MAMMALIAN HAIR DIAMETER AS A POSSIBLE MECHANISM FOR HOST SPECIALIZATION IN CHEWING LICE

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We examined the relationship between mammalian hair diameter and body mass at several taxonomic levels (interordinal, intrafamilial, intrageneric, and intraspecific) and showed a significant, positive allometric relationship between hair diameter and body size at all taxonomic levels examined. The allometric coefficient (α) ranged from 0.13 to 0.33. Within pocket gophers (Geomyidae), a significant positive relationship exists between hair diameter and rostral groove dimensions of their chewing lice, *Geomydoecus,* which use the rostral groove to grasp hairs of their host. Coupled with previous evidence of a strong allometric relationship between rostral groove width and louse body size, our findings suggest that hair diameter of the host is an important determinant of body size in chewing lice that parasitize pocket gophers.

Key words: body mass, Geomyidae, hair diameter, host, parasite, Phthiraptera, Rodentia, Trichodectidae

Body size of host and parasite often are correlated positively. Harvey and Keymer (1991) and Morand et al. (2000) demonstrated this trend for chewing lice (Phthiraptera: Trichodectidae) and their pocket gopher hosts (Rodentia: Geomyidae). Specifically, Harvey and Keymer (1991) used the comparative method to demonstrate that increased body size in pocket gophers is associated invariably with increased size of their ectoparasites. They suggested that lice grow larger on larger hosts because those hosts presumably live longer, allowing their lice more time to grow. Although intriguing, this explanation seems unlikely, given that generation time of chewing lice (about 40 days—Rust 1974) is almost an order of magnitude less than generation time of even the shortest-lived species of pocket gopher (about 1 year—Nowak 1999).

Other potential explanations exist for the body-size correlation documented by Harvey and Keymer (1991). For example, ability of the host to detect and destroy ectoparasites may scale with host body size, thereby placing an upper limit on body size of the parasite. Eolutionary changes in the body mass of the host also might alter habitat of chewing lice in terms of temperature, humidity, hair length and diameter, and other habitat parameters. Because lice are extremely host specific (Price and Emerson 1971; Reed and Hafner 1997) and inextricably tied to their host for survival (Kellogg 1913; Marshall 1981), it seems likely that lice would show finely tuned adaptations for life on their host. Characteristics of the hair, particularly hair diameter, should be important components of the environment of the louse (Fig. 1) because of the pivotal role that hair plays in louse feeding, locomotion, ovipositing, and survival (Murray 1957).

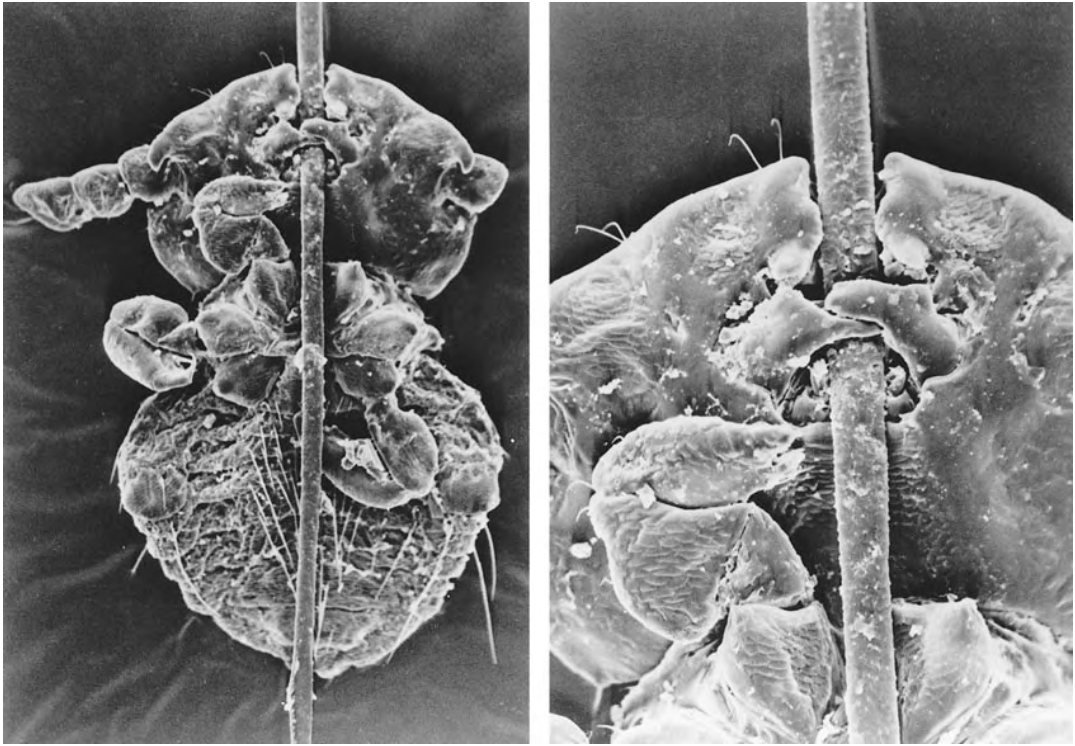Mammal pelage consists of 2 basic types of hairs: guard hairs, which are relatively

FIG. 1.—Electron micrograph (left) of a chewing louse (*Geomydoecus aurei*) attached to the hair shaft of a pocket gopher (*Thomomys bottae*). Magnified view (right) of rostral groove and hair shaft.

long and thick, and wool hairs (or underfur), which are shorter, thinner hairs (Mayer 1952). Our observations of chewing lice reveal that lice spend most of their time moving among guard hairs and are seldom seen attached to wool hairs. Accordingly, we focused this investigation on mammalian guard hairs. We examined the relationship between the diameter of guard hair and body mass at several taxonomic levels in mammals (interordinal, intrafamilial, intrageneric, and intraspecific) to determine the generality of the hair size–body size relationship in mammals. We also investigated whether hair diameter of the host was correlated with host and parasite body size in geomyid rodents.

MATERIALS AND METHODS

A single adult individual from each of 18 species of nongeomyid mammals (representing 17 families in 9 orders; Appendix I) was examined to assess variