267267	Chiengmai	-	-	-
USNM 292654	Mt. Kinabalu	-	108.62	14.61
USNM 397068	Alger Co.	-	83.22	11.49
USNM 551841	Schoolcraft Co.	93.00	91.87	13.60
USNM 398288	Sierra Co.	188.00	103.37	15.19
USNM 235940	Peace Point	-	100.70	15.87
USNM 332333	Carter Co.	97.00	81.31	12.42
USNM 267440	Roan Mt.	-	93.74	12.15
USNM 524544	Schoolcraft Co.	107.00	91.04	13.34
USNM 524543	Schoolcraft Co.	122.00	99.93	13.42
USNM 397065	Chippewa Co.	-	97.48	14.42
USNM 397040	Cheyboygan Co.	-	92.36	12.65
USNM 397021		-	97.84	14.58
USNM 397022	Chippewa Co.	132.00	99.11	15.27
USNM 398287	Chelan Co.	196.00	107.11	16.04
USNM 397017	Chippewa Co.	108.00	93.23	14.96
USNM 528045	Wake Co., Raleigh	-	133.20	24.56
USNM 500992	Middlesex Co.	-	146.13	25.46
USNM 503982	Arlington Co.	-	139.22	24.82
USNM 528175	Monogalia Co.	-	131.57	-
USNM 396202	Fairfax Co.	-	141.12	23.10
USNM 398003	Montgomery Co.	-	145.13	24.83
USNM 244953	Peten, Remote	-	114.98	18.21
USNM 244934	Peten, Chuntuqui	-	-	17.53
USNM 244938	Peten, Chuntuqui	-	109.83	17.45
USNM 244954	Peten, Remote	-	112.84	18.54

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Museum #	Site	Mass in g.	Skeletal Trunk Length	Length of Cervical Vertebrae
USNM 244956	Peten, Libertad	-	111.55	18.74
USNM 244958	Peten, Libertad	-	108.60	17.10
USNM 397160	Wayne Co.	-	157.75	26.85
USNM 270303	Georgetown	-	180.67	30.31
USNM 564075	St. Peter	-	179.51	29.94
USNM 261765	Aireys	-	169.62	28.08
USNM 257984	Tallahassee	-	183.75	29.90
USNM 548038	Chicago	-	167.61	26.05

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Museum #	Length of Thoracic Vertebrae	Length of Lumbar Vertebrae	Length of Sacral Vertebrae	Humerus Length	Radius Length	Ulna Length
USNM 84546	-	-	-	-	64.42	75.14
USNM 84547	-	-	-	-	-	-
USNM 466118	-	-	26.49	68.15	56.21	65.28
USNM 466119	80.81	85.05	28.97	70.55	60.86	73.80
USNM 466120	71.09	78.24	25.96	64.43	54.88	65.97
USNM 466121	58.03	61.67	24.58	59.99	52.35	64.24
USNM 429832	106.94	127.95	43.16	96.19	79.68	99.48
USNM 466126	-	-	-	71.21	58.70	74.66
USNM 399470	100.58	110.93	36.10	-	76.53	93.77
USNM 396650	63.25	16.09	10.79	80.22	111.81	-
USNM 396640	65.88	16.08	10.11	76.35	109.92	-
USNM 396675	72.19	19.18	12.06	84.91	117.88	-
USNM 463935	61.69	14.85	8.87	81.35	113.85	-
USNM 464511	80.67	19.55	7.70	85.39	116.22	-
USNM 464514	58.50	14.40	7.59	79.45	108.72	-
USNM 464996	64.20	15.66	9.30	75.02	104.17	-
USNM 464998	66.15	16.10	7.81	77.37	108.31	-
USNM 573383	25.22	9.14	4.73	34.96	54.81	-
USNM 573387	22.41	7.67	4.49	33.95	52.66	-
USNM 573400	25.14	8.45	4.90	36.47	57.02	-
USNM 573403	30.67	10.00	6.00	34.13	55.09	-
USNM 573409	26.86	9.39	5.12	37.11	57.41	-
USNM 573410	27.83	9.83	4.17	36.17	55.94	-
USNM 396827	46.00	12.83	7.83	50.00	93.04	-
USNM 577065	15.59	4.04	6.17	24.21	44.60	-
USNM 362098	20.67	9.67	5.33	32.31	53.10	-
USNM 365686	14.69	11.18	5.14	25.91	41.21	-
USNM 523439	17.67	12.00	4.00	34.60	53.08	-
USNM 102922	10.91	4.73	7.51	14.85	31.26	-
USNM 549507	4.57	8.49	2.12	17.83	31.67	-
USNM 120576	16.17	7.67	7.17	25.97	41.91	-
FMNH 61032	88.34	41.38	30.24	105.12	117.97	127.97
FMNH 56442	92.78	41.54	30.89	101.21	120.49	130.82
FMNH 62067	75.01	34.99	26.43	101.26	113.15	122.91
FMNH 61030	94.89	42.21	31.04	110.23	125.37	136.94
FMNH 56441	98.39	38.50	28.76	103.50	123.91	134.56
USNM 144662	-	-	-	90.82	101.22	99.89
USNM 239191	-	-	-	105.52	126.53	135.27
USNM 578084	70.88	34.53	25.68	96.67	109.42	119.57
Uncatalogued	73.86	38.32	28.78	102.19	113.99	125.78
USNM 155363	49.35	40.40	26.75	-	-	-
USNM 154600	45.97	32.52	20.07	79.27	94.47	103.03
USNM 49640	79.77	38.55	29.80	104.25	137.78	146.56
USNM 49693	75.64	38.39	28.01	108.23	142.53	150.00
USNM 198704	57.73	33.67	25.38	104.24	135.16	143.36
USNM 197202	79.49	42.63	31.02	116.84	151.05	-

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Museum #	Length of Thoracic Vertebrae	Length of Lumbar Vertebrae	Length of Sacral Vertebrae	Humerus Length	Radius Length	Ulna Length
USNM 196905	60.91	44.16	26.83	103.00	135.65	144.65
USNM 151887	61.56	31.79	24.08	92.07	-	-
USNM 317118	71.07	35.40	26.43	107.96	152.74	140.65
USNM 49470	66.95	38.67	29.35	105.66	144.14	152.19
USNM 197203	42.96	21.61	16.21	61.20	70.59	76.54
USNM 221150	83.39	67.61	22.54	60.13	68.00	78.02
USNM 237728	43.53	40.00	12.30	32.10	-	-
USNM 221215	48.89	39.11	13.10	32.31	37.90	43.67
USNM 319791	44.19	41.04	11.98	31.42	36.54	42.28
USNM 221218	43.19	37.33	13.68	30.86	36.39	42.23
USNM 297823	45.03	39.72	12.91	32.00	35.28	41.00
USNM 270812	41.77	40.40	12.46	32.49	37.10	42.50
USNM 49937	40.28	35.38	10.98	28.24	33.29	38.23
USNM 396817	37.26	37.94	11.41	28.42	-	-
USNM 543146	39.12	33.58	10.70	29.28	33.31	38.10
USNM 534229	38.46	36.95	10.80	28.46	33.60	38.39
USNM 293168	-	-	-	-	-	-
USNM 362186	54.18	53.72	16.90	44.51	51.37	58.58
USNM 221137	128.96	112.10	40.55	81.56	68.33	-
USNM 238417	105.48	93.65	31.23	70.54	56.62	71.16
USNM 238366	95.97	78.88	30.19	50.02	48.07	59.05
USNM 237653	83.05	82.62	23.72	51.57	52.01	63.20
USNM 237694	90.03	75.62	30.41	47.97	47.93	57.77
USNM 238391	109.63	85.22	31.02	46.12	48.80	59.94
USNM 238396	99.70	78.89	33.99	56.71	53.61	66.68
USNM 221155	92.19	78.76	27.56	43.75	43.82	51.42
USNM 238377	94.34	76.90	29.97	49.06	49.05	60.06
USNM 277372	99.60	76.13	27.97	46.97	47.89	57.92
USNM 582004	16.50	13.17	5.42	13.07	15.08	18.00
USNM 481774	85.05	53.96	30.26	64.30	61.91	73.49
USNM 511930	69.39	52.19	26.82	54.69	51.24	58.00
USNM 256737	56.13	55.19	11.00	61.21	-	-
USNM 300000	88.57	55.83	27.26	66.27	61.77	71.59
USNM 397984	50.54	41.12	14.36	33.56	30.02	36.59
USNM 574901	50.62	43.93	15.78	34.16	33.56	40.48
USNM 252306	192.96	39.81	66.25	173.00	153.00	169.00
USNM 252299	175.00	41.08	73.00	150.00	136.00	147.50
USNM 256676	185.53	51.59	69.07	161.90	148.00	158.00
USNM 548401	339.11	49.06	83.00	160.50	185.50	199.25
USNM 260868	252.83	39.99	62.00	134.50	146.50	156.00
USNM 257009	298.21	49.46	81.00	162.75	180.75	189.25
USNM 200353	50.67	7.00	14.83	23.76	15.67	23.84
USNM 283876	68.21	10.33	17.83	24.62	17.68	25.70
USNM 583067	69.39	9.80	17.05	26.83	19.10	27.39
USNM 256914	-	-	-	101.10	100.39	115.33
USNM 258016	-	-	-	-	102.61	-

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Museum #	Length of Thoracic Vertebrae	Length of Lumbar Vertebrae	Length of Sacral Vertebrae	Humerus Length	Radius Length	Ulna Length
USNM 174080	100.14	118.19	-	-	-	-
USNM 174079	91.89	107.60	32.06	-	-	-
USNM 332937	74.00	89.42	28.78	61.08	-	-
USNM 267209	-	-	-	-	-	-
USNM 258017	-	-	-	-	100.59	115.75
USNM 197320	100.25	124.77	20.08	96.23	96.08	109.82
USNM 173374	92.79	114.38	30.69	-	-	-
USNM 20941	86.86	112.93	28.86	70.40	-	-
USNM 257844	-	-	-	110.56	105.46	121.50
USNM 292647	85.22	102.23	29.68	71.30	71.53	82.69
USNM 254807	63.75	75.15	21.04	42.87	51.07	60.29
USNM 49660	108.53	122.33	32.69	87.74	82.36	96.52
USNM 307073	60.72	71.39	23.97	57.23	53.10	-
USNM 258520	54.90	67.40	20.94	46.87	47.80	57.09
USNM 268872	78.91	94.74	24.77	63.16	63.67	73.75
USNM 196743	-	113.39	29.30	96.65	93.39	104.90
USNM 173363	70.99	78.57	24.15	52.91	54.47	65.10
USNM 173365	70.43	78.49	25.32	51.60	53.24	63.60
USNM 353243	70.04	74.62	23.45	53.00	-	-
USNM 173361	69.75	79.80	24.38	53.64	54.10	65.45
USNM 267267	-	-	-	-	78.26	87.96
USNM 292654	43.98	50.32	14.32	-	-	-
USNM 397068	30.84	39.89	12.49	30.75	32.61	38.26
USNM 551841	37.36	41.15	13.36	31.28	32.69	38.14
USNM 398288	41.88	47.66	13.83	33.90	36.77	43.31
USNM 235940	43.24	42.94	14.52	34.52	36.40	-
USNM 332333	33.86	35.09	12.36	30.66	-	-
USNM 267440	38.54	42.14	13.06	30.44	32.74	38.69
USNM 524544	38.48	40.02	12.54	30.21	33.82	39.07
USNM 524543	41.03	45.51	13.39	30.18	33.49	39.07
USNM 397065	40.12	44.21	13.15	32.72	34.55	40.44
USNM 397040	38.18	41.63	12.55	30.85	33.20	38.81
USNM 397021	39.17	45.06	13.61	32.30	35.31	40.87
USNM 397022	39.95	44.86	14.30	32.16	34.74	39.89
USNM 398287	42.45	49.72	14.94	35.45	38.31	45.20
USNM 397017	37.13	43.10	13.00	31.80	34.51	39.91
USNM 528045	60.95	52.64	19.61	40.05	36.61	46.64
USNM 500992	61.20	63.36	21.57	43.20	39.89	50.12
USNM 503982	58.88	59.92	20.42	43.09	39.22	50.28
USNM 528175	57.45	54.08	20.04	39.25	36.46	46.50
USNM 396202	61.47	59.65	20.00	41.98	38.58	48.44
USNM 398003	62.72	61.11	21.30	42.63	38.72	49.46
USNM 244953	49.17	49.15	16.66	34.77	32.66	39.95
USNM 244934	48.50	-	15.83	34.80	31.72	39.00
USNM 244938	48.17	45.85	15.81	34.52	30.59	37.52
USNM 244954	49.82	46.26	16.76	34.54	31.58	38.93

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Museum #	Length of Thoracic Vertebrae	Length of Lumbar Vertebrae	Length of Sacral Vertebrae	Humerus Length	Radius Length	Ulna Length
USNM 244956	49.12	47.00	15.43	34.45	31.56	-
USNM 244958	46.06	46.23	16.31	34.44	31.76	38.44
USNM 397160	71.84	61.77	24.14	47.02	42.65	53.85
USNM 270303	78.40	76.07	26.20	52.74	46.58	58.52
USNM 564075	81.15	72.87	25.49	48.46	44.92	56.32
USNM 261765	77.90	64.90	26.82	49.04	47.32	58.26
USNM 257984	78.45	77.90	27.40	54.33	49.59	61.31
USNM 548038	69.24	75.15	23.22	45.39	41.31	51.79

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Museum #	Medio-lateral Midshaft Diameter of the Humerus	Anterior-posterior Midshaft Diameter of the Humerus	Medio-lateral Midshaft Diameter of the Radius	Anterior-posterior Midshaft Diameter of the Radius	Medio-lateral Midshaft Diameter of the Ulna	Anterior-posterior Midshaft Diameter of the Ulna
USNM 84546	-		2.96	2.18	1.77	3.41
USNM 84547	-	-	-	-	-	-
USNM 466118	3.91	4.11	2.56	1.69	1.63	2.66
USNM 466119	4.17	4.35	2.60	2.09	2.25	2.73
USNM 466120	3.94	4.19	2.68	1.88	1.71	2.86
USNM 466121	3.25	3.67	2.11	1.74	1.54	2.91
USNM 429832	6.02	7.11	3.56	3.24	2.50	4.05
USNM 466126	3.86	4.19	2.48	2.30	1.81	2.92
USNM 399470	-	-	3.14	2.83	2.10	3.32
USNM 396650	4.74	4.40	3.36	3.39	-	-
USNM 396640	4.42	4.14	3.98	3.86	-	-
USNM 396675	5.11	4.77	3.98	3.94	-	-
USNM 463935	4.45	4.17	3.61	3.44	-	-
USNM 464511	4.89	4.76	4.11	4.03	-	-
USNM 464514	4.36	4.22	3.50	3.54	-	-
USNM 464996	4.27	4.18	3.32	3.49	-	-
USNM 464998	4.16	3.93	3.25	3.34	-	-
USNM 573383	1.85	1.84	1.58	1.66	-	-
USNM 573387	1.75	1.73	1.33	1.40	-	-
USNM 573400	1.95	1.88	1.62	1.75	-	-
USNM 573403	1.85	1.97	1.57	1.70	-	-
USNM 573409	2.06	1.91	1.69	1.63	-	-
USNM 573410	1.90	1.87	1.60	1.61	-	-
USNM 396827	3.33	3.16	2.95	3.10	-	-
USNM 577065	1.33	1.17	1.27	1.16	-	-
USNM 362098	2.40	2.15	2.07	1.74	-	-
USNM 365686	1.50	1.43	1.69	1.42	-	-
USNM 523439	2.08	1.89	2.34	1.46	-	-
USNM 102922	0.87	0.81	0.79	0.71	-	-
USNM 549507	0.92	0.86	0.91	0.69	-	-
USNM 120576	1.42	1.42	1.41	1.36	-	-
FMNH 61032	5.61	6.45	4.56	4.20	1.26	1.68
FMNH 56442	6.58	6.53	4.69	4.67	1.76	2.36
FMNH 62067	6.17	6.55	4.77	4.58	1.59	1.85
FMNH 61030	6.29	7.05	5.23	4.24	1.81	1.92
FMNH 56441	6.76	6.13	4.47	4.32	1.26	2.12
USNM 144662	5.45	6.66	4.52	3.97	1.89	0.79
USNM 239191	5.54	6.65	4.20	4.27	1.08	1.84
USNM 578084	5.46	6.45	3.91	4.32	1.06	2.26
Uncatalogued	6.72	6.17	4.73	4.33	1.10	2.41
USNM 155363	-	-	-	-	-	-
USNM 154600	4.34	4.90	3.08	3.49	0.64	1.81
USNM 49640	6.27	5.55	3.77	3.79	1.07	2.28
USNM 49693	6.18	5.52	3.95	3.42	0.97	1.58
USNM 198704	5.34	4.98	3.48	3.18	0.70	2.16
USNM 197202	5.68	5.70	4.27	3.67	-	-

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Museum #	Medio-lateral Midshaft Diameter of the Humerus	Anterior-posterior Midshaft Diameter of the Humerus	Medio-lateral Midshaft Diameter of the Radius	Anterior-posterior Midshaft Diameter of the Radius	Medio-lateral Midshaft Diameter of the Ulna	Anterior-posterior Midshaft Diameter of the Ulna
USNM 196905	5.56	5.42	3.99	3.44	0.93	2.26
USNM 151887	5.15	4.68	-	-	-	-
USNM 317118	6.30	6.02	4.28	3.90	1.90	1.05
USNM 49470	6.24	5.68	3.96	3.41	0.99	2.10
USNM 197203	3.32	3.77	2.67	2.62	0.52	1.45
USNM 221150	3.96	4.53	3.65	2.35	3.24	2.33
USNM 237728	2.30	2.78	-	-	-	-
USNM 221215	2.33	2.31	2.00	1.31	2.06	1.25
USNM 319791	2.42	2.64	2.20	1.17	2.08	1.08
USNM 221218	2.37	2.47	1.99	1.32	2.01	1.34
USNM 297823	2.18	3.34	2.50	1.30	2.32	1.20
USNM 270812	2.23	2.56	2.05	1.17	2.00	1.05
USNM 49937	2.08	2.54	1.78	1.31	1.92	1.22
USNM 396817	1.87	1.91	-	-	-	-
USNM 543146	2.11	2.28	1.87	1.13	1.75	1.04
USNM 534229	1.95	2.22	1.75	0.95	1.78	0.93
USNM 293168	-	-	-	-	-	-
USNM 362186	2.76	3.06	2.81	1.95	2.17	1.74
USNM 221137	4.32	4.75	4.39	2.93	3.74	2.57
USNM 238417	3.74	3.79	3.52	2.33	3.24	2.03
USNM 238366	4.06	4.31	3.29	2.15	3.15	2.14
USNM 237653	4.57	5.10	3.62	2.77	4.20	3.46
USNM 237694	4.11	4.53	3.29	2.57	3.45	2.14
USNM 238391	4.34	5.72	3.90	2.16	3.52	2.18
USNM 238396	4.82	5.43	3.88	2.36	3.60	2.42
USNM 221155	3.83	5.11	2.64	2.60	3.24	2.11
USNM 238377	4.33	5.74	3.26	2.55	3.82	2.40
USNM 277372	4.16	4.83	3.04	2.44	3.40	2.64
USNM 582004	0.92	0.90	0.76	0.60	0.76	0.40
USNM 481774	4.23	4.90	4.32	2.83	2.45	3.42
USNM 511930	3.31	3.59	2.40	2.04	1.84	1.86
USNM 256737	2.99	2.86	-	-	-	-
USNM 300000	5.01	5.38	3.73	3.39	2.75	3.42
USNM 397984	2.30	2.63	1.53	1.45	2.25	1.08
USNM 574901	2.88	3.03	1.89	2.02	2.42	1.27
USNM 252306	10.16	9.78	7.06	5.94	4.60	5.79
USNM 252299	8.83	9.35	6.00	5.18	4.43	5.37
USNM 256676	9.69	10.29	6.94	4.92	4.91	5.42
USNM 548401	12.58	12.44	13.19	7.54	5.83	8.39
USNM 260868	8.39	10.07	9.45	4.76	5.43	3.62
USNM 257009	9.22	9.85	9.60	4.95	4.59	4.15
USNM 200353	3.92	2.67	2.33	2.00	1.33	2.33
USNM 283876	4.61	3.08	3.11	2.01	1.89	2.79
USNM 583067	4.85	2.88	2.72	2.14	1.72	2.86
USNM 256914	6.07	6.43	4.45	4.31	2.07	2.45
USNM 258016	-	-	4.59	3.89	1.98	2.45

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Museum #	Medio-lateral Midshaft Diameter of the Humerus	Anterior-posterior Midshaft Diameter of the Humerus	Medio-lateral Midshaft Diameter of the Radius	Anterior-posterior Midshaft Diameter of the Radius	Medio-lateral Midshaft Diameter of the Ulna	Anterior-posterior Midshaft Diameter of the Ulna
USNM 174080	-	-	-	-	-	-
USNM 174079	-	-	-	-	-	-
USNM 332937	4.05	4.20	-	-	-	-
USNM 267209	-	-	-	-	-	-
USNM 258017	-	-	4.72	4.05	2.40	2.51
USNM 197320	5.51	6.26	4.02	3.84	2.37	2.12
USNM 173374	-	-	-	-	-	-
USNM 20941	4.50	4.86	-	-	-	-
USNM 257844	5.43	6.86	4.53	4.03	2.37	2.23
USNM 292647	4.55	4.95	3.20	2.71	1.72	1.69
USNM 254807	3.23	3.40	2.62	2.11	1.05	0.87
USNM 49660	4.87	5.58	3.63	3.63	2.02	2.07
USNM 307073	3.58	4.00	2.93	2.51	-	-
USNM 258520	2.96	3.21	2.76	2.05	1.00	0.90
USNM 268872	3.61	4.31	3.00	2.73	1.07	0.93
USNM 196743	4.72	5.08	3.85	2.93	1.74	1.12
USNM 173363	3.69	4.06	2.79	2.65	2.14	1.47
USNM 173365	3.55	3.68	2.85	2.24	1.95	1.39
USNM 353243	3.36	4.39	-	-	-	-
USNM 173361	3.07	3.56	2.57	2.12	1.94	1.01
USNM 267267	-	-	3.15	3.36	2.46	1.98
USNM 292654	-	-	-	-	-	-
USNM 397068	1.71	2.10	1.45	1.39	0.58	0.49
USNM 551841	1.73	2.04	1.36	1.21	0.52	0.37
USNM 398288	2.33	2.40	1.75	1.53	1.19	0.71
USNM 235940	2.08	2.31	1.79	1.44	-	-
USNM 332333	1.96	2.33	-	-	-	-
USNM 267440	1.92	2.27	1.61	1.40	0.63	0.56
USNM 524544	1.85	2.00	1.58	1.23	0.70	0.58
USNM 524543	1.88	2.14	1.60	1.34	0.65	0.54
USNM 397065	2.00	2.21	1.75	1.42	0.79	0.43
USNM 397040	1.98	2.22	1.63	1.26	1.04	0.60
USNM 397021	2.08	2.29	1.77	1.47	0.93	0.58
USNM 397022	1.92	2.15	1.68	1.33	0.96	0.55
USNM 398287	2.37	2.52	2.17	1.52	0.94	0.64
USNM 397017	1.78	1.91	1.69	1.47	0.89	0.46
USNM 528045	3.37	4.22	2.84	1.89	3.85	1.36
USNM 500992	3.76	4.47	2.82	2.19	4.47	1.69
USNM 503982	3.76	4.74	2.90	2.33	3.90	1.79
USNM 528175	3.25	3.72	2.56	1.96	3.35	1.70
USNM 396202	3.53	4.20	2.47	2.21	3.63	1.45
USNM 398003	3.31	4.00	2.71	2.17	3.52	1.68
USNM 244953	2.76	3.29	2.30	1.51	2.65	1.22
USNM 244934	2.66	2.96	2.08	1.79	2.76	1.34
USNM 244938	2.72	3.21	1.94	1.45	2.63	1.13
USNM 244954	2.46	3.11	1.98	1.28	2.53	1.21

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Museum #	Medio-lateral Midshaft Diameter of the Humerus	Anterior-posterior Midshaft Diameter of the Humerus	Medio-lateral Midshaft Diameter of the Radius	Anterior-posterior Midshaft Diameter of the Radius	Medio-lateral Midshaft Diameter of the Ulna	Anterior-posterior Midshaft Diameter of the Ulna
USNM 244956	2.53	3.24	2.13	1.39	-	-
USNM 244958	2.72	3.28	2.01	1.49	2.29	1.14
USNM 397160	3.98	4.89	2.92	2.72	4.24	1.70
USNM 270303	4.25	5.63	3.16	2.65	4.34	1.75
USNM 564075	3.93	5.34	3.09	2.61	4.04	2.14
USNM 261765	4.43	5.33	2.89	2.68	4.02	1.72
USNM 257984	4.16	5.50	3.36	2.50	4.50	1.87
USNM 548038	3.90	5.05	2.83	2.25	4.24	1.76

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Museum #	Length of First Metacarpal	Length of Second Metacarpal	Length of Third Metacarpal	Length of Fourth metacarpal	Length of Fifth Metacarpal	Length of First Proximal Carpal Phalanx
USNM 84546	-	-	-	-	-	-
USNM 84547	3.04	9.63	10.78	11.10	9.96	3.84
USNM 466118	-	-	-	-	-	-
USNM 466119	-	-	-	-	-	-
USNM 466120	-	-	-	-	-	-
USNM 466121	-	-	-	-	-	-
USNM 429832	-	-	-	-	-	-
USNM 466126	-	-	-	-	-	-
USNM 399470	-	-	-	-	-	-
USNM 396650	18.08	65.97	87.79	88.71	85.61	22.12
USNM 396640	17.52	65.03	84.36	84.28	82.31	22.51
USNM 396675	18.86	54.39	90.12	88.74	87.07	23.12
USNM 463935	17.53	65.88	86.25	86.52	83.32	-
USNM 464511	17.34	71.04	88.92	89.11	87.44	-
USNM 464514	17.86	67.29	84.81	84.02	82.42	-
USNM 464996	19.54	63.40	81.63	81.79	77.65	19.87
USNM 464998	17.44	63.76	83.74	83.10	83.28	22.47
USNM 573383	8.29	30.86	40.45	36.93	37.60	14.23
USNM 573387	7.55	27.08	37.07	34.68	34.78	13.00
USNM 573400	8.10	28.28	42.28	38.13	38.77	13.33
USNM 573403	7.00	26.67	40.26	36.86	37.35	13.17
USNM 573409	8.26	29.28	40.98	38.23	39.31	14.19
USNM 573410	7.28	25.23	39.73	36.40	38.05	13.29
USNM 396827	9.32	81.98	69.87	75.65	78.65	7.45
USNM 577065	-	39.77	39.38	38.56	37.42	-
USNM 362098	4.15	43.89	52.34	52.11	53.26	6.51
USNM 365686	3.43	42.75	37.86	37.82	46.09	4.57
USNM 523439	7.34	44.18	52.16	51.86	49.93	6.93
USNM 102922	-	-	31.46	31.17	29.09	-
USNM 549507	1.80	25.33	31.00	27.17	-	-
USNM 120576	2.73	37.25	42.85	41.39	38.34	4.53
FMNH 61032	13.38	24.73	27.38	28.37	27.33	16.60
FMNH 56442	13.19	24.26	27.21	28.62	27.98	15.67
FMNH 62067	-	-	-	-	-	-
FMNH 61030	12.42	23.42	26.83	27.75	26.33	15.50
FMNH 56441	-	-	-	-	-	-
USNM 144662	10.55	20.30	23.22	24.11	23.27	12.04
USNM 239191	11.49	21.84	24.89	26.46	25.19	14.44
USNM 578084	12.31	20.61	23.49	24.35	24.24	-
Uncatalogued	12.48	23.73	26.84	27.63	26.13	15.35
USNM 155363	-	-	-	-	-	-
USNM 154600	-	-	-	-	-	-
USNM 49640	11.57	20.69	25.09	26.60	25.72	12.05
USNM 49693	11.91	19.88	23.56	25.80	25.25	11.79
USNM 198704	-	-	-	-	-	-
USNM 197202	-	-	-	-	-	-

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Museum #	Length of First Metacarpal	Length of Second Metacarpal	Length of Third Metacarpal	Length of Fourth metacarpal	Length of Fifth Metacarpal	Length of First Proximal Carpal Phalanx
USNM 196905	-	-	-	-	-	-
USNM 151887	-	-	-	-	-	-
USNM 317118	13.66	24.15	28.78	30.20	29.54	-
USNM 49470	12.75	21.77	26.18	28.07	27.85	12.80
USNM 197203	-	-	-	-	-	-
USNM 221150	5.14	7.60	9.57	10.57	13.56	6.14
USNM 237728	3.15	4.47	5.64	-	-	-
USNM 221215	3.55	5.45	6.05	6.72	6.73	3.55
USNM 319791	-	-	-	-	-	-
USNM 221218	3.41	4.84	5.85	6.10	6.06	3.59
USNM 297823	3.10	5.01	5.86	5.84	5.88	3.79
USNM 270812	-	-	-	-	-	-
USNM 49937	2.91	4.55	5.27	6.34	5.98	3.04
USNM 396817	-	-	-	-	-	-
USNM 543146	2.99	4.50	5.84	6.28	6.45	3.58
USNM 534229	-	5.52	6.22	6.62	6.20	-
USNM 293168	-	-	-	-	-	-
USNM 362186	4.63	-	-	-	-	-
USNM 221137	7.87	9.35	12.45	12.26	10.34	10.87
USNM 238417	5.42	6.82	8.93	8.36	5.88	8.46
USNM 238366	6.16	7.80	9.41	8.73	6.32	8.28
USNM 237653	6.70	8.69	10.82	10.08	7.43	8.24
USNM 237694	3.45	2.14	6.03	7.61	10.09	9.27
USNM 238391	3.52	2.18	5.22	6.78	8.24	7.67
USNM 238396	6.94	8.33	9.47	9.88	10.86	8.65
USNM 221155	5.06	7.84	9.22	7.84	6.37	6.61
USNM 238377	5.88	8.57	9.31	9.51	7.35	8.33
USNM 277372	5.35	7.76	9.18	8.94	6.73	7.67
USNM 582004	1.56	2.32	2.84	2.84	1.56	1.76
USNM 481774	9.55	8.24	11.67	12.98	12.16	10.04
USNM 511930	-	-	-	-	-	-
USNM 256737	-	-	-	-	-	-
USNM 300000	9.17	8.67	11.83	11.17	10.50	8.33
USNM 397984	4.54	8.41	10.29	9.27	6.20	3.70
USNM 574901	5.88	9.27	10.78	9.67	6.41	4.49
USNM 252306	-	22.94	22.19	18.16	-	-
USNM 252299	-	20.36	21.22	22.88	-	-
USNM 256676	-	26.28	27.36	24.66	-	-
USNM 548401	27.46	38.38	36.66	27.85	-	-
USNM 260868	11.75	30.38	29.53	15.55	-	-
USNM 257009	22.97	35.76	38.21	21.24	-	-
USNM 200353	-	-	-	-	-	-
USNM 283876	-	5.00	4.25	4.17	-	-
USNM 583067	-	6.00	5.00	5.67	-	-
USNM 256914	-	-	-	-	-	-
USNM 258016	-	-	-	-	-	-

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Museum #	Length of First Metacarpal	Length of Second Metacarpal	Length of Third Metacarpal	Length of Fourth metacarpal	Length of Fifth Metacarpal	Length of First Proximal Carpal Phalanx
USNM 174080	-	-	-	-	-	-
USNM 174079	-	-	-	-	-	-
USNM 332937	-	-	-	-	-	-
USNM 267209	-	-	-	-	-	-
USNM 258017	-	-	-	-	-	-
USNM 197320	-	-	-	-	-	-
USNM 173374	-	-	-	-	-	-
USNM 20941	-	-	-	-	-	-
USNM 257844	-	-	-	-	-	-
USNM 292647	-	-	-	-	-	-
USNM 254807	-	-	-	-	-	-
USNM 49660	-	-	-	-	-	-
USNM 307073	-	-	-	-	-	-
USNM 258520	2.75	7.62	9.70	10.18	7.78	-
USNM 268872	3.90	7.73	10.00	10.89	8.45	-
USNM 196743	-	-	-	-	-	-
USNM 173363	-	-	-	-	-	-
USNM 173365	-	-	-	-	-	-
USNM 353243	-	-	-	-	-	-
USNM 173361	-	-	-	-	-	-
USNM 267267	-	-	-	-	-	-
USNM 292654	-	-	-	6.86	-	-
USNM 397068	1.26	4.78	6.15	6.47	5.03	-
USNM 551841	1.17	4.64	6.08	6.18	4.98	-
USNM 398288	-	-	-	-	-	-
USNM 235940	-	-	-	-	-	-
USNM 332333	-	-	-	-	-	-
USNM 267440	-	-	-	-	-	-
USNM 524544	1.28	4.25	6.75	6.83	4.96	-
USNM 524543	-	-	-	-	-	-
USNM 397065	1.19	4.80	5.79	6.39	4.76	-
USNM 397040	1.06	4.24	5.56	5.60	4.31	-
USNM 397021	-	-	-	-	-	-
USNM 397022	-	-	-	-	-	-
USNM 398287	-	-	-	-	-	-
USNM 397017	-	-	-	-	-	-
USNM 528045	1.97	8.20	11.09	10.85	8.29	1.89
USNM 500992	1.35	8.91	12.95	12.91	8.54	1.53
USNM 503982	1.72	8.67	12.17	12.83	8.67	1.96
USNM 528175	1.64	8.74	11.25	12.08	8.67	-
USNM 396202	1.54	8.57	12.42	12.58	8.25	-
USNM 398003	1.59	8.90	12.10	12.24	8.78	-
USNM 244953	1.12	6.61	9.84	10.16	7.26	1.23
USNM 244934	-	6.19	9.44	9.84	6.75	-
USNM 244938	1.18	6.59	9.92	10.32	6.83	1.20
USNM 244954	1.17	6.45	9.33	9.64	6.63	1.12

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Museum #	Length of First Metacarpal	Length of Second Metacarpal	Length of Third Metacarpal	Length of Fourth metacarpal	Length of Fifth Metacarpal	Length of First Proximal Carpal Phalanx
USNM 244956	1.60	6.15	9.31	9.68	6.79	1.18
USNM 244958	1.23	6.51	9.23	9.76	6.75	1.22
USNM 397160	1.60	9.57	13.40	13.36	9.86	1.78
USNM 270303	2.04	9.92	13.80	14.16	9.59	2.04
USNM 564075	1.70	10.24	14.45	14.29	10.16	1.67
USNM 261765	1.76	10.37	14.41	15.06	10.29	2.12
USNM 257984	1.86	11.11	15.80	16.86	12.11	-
USNM 548038	1.84	9.67	13.22	13.10	9.02	1.80

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Museum #	Length of Second Proximal Carpal Phalanx	Length of Third Proximal Carpal Phalanx	Length of Fourth Proximal Carpal Phalanx	Length of Fifth Proximal Carpal Phalanx	Length of Second Intermediate Carpal Phalanx	Length of Third Intermediate Carpal Phalanx
USNM 84546	-	-	-	-	-	-
USNM 84547	-	-	-	-	-	-
USNM 466118	-	-	-	-	-	-
USNM 466119	-	-	-	-	-	-
USNM 466120	-	-	-	-	-	-
USNM 466121	-	-	-	-	-	-
USNM 429832	-	-	-	-	-	-
USNM 466126	-	-	-	-	-	-
USNM 399470	-	-	-	-	-	-
USNM 396650	11.60	58.60	43.23	41.04	8.28	89.63
USNM 396640	-	-	22.54	-	-	-
USNM 396675	12.70	-	-	-	8.04	-
USNM 463935	-	-	-	-	-	-
USNM 464511	-	-	-	-	8.69	-
USNM 464514	-	-	-	-	-	-
USNM 464996	10.12	37.44	-	-	7.54	-
USNM 464998	11.51	-	-	-	8.66	-
USNM 573383	9.06	28.67	21.47	19.57	5.14	33.30
USNM 573387	6.93	25.42	19.50	18.33	3.35	30.40
USNM 573400	6.85	27.05	19.97	18.39	3.73	34.93
USNM 573403	7.67	26.47	19.62	17.34	4.83	37.50
USNM 573409	9.14	28.01	21.14	18.78	3.96	34.78
USNM 573410	7.06	27.03	21.06	18.69	4.65	35.50
USNM 396827	15.48	42.30	24.22	32.14	-	79.00
USNM 577065	11.27	14.37	17.00	-	13.63	14.69
USNM 362098	4.97	14.96	11.74	15.25	-	26.72
USNM 365686	-	15.67	15.50	20.42	-	9.41
USNM 523439	8.68	11.20	-	10.02	-	17.92
USNM 102922	-	14.50	9.85	8.17	-	9.17
USNM 549507	-	5.33	6.33	-	-	19.00
USNM 120576	2.37	11.10	10.29	6.29	-	6.37
FMNH 61032	17.12	17.90	18.76	19.02	20.57	21.79
FMNH 56442	16.28	17.34	17.80	17.96	19.91	21.38
FMNH 62067	-	-	-	-	-	-
FMNH 61030	16.83	17.50	18.75	19.50	-	-
FMNH 56441	-	-	-	-	-	-
USNM 144662	12.08	12.57	13.12	14.26	18.66	20.28
USNM 239191	-	16.47	17.03	-	-	21.92
USNM 578084	-	-	16.87	17.64	-	-
Uncatalogued	15.53	17.07	17.64	17.90	20.05	21.90
USNM 155363	-	-	-	-	-	-
USNM 154600	-	-	-	-	-	-
USNM 49640	13.41	14.52	15.18	16.55	17.38	22.42
USNM 49693	13.52	15.14	15.96	16.96	17.92	21.57
USNM 198704	-	-	-	-	-	-
USNM 197202	-	-	-	-	-	-

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Museum #	Length of Second Proximal Carpal Phalanx	Length of Third Proximal Carpal Phalanx	Length of Fourth Proximal Carpal Phalanx	Length of Fifth Proximal Carpal Phalanx	Length of Second Intermediate Carpal Phalanx	Length of Third Intermediate Carpal Phalanx
USNM 196905	-	-	-	-	-	-
USNM 151887	-	-	-	-	-	-
USNM 317118	-	-	-	-	-	-
USNM 49470	13.94	15.35	16.05	17.18	18.81	23.18
USNM 197203	-	-	-	-	-	-
USNM 221150	7.68	9.19	10.40	10.44	-	-
USNM 237728	4.94	5.84	-	-	2.72	2.95
USNM 221215	5.45	6.05	6.72	6.73	2.33	3.72
USNM 319791	-	-	-	-	-	-
USNM 221218	4.64	6.02	6.94	6.76	-	-
USNM 297823	4.74	5.92	6.78	6.71	2.74	3.41
USNM 270812	-	-	-	-	-	-
USNM 49937	4.57	6.12	6.38	6.53	2.50	3.55
USNM 396817	-	-	-	-	-	-
USNM 543146	4.76	5.70	6.39	6.45	2.57	3.28
USNM 534229	5.25	6.21	7.29	6.99	-	-
USNM 293168	-	-	-	-	-	-
USNM 362186	-	-	-	-	-	-
USNM 221137	13.70	15.32	15.95	15.52	-	-
USNM 238417	10.32	12.10	13.06	12.03	5.26	5.98
USNM 238366	9.18	9.79	10.48	10.11	4.41	4.89
USNM 237653	8.73	9.88	10.65	9.47	-	-
USNM 237694	7.27	-	-	-	-	-
USNM 238391	5.96	7.10	7.43	8.08	8.73	7.76
USNM 238396	9.31	8.98	10.53	10.61	4.98	4.73
USNM 221155	6.61	7.59	8.24	7.27	4.08	3.92
USNM 238377	8.53	9.51	10.20	9.39	4.04	5.39
USNM 277372	7.80	8.86	9.18	8.61	3.88	4.37
USNM 582004	2.08	2.64	3.20	2.32	1.16	1.48
USNM 481774	-	14.83	18.00	15.00	-	7.84
USNM 511930	-	-	-	-	-	-
USNM 256737	-	-	-	-	-	-
USNM 300000	9.67	13.50	14.67	12.67	4.67	8.50
USNM 397984	5.14	5.35	5.47	4.65	-	-
USNM 574901	6.20	5.88	5.84	-	4.16	4.00
USNM 252306	6.34	5.74	5.81	-	33.86	32.86
USNM 252299	5.16	5.05	5.54	-	30.46	31.90
USNM 256676	-	-	-	-	31.04	31.27
USNM 548401	8.61	7.31	-	-	46.20	44.26
USNM 260868	7.97	7.79	-	-	32.79	32.45
USNM 257009	8.60	9.21	-	-	46.05	47.91
USNM 200353	-	-	-	-	-	-
USNM 283876	2.67	7.67	-	-	4.17	-
USNM 583067	3.33	1.83	2.50	-	4.17	7.00
USNM 256914	-	-	-	-	-	-
USNM 258016	-	-	-	-	-	-

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Museum #	Length of Second Proximal Carpal Phalanx	Length of Third Proximal Carpal Phalanx	Length of Fourth Proximal Carpal Phalanx	Length of Fifth Proximal Carpal Phalanx	Length of Second Intermediate Carpal Phalanx	Length of Third Intermediate Carpal Phalanx
USNM 174080	-	-	-	-	-	-
USNM 174079	-	-	-	-	-	-
USNM 332937	-	-	-	-	-	-
USNM 267209	-	-	-	-	-	-
USNM 258017	-	-	-	-	-	-
USNM 197320	-	-	-	-	-	-
USNM 173374	-	-	-	-	-	-
USNM 20941	-	-	-	-	-	-
USNM 257844	-	-	-	-	-	-
USNM 292647	-	-	-	-	-	-
USNM 254807	-	-	-	-	-	-
USNM 49660	-	-	-	-	-	-
USNM 307073	-	-	-	-	-	-
USNM 258520	8.21	9.79	10.14	9.14	-	-
USNM 268872	9.00	10.56	10.94	10.12	6.96	7.64
USNM 196743	-	-	-	-	-	-
USNM 173363	-	-	-	-	-	-
USNM 173365	-	-	-	-	-	-
USNM 353243	-	-	-	-	-	-
USNM 173361	-	-	-	-	-	-
USNM 267267	-	-	-	-	-	-
USNM 292654	-	-	6.61	-	-	-
USNM 397068	5.00	-	6.05	5.46	-	-
USNM 551841	4.85	5.25	5.22	4.99	3.55	4.13
USNM 398288	-	-	-	-	-	-
USNM 235940	-	-	-	-	-	-
USNM 332333	-	-	-	-	-	-
USNM 267440	-	-	-	-	-	-
USNM 524544	5.17	5.50	5.75	5.08	-	4.50
USNM 524543	-	-	-	-	-	-
USNM 397065	-	5.48	5.71	-	-	-
USNM 397040	4.49	5.16	5.02	4.69	3.92	3.85
USNM 397021	-	-	-	-	-	-
USNM 397022	-	-	-	-	-	-
USNM 398287	-	-	-	-	-	-
USNM 397017	-	-	-	-	-	-
USNM 528045	7.44	8.43	9.07	7.74	5.24	6.94
USNM 500992	8.70	10.00	10.45	8.53	6.12	7.96
USNM 503982	8.50	9.50	10.17	7.67	8.17	8.00
USNM 528175	8.33	9.67	11.08	8.50	6.08	8.00
USNM 396202	-	9.44	10.00	7.78	-	7.62
USNM 398003	8.41	8.69	10.08	8.33	5.55	7.59
USNM 244953	6.43	7.82	8.06	6.35	4.17	6.23
USNM 244934	6.43	-	7.30	6.35	3.97	-
USNM 244938	6.01	7.46	7.86	6.37	3.66	5.65
USNM 244954	5.87	7.18	7.42	5.93	3.98	5.77

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Museum #	Length of Second Proximal Carpal Phalanx	Length of Third Proximal Carpal Phalanx	Length of Fourth Proximal Carpal Phalanx	Length of Fifth Proximal Carpal Phalanx	Length of Second Intermediate Carpal Phalanx	Length of Third Intermediate Carpal Phalanx
USNM 244956	6.13	7.54	7.88	6.39	3.97	6.25
USNM 244958	6.11	7.66	8.06	6.43	3.89	5.95
USNM 397160	8.49	9.77	10.19	-	-	-
USNM 270303	9.63	11.10	11.55	8.29	6.65	9.06
USNM 564075	8.94	10.69	10.94	9.18	6.24	8.82
USNM 261765	9.31	10.94	11.18	9.22	5.88	8.16
USNM 257984	10.02	12.44	13.54	10.43	7.36	9.86
USNM 548038	-	10.16	10.45	8.78	-	-

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Museum #	Length of Fourth Intermediate Carpal Phalanx	Length of Fifth Intermediate Carpal Phalanx	Femur Length	Tibia Length	Fibula Length	Medio-lateral Midshaft Diameter of the Femur
USNM 84546	-	-	-	-	-	-
USNM 84547	-	-	82.94	79.38	77.83	5.06
USNM 466118	-	-	76.23	72.64	70.69	4.56
USNM 466119	-	-	79.75	80.45	77.94	5.17
USNM 466120	-	-	74.23	73.46	71.51	4.78
USNM 466121	-	-	69.93	69.84	62.82	3.90
USNM 429832	-	-	110.68	-	-	7.40
USNM 466126	-	-	78.29	82.07	-	4.70
USNM 399470	-	-	103.49	105.13	102.06	5.90
USNM 396650	41.42	39.79	33.39	46.22	-	2.95
USNM 396640	-	-	31.70	44.43	-	2.64
USNM 396675	-	-	34.19	48.62	-	3.12
USNM 463935	-	-	32.10	45.78	-	2.74
USNM 464511	-	-	34.27	49.38	-	3.03
USNM 464514	-	-	31.03	43.96	-	2.71
USNM 464996	39.86	-	30.76	43.79	-	2.82
USNM 464998	-	-	30.03	44.74	-	2.63
USNM 573383	23.79	19.87	16.88	19.67	-	1.15
USNM 573387	19.86	16.56	16.33	18.25	-	1.06
USNM 573400	22.54	20.23	17.05	20.65	-	1.09
USNM 573403	22.51	23.50	17.25	20.67	-	1.16
USNM 573409	23.78	20.78	17.92	21.50	-	1.17
USNM 573410	24.00	21.75	17.29	21.50	-	1.21
USNM 396827	30.76	20.23	41.95	43.48	-	1.79
USNM 577065	-	-	16.67	16.50	-	0.72
USNM 362098	18.20	13.44	23.19	20.52	-	1.46
USNM 365686	9.08	20.25	15.10	13.17	-	1.06
USNM 523439	16.86	13.60	23.79	23.29	-	2.02
USNM 102922	5.44	5.83	15.25	14.50	-	0.51
USNM 549507	8.83	-	17.67	13.67	-	0.48
USNM 120576	13.14	11.31	17.88	22.83	-	6.37
FMNH 61032	22.53	24.00	119.41	117.68	117.09	5.55
FMNH 56442	22.32	23.17	116.23	118.13	116.13	5.68
FMNH 62067	-	-	117.47	111.04	107.49	5.95
FMNH 61030	21.25	22.33	-	127.04	126.83	-
FMNH 56441	-	-	121.06	121.09	119.29	5.75
USNM 144662	20.57	21.27	104.06	100.43	94.03	5.43
USNM 239191	22.55	-	124.35	123.49	123.39	5.60
USNM 578084	-	-	105.41	110.16	108.71	5.46
Uncatalogued	22.71	23.36	115.05	114.76	114.42	5.80
USNM 155363	-	-	-	-	-	-
USNM 154600	-	-	89.40	88.89	87.74	4.25
USNM 49640	23.98	24.10	120.93	115.00	-	5.26
USNM 49693	22.80	24.82	124.52	119.88	120.45	5.02
USNM 198704	-	-	116.58	119.99	-	4.90
USNM 197202	-	-	132.88	128.24	127.29	4.79

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Museum #	Length of Fourth Intermediate Carpal Phalanx	Length of Fifth Intermediate Carpal Phalanx	Femur Length	Tibia Length	Fibula Length	Medio-lateral Midshaft Diameter of the Femur
USNM 196905	-	-	121.82	115.41	115.07	4.34
USNM 151887	-	-	-	-	-	-
USNM 317118	-	-	129.23	128.80	129.66	4.91
USNM 49470	24.57	25.07	125.21	121.36	121.12	4.86
USNM 197203	-	-	67.45	65.28	60.59	3.61
USNM 221150	6.67	6.64	72.04	78.29	80.15	4.30
USNM 237728	-	-	39.43	44.56	44.42	2.29
USNM 221215	-	-	39.63	43.72	45.06	2.36
USNM 319791	-	-	39.02	40.34	43.24	2.16
USNM 221218	-	-	38.16	41.08	42.90	2.32
USNM 297823	3.96	4.38	36.68	38.90	40.12	2.44
USNM 270812	-	-	37.82	42.10	42.83	2.29
USNM 49937	3.94	3.91	35.26	38.95	39.09	2.10
USNM 396817	-	-	35.71	-	-	2.08
USNM 543146	-	4.22	34.03	36.43	37.59	2.15
USNM 534229	-	4.24	34.95	37.25	37.31	2.01
USNM 293168	-	-	-	-	-	-
USNM 362186	-	-	55.10	58.33	59.63	2.80
USNM 221137	-	-	99.53	98.07	102.24	5.06
USNM 238417	6.77	6.15	89.60	85.57	86.55	4.49
USNM 238366	5.08	-	63.49	58.74	60.66	4.31
USNM 237653	-	4.73	65.80	65.53	66.55	5.19
USNM 237694	-	-	-	-	60.93	4.74
USNM 238391	2.86	3.67	3.76	3.43	56.93	4.97
USNM 238396	5.88	5.39	67.70	62.11	66.49	5.04
USNM 221155	-	4.49	59.62	53.00	59.23	4.50
USNM 238377	5.71	4.86	63.93	60.32	62.04	4.85
USNM 277372	5.22	4.57	63.10	59.37	63.91	4.44
USNM 582004	1.68	1.56	15.00	20.17	20.00	0.94
USNM 481774	10.20	8.57	76.75	69.15	67.76	5.04
USNM 511930	-	-	62.76	53.91	52.97	3.60
USNM 256737	-	-	70.07	66.62	65.90	3.09
USNM 300000	9.67	8.33	74.18	67.70	65.76	5.15
USNM 397984	-	-	42.33	44.13	43.22	2.90
USNM 574901	3.84	-	46.26	46.76	46.94	3.97
USNM 252306	31.83	-	99.17	88.90	86.96	11.43
USNM 252299	31.03	-	88.75	80.25	80.50	10.37
USNM 256676	28.85	-	91.85	79.55	78.58	11.70
USNM 548401	-	-	157.75	146.35	146.00	14.20
USNM 260868	-	-	131.50	119.25	120.00	10.70
USNM 257009	-	-	155.00	139.25	138.25	10.95
USNM 200353	-	-	29.54	32.23	29.60	3.66
USNM 283876	-	-	33.35	35.61	34.50	4.56
USNM 583067	-	-	33.56	38.25	35.12	5.05
USNM 256914	-	-	-	129.17	124.61	-
USNM 258016	-	-	-	133.97	129.66	-

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Museum #	Length of Fourth Intermediate Carpal Phalanx	Length of Fifth Intermediate Carpal Phalanx	Femur Length	Tibia Length	Fibula Length	Medio-lateral Midshaft Diameter of the Femur
USNM 174080	-	-	-	-	-	-
USNM 174079	-	-	-	-	-	-
USNM 332937	-	-	82.31	-	-	4.74
USNM 267209	-	-	-	90.70	87.20	-
USNM 258017	-	-	-	126.86	123.83	-
USNM 197320	-	-	115.94	118.21	116.06	6.53
USNM 173374	-	-	-	-	-	-
USNM 20941	-	-	93.43	-	-	5.16
USNM 257844	-	-	134.28	134.35	131.55	6.87
USNM 292647	-	-	95.28	97.15	94.99	5.59
USNM 254807	-	-	60.03	65.78	-	3.38
USNM 49660	-	-	108.10	105.97	102.18	5.91
USNM 307073	-	-	70.93	73.39	-	3.87
USNM 258520	-	-	58.67	63.72	-	3.57
USNM 268872	8.45	7.05	80.04	80.17	78.31	4.30
USNM 196743	-	-	111.15	113.42	110.87	5.83
USNM 173363	-	-	68.83	-	-	4.29
USNM 173365	-	-	67.75	71.44	69.01	3.95
USNM 353243	-	-	67.48	71.24	69.89	3.99
USNM 173361	-	-	71.06	74.95	73.16	4.00
USNM 267267	-	-	-	104.46	102.40	-
USNM 292654	5.22	-	44.79	-	-	2.64
USNM 397068	4.20	-	36.55	40.45	39.15	2.07
USNM 551841	4.27	3.60	36.66	41.03	40.27	2.06
USNM 398288	-	-	39.30	42.55	42.17	2.53
USNM 235940	-	-	40.96	45.63	44.42	2.42
USNM 332333	-	-	35.94	-	-	2.23
USNM 267440	-	-	37.25	41.66	40.44	2.16
USNM 524544	4.42	3.83	36.71	42.20	41.24	2.16
USNM 524543	-	-	36.16	40.54	39.93	2.16
USNM 397065	-	-	38.40	43.90	42.47	2.38
USNM 397040	3.92	-	36.88	41.55	39.98	2.27
USNM 397021	-	-	38.80	43.32	-	2.42
USNM 397022	-	-	38.34	43.26	-	2.21
USNM 398287	-	-	41.71	46.43	44.70	2.71
USNM 397017	-	-	38.17	43.85	42.63	2.03
USNM 528045	7.38	5.26	52.30	55.26	54.47	4.24
USNM 500992	8.65	6.08	57.14	63.03	61.22	4.86
USNM 503982	8.50	5.83	54.92	60.10	57.65	4.80
USNM 528175	8.67	6.00	50.57	57.91	52.57	4.02
USNM 396202	-	-	56.41	60.60	57.85	4.50
USNM 398003	8.33	5.80	55.74	59.27	56.79	4.05
USNM 244953	6.92	4.56	45.80	49.94	49.29	3.56
USNM 244934	-	4.13	45.13	48.29	46.90	3.34
USNM 244938	6.25	4.21	44.11	46.47	45.44	3.63
USNM 244954	6.37	4.11	-	47.39	46.81	-

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Museum #	Length of Fourth Intermediate Carpal Phalanx	Length of Fifth Intermediate Carpal Phalanx	Femur Length	Tibia Length	Fibula Length	Medio-lateral Midshaft Diameter of the Femur
USNM 244956	6.43	4.46	43.94	46.58	46.39	3.15
USNM 244958	6.59	4.29	43.25	41.93	45.76	3.51
USNM 397160	-	-	60.73	63.69	62.48	5.18
USNM 270303	9.63	6.45	66.41	69.20	69.18	5.60
USNM 564075	8.98	6.41	63.51	67.84	66.55	5.30
USNM 261765	9.31	5.96	63.58	69.03	-	5.07
USNM 257984	11.07	6.81	70.06	75.85	73.91	5.45
USNM 548038	8.82	-	57.16	62.24	59.68	4.95

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Museum #	Anterior-posterior Midshaft Dameter of the Femur	Medio-lateral Midshaft Diameter of the Tibia	Anterior-posterior Midshaft Dameter of the Tibia	Medio-lateral Midshaft Diameter of the Fibula	Anterior-posterior Midshaft Dameter of the Fibula	Length of the Dorsal Spine of the Scapula
USNM 84546	-	-	-	-	-	-
USNM 84547	4.56	3.77	4.38	1.48	1.79	-
USNM 466118	4.40	3.28	4.36	1.06	1.33	30.97
USNM 466119	4.31	3.38	4.50	1.08	1.45	34.52
USNM 466120	4.28	3.66	4.13	1.19	1.74	28.68
USNM 466121	3.47	2.96	3.68	0.95	1.51	26.18
USNM 429832	6.98	-	-	-	-	44.34
USNM 466126	4.58	-	-	3.61	4.47	28.81
USNM 399470	5.52	4.39	5.31	1.22	1.86	-
USNM 396650	2.22	2.20	1.74	-	-	19.67
USNM 396640	2.26	1.84	1.64	-	-	19.43
USNM 396675	2.32	1.94	1.93	-	-	22.22
USNM 463935	2.21	1.84	1.76	-	-	21.45
USNM 464511	2.35	1.88	1.85	-	-	22.97
USNM 464514	2.06	1.71	1.83	-	-	19.94
USNM 464996	2.13	1.86	1.76	-	-	21.42
USNM 464998	2.09	1.99	1.71	-	-	20.08
USNM 573383	1.06	0.91	0.88	-	-	9.57
USNM 573387	0.96	0.84	0.79	-	-	8.37
USNM 573400	1.11	0.93	0.87	-	-	9.64
USNM 573403	1.08	0.85	0.86	-	-	9.46
USNM 573409	1.16	0.98	1.01	-	-	10.08
USNM 573410	1.10	1.00	0.90	-	-	9.92
USNM 396827	1.94	1.34	1.89	-	-	16.10
USNM 577065	0.69	4.63	0.56	-	-	7.39
USNM 362098	1.22	0.91	0.94	-	-	10.59
USNM 365686	0.99	0.70	0.96	-	-	7.47
USNM 523439	1.47	1.21	1.19	-	-	11.75
USNM 102922	0.41	0.33	0.34	-	-	5.75
USNM 549507	0.49	0.48	0.34	-	-	5.08
USNM 120576	1.10	1.19	0.82	-	-	8.17
FMNH 61032	5.63	4.93	4.68	2.03	1.45	36.64
FMNH 56442	6.48	5.26	5.04	2.23	1.80	38.05
FMNH 62067	6.64	5.28	5.42	2.35	1.80	34.58
FMNH 61030	-	5.19	5.51	1.65	2.06	36.09
FMNH 56441	6.81	5.62	5.38	1.45	2.18	33.54
USNM 144662	5.98	4.87	4.40	1.88	1.46	-
USNM 239191	5.97	5.28	4.47	1.84	1.72	-
USNM 578084	5.59	4.71	4.18	1.67	1.64	-
Uncatalogued	6.11	4.86	4.91	1.45	1.57	34.26
USNM 155363	-	-	-	-	-	32.83
USNM 154600	4.56	3.49	3.36	1.19	1.54	23.78
USNM 49640	5.49	4.56	4.79	-	-	31.49
USNM 49693	6.42	4.59	4.15	1.23	2.00	33.55
USNM 198704	5.48	4.01	4.06	-	-	32.76
USNM 197202	6.18	4.40	4.97	1.30	1.24	-

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Museum #	Anterior-posterior Midshaft Dameter of the Femur	Medio-lateral Midshaft Diameter of the Tibia	Anterior-posterior Midshaft Dameter of the Tibia	Medio-lateral Midshaft Diameter of the Fibula	Anterior-posterior Midshaft Dameter of the Fibula	Length of the Dorsal Spine of the Scapula
USNM 196905	5.96	4.81	4.01	1.40	1.58	32.58
USNM 151887	-	-	-	-	-	27.02
USNM 317118	6.77	4.57	4.49	1.86	1.28	35.32
USNM 49470	5.56	4.33	4.43	1.95	1.51	32.26
USNM 197203	3.60	2.98	3.32	1.58	0.96	20.95
USNM 221150	4.59	2.93	3.92	2.22	2.04	25.92
USNM 237728	2.42	1.60	2.14	1.40	1.28	17.56
USNM 221215	2.31	1.65	2.12	1.36	1.27	17.26
USNM 319791	2.45	1.43	1.90	0.99	1.30	17.41
USNM 221218	2.40	1.61	2.33	1.24	1.40	17.41
USNM 297823	2.56	1.72	2.13	1.31	1.39	17.42
USNM 270812	2.48	1.54	2.06	1.22	1.39	17.36
USNM 49937	2.20	1.52	1.91	1.01	1.19	14.58
USNM 396817	2.03	-	-	-	-	14.13
USNM 543146	2.15	1.40	2.13	1.06	1.38	15.45
USNM 534229	2.15	1.28	2.00	0.96	1.21	14.63
USNM 293168	-	-	-	-	-	-
USNM 362186	2.92	1.77	2.71	1.34	1.52	20.77
USNM 221137	5.74	3.83	4.95	2.48	3.07	38.83
USNM 238417	4.67	2.89	3.94	1.99	2.75	34.80
USNM 238366	4.92	2.92	4.08	1.97	2.56	28.45
USNM 237653	5.69	3.38	4.74	2.57	2.80	35.28
USNM 237694	4.83	2.70	4.49	2.00	2.69	-
USNM 238391	5.27	3.24	3.98	2.28	2.86	5.39
USNM 238396	5.18	3.03	4.79	2.43	2.70	34.20
USNM 221155	4.85	2.64	4.12	2.16	2.77	29.33
USNM 238377	5.10	3.02	4.52	2.15	2.94	32.54
USNM 277372	5.68	2.77	4.43	2.10	2.62	31.14
USNM 582004	0.94	0.58	0.94	0.48	0.46	8.20
USNM 481774	4.31	3.67	-	2.40	1.95	28.16
USNM 511930	3.46	2.42	2.56	1.52	1.38	21.72
USNM 256737	2.63	2.31	1.69	1.31	1.43	20.75
USNM 300000	4.29	4.25	3.60	2.48	6.98	33.20
USNM 397984	2.79	2.31	2.83	1.08	1.17	24.08
USNM 574901	3.19	2.59	3.43	0.95	1.29	24.64
USNM 252306	7.98	7.00	6.54	4.03	5.34	45.67
USNM 252299	7.51	6.57	5.37	4.03	4.19	40.59
USNM 256676	8.38	6.84	6.62	3.82	5.53	45.34
USNM 548401	13.14	9.70	9.15	3.93	7.50	57.94
USNM 260868	9.04	6.63	5.65	4.21	3.77	48.44
USNM 257009	9.36	7.32	6.45	3.75	5.07	49.73
USNM 200353	2.39	1.74	2.14	1.02	1.46	16.84
USNM 283876	2.76	2.59	2.59	1.10	1.96	20.55
USNM 583067	2.40	1.98	2.72	1.02	1.82	19.75
USNM 256914	-	5.36	6.52	0.91	2.12	-
USNM 258016	-	5.13	6.53	1.21	1.94	-

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Museum #	Anterior-posterior Midshaft Dameter of the Femur	Medio-lateral Midshaft Diameter of the Tibia	Anterior-posterior Midshaft Dameter of the Tibia	Medio-lateral Midshaft Diameter of the Fibula	Anterior-posterior Midshaft Dameter of the Fibula	Length of the Dorsal Spine of the Scapula
USNM 174080	-	-	-	-	-	36.94
USNM 174079	-	-	-	-	-	35.02
USNM 332937	4.52	-	-	-	-	29.13
USNM 267209	-	3.75	4.60	0.97	2.02	-
USNM 258017	-	5.28	6.36	1.19	2.54	-
USNM 197320	6.77	4.62	6.18	1.12	1.47	39.93
USNM 173374	-	-	-	-	-	33.76
USNM 20941	5.13	-	-	-	-	37.36
USNM 257844	6.89	5.20	6.35	1.21	1.75	34.01
USNM 292647	5.15	4.06	4.44	1.00	1.48	32.77
USNM 254807	3.51	2.74	3.35	0.62	0.85	23.41
USNM 49660	5.49	4.32	5.20	0.82	1.28	-
USNM 307073	4.01	3.50	3.75	1.10	1.16	25.12
USNM 258520	3.63	3.05	3.27	-	-	22.64
USNM 268872	4.65	3.72	4.34	0.81	1.11	32.09
USNM 196743	5.30	4.29	5.31	1.00	1.31	41.47
USNM 173363	4.27	-	-	-	-	29.10
USNM 173365	4.51	3.16	3.93	0.90	1.41	27.74
USNM 353243	4.16	3.38	3.85	0.97	1.13	23.83
USNM 173361	3.84	3.24	3.55	0.67	1.11	27.96
USNM 267267	-	4.10	4.45	1.16	2.14	-
USNM 292654	2.65	-	-	-	-	18.77
USNM 397068	2.11	1.80	2.06	0.45	0.55	16.52
USNM 551841	1.85	1.64	1.86	0.37	0.52	16.63
USNM 398288	2.32	2.07	2.18	0.47	0.79	19.38
USNM 235940	2.33	1.99	2.15	0.46	0.63	-
USNM 332333	2.07	-	-	-	-	16.32
USNM 267440	2.10	1.85	1.92	0.46	0.55	16.54
USNM 524544	2.01	1.75	1.90	0.39	0.52	16.33
USNM 524543	2.21	1.79	1.92	0.46	0.56	15.61
USNM 397065	2.22	1.98	2.02	0.48	0.63	16.74
USNM 397040	2.11	1.77	2.10	0.38	0.71	15.68
USNM 397021	2.23	1.91	2.11	0.45	0.59	16.29
USNM 397022	2.23	1.87	1.90	-	-	16.14
USNM 398287	2.59	2.17	2.51	0.68	0.88	18.41
USNM 397017	1.80	1.89	1.94	0.44	0.58	18.79
USNM 528045	3.97	3.36	3.80	1.14	1.67	28.17
USNM 500992	4.44	3.56	3.96	1.03	1.52	31.34
USNM 503982	4.08	3.85	4.34	1.18	1.87	29.42
USNM 528175	3.56	2.87	3.38	1.05	1.35	26.27
USNM 396202	3.91	3.43	3.87	0.96	1.76	29.25
USNM 398003	3.72	3.15	3.79	0.95	1.79	27.49
USNM 244953	3.10	2.82	2.89	0.68	0.99	22.90
USNM 244934	3.08	2.66	2.79	0.73	0.90	22.93
USNM 244938	3.10	2.78	2.76	0.79	0.95	22.65
USNM 244954	-	2.47	2.69	0.65	0.77	22.85

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Museum #	Anterior-posterior Midshaft Dameter of the Femur	Medio-lateral Midshaft Diameter of the Tibia	Anterior-posterior Midshaft Dameter of the Tibia	Medio-lateral Midshaft Diameter of the Fibula	Anterior-posterior Midshaft Dameter of the Fibula	Length of the Dorsal Spine of the Scapula
USNM 244956	2.93	2.47	2.71	0.64	1.18	-
USNM 244958	2.92	2.63	3.04	0.73	1.19	22.38
USNM 397160	5.13	4.48	5.05	1.09	1.73	31.68
USNM 270303	5.16	4.49	5.21	1.53	1.52	34.46
USNM 564075	4.75	4.61	5.07	1.21	1.44	32.67
USNM 261765	4.69	4.49	4.68	-	-	34.44
USNM 257984	4.82	4.49	4.97	1.27	1.69	36.72
USNM 548038	4.29	4.35	4.74	0.97	1.44	22.16

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Museum #	Length of the Vertebral Border of the Scapula	Clavicle Length	Anterior-posterior Midshaft Diameter of the Clavicle	Medio-lateral Midshaft Diameter of the Clavicle
USNM 84546	-	-	-	-
USNM 84547	-	-	-	-
USNM 466118	28.54	23.96	1.21	1.82
USNM 466119	31.96	24.86	1.23	1.98
USNM 466120	28.37	24.26	1.22	1.89
USNM 466121	22.49	19.07	1.09	1.52
USNM 429832	45.40	34.91	2.14	2.86
USNM 466126	-	-	-	-
USNM 399470	-	28.89	1.59	2.63
USNM 396650	32.24	34.39	1.86	3.40
USNM 396640	32.22	35.18	1.67	3.38
USNM 396675	37.62	41.64	2.13	4.74
USNM 463935	33.52	33.29	1.56	3.41
USNM 464511	38.08	41.94	1.60	4.21
USNM 464514	33.22	33.19	1.71	3.17
USNM 464996	32.01	34.11	1.52	3.50
USNM 464998	32.85	33.97	1.67	3.14
USNM 573383	16.47	13.80	0.82	1.41
USNM 573387	15.20	13.45	0.67	1.33
USNM 573400	17.30	13.98	0.75	1.52
USNM 573403	17.75	14.42	0.76	1.54
USNM 573409	18.00	15.00	0.83	1.54
USNM 573410	16.83	14.75	0.88	1.50
USNM 396827	30.46	19.46	1.17	2.93
USNM 577065	10.57	10.69	1.04	0.53
USNM 362098	18.33	8.70	1.34	1.05
USNM 365686	12.70	13.43	1.09	0.62
USNM 523439	18.44	15.48	1.41	0.90
USNM 102922	8.92	8.58	0.56	0.43
USNM 549507	7.92	8.25	0.67	0.42
USNM 120576	12.83	13.99	1.06	0.65
FMNH 61032	41.95	35.77	1.86	2.77
FMNH 56442	41.96	40.07	2.24	2.93
FMNH 62067	42.75	35.04	2.21	2.80
FMNH 61030	47.05	38.98	2.40	2.99
FMNH 56441	48.46	36.21	2.06	2.93
USNM 144662	-	-	-	-
USNM 239191	-	-	-	-
USNM 578084	-	36.02	2.15	2.92
Uncatalogued	-	-	-	-
USNM 155363	39.97	35.69	1.75	2.73
USNM 154600	23.36	25.01	1.30	1.87
USNM 49640	38.37	34.27	1.87	2.90
USNM 49693	40.54	35.50	1.94	2.65
USNM 198704	37.37	36.02	1.74	2.26
USNM 197202	44.48	-	-	-

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Museum #	Length of the Vertebral Border of the Scapula	Clavicle Length	Anterior-posterior Midshaft Diameter of the Clavicle	Medio-lateral Midshaft Diameter of the Clavicle
USNM 196905	39.28	31.97	1.45	2.79
USNM 151887	35.88	30.79	1.69	2.22
USNM 317118	41.75	34.51	1.76	3.30
USNM 49470	41.79	34.32	1.49	2.58
USNM 197203	18.58	22.90	1.26	1.67
USNM 221150	24.73	25.98	1.44	2.23
USNM 237728	13.50	16.33	0.73	1.24
USNM 221215	13.31	16.21	0.81	1.14
USNM 319791	15.38	15.85	0.75	1.26
USNM 221218	12.85	16.43	0.76	1.27
USNM 297823	14.20	17.30	0.82	1.28
USNM 270812	14.02	16.15	0.64	1.28
USNM 49937	12.39	14.47	0.72	0.94
USNM 396817	11.24	13.03	0.56	0.91
USNM 543146	10.55	14.10	0.71	1.14
USNM 534229	10.77	14.95	0.65	1.05
USNM 293168	-	-	-	-
USNM 362186	18.21	18.98	0.77	1.37
USNM 221137	27.22	28.92	1.52	2.54
USNM 238417	25.10	25.82	1.44	1.97
USNM 238366	22.44	25.61	1.54	2.11
USNM 237653	27.48	24.14	1.19	2.75
USNM 237694	-	30.69	23.69	23.56
USNM 238391	4.82	29.62	21.58	25.21
USNM 238396	27.25	24.98	1.58	2.19
USNM 221155	27.70	21.78	1.18	2.17
USNM 238377	26.37	22.25	1.31	2.70
USNM 277372	27.40	22.28	1.09	2.10
USNM 582004	5.02	8.20	0.35	0.46
USNM 481774	29.46	30.51	1.98	3.08
USNM 511930	23.77	18.24	0.94	1.64
USNM 256737	18.48	19.91	1.20	1.56
USNM 300000	34.01	31.34	2.03	2.66
USNM 397984	20.07	15.52	0.94	0.98
USNM 574901	18.14	17.89	1.22	1.40
USNM 252306	65.42	20.79	1.95	2.35
USNM 252299	54.69	-	-	-
USNM 256676	66.39	-	-	-
USNM 548401	81.09	50.00	2.55	4.34
USNM 260868	53.49	36.45	1.89	3.05
USNM 257009	54.98	38.47	2.07	3.21
USNM 200353	18.86	12.50	1.33	0.58
USNM 283876	22.81	16.79	1.42	0.82
USNM 583067	24.09	15.95	1.40	0.81
USNM 256914	-	-	-	-
USNM 258016	-	-	-	-

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Museum #	Length of the Vertebral Border of the Scapula	Clavicle Length	Anterior-posterior Midshaft Diameter of the Clavicle	Medio-lateral Midshaft Diameter of the Clavicle
USNM 174080	30.68	30.58	1.78	2.40
USNM 174079	30.40	29.26	1.54	2.14
USNM 332937	23.95	23.70	1.42	1.87
USNM 267209	-	-	-	-
USNM 258017	-	-	-	-
USNM 197320	37.26	35.26	2.27	2.74
USNM 173374	27.94	29.00	1.73	2.18
USNM 20941	28.22	29.27	1.76	2.34
USNM 257844	28.44	-	-	-
USNM 292647	26.45	28.16	1.51	1.97
USNM 254807	16.87	-	-	-
USNM 49660	-	-	-	-
USNM 307073	19.50	20.50	1.24	1.52
USNM 258520	16.08	19.91	0.94	1.45
USNM 268872	26.83	26.86	1.31	1.90
USNM 196743	36.50	35.13	1.60	2.38
USNM 173363	23.07	25.47	1.40	1.74
USNM 173365	23.36	24.92	1.21	1.94
USNM 353243	23.11	25.54	1.52	1.79
USNM 173361	22.17	24.61	1.23	1.25
USNM 267267	-	-	-	-
USNM 292654	15.05	16.75	0.75	1.21
USNM 397068	13.75	15.07	0.70	0.92
USNM 551841	11.78	14.85	0.66	0.89
USNM 398288	16.59	17.45	0.93	1.06
USNM 235940	-	17.21	0.80	1.08
USNM 332333	12.96	-	-	-
USNM 267440	14.10	14.14	0.82	0.96
USNM 524544	12.58	14.17	0.77	1.05
USNM 524543	-	14.02	0.87	1.02
USNM 397065	13.33	-	-	-
USNM 397040	12.69	14.47	0.77	1.15
USNM 397021	13.07	15.72	0.72	1.03
USNM 397022	13.90	15.53	0.72	1.13
USNM 398287	14.47	17.16	0.87	1.19
USNM 397017	13.95	16.81	0.72	0.97
USNM 528045	22.75	20.02	1.10	1.86
USNM 500992	25.59	22.20	1.18	2.12
USNM 503982	25.32	21.76	1.31	2.12
USNM 528175	20.49	19.50	1.14	1.78
USNM 396202	23.08	21.26	1.10	1.87
USNM 398003	22.14	19.91	0.98	1.98
USNM 244953	19.39	17.25	0.93	1.59
USNM 244934	20.25	15.71	0.98	1.35
USNM 244938	18.47	16.53	0.98	1.61
USNM 244954	19.49	16.40	0.90	1.29

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Museum #	Length of the Vertebral Border of the Scapula	Clavicle Length	Anterior-posterior Midshaft Diameter of the Clavicle	Medio-lateral Midshaft Diameter of the Clavicle
USNM 244956	-	16.72	0.81	1.76
USNM 244958	20.73	17.25	0.91	1.45
USNM 397160	28.91	23.17	1.21	2.12
USNM 270303	30.14	24.85	1.44	2.39
USNM 564075	28.43	24.65	1.35	2.30
USNM 261765	26.56	23.75	1.31	2.29
USNM 257984	33.28	27.02	1.49	2.78
USNM 548038	24.66	22.17	1.28	2.14

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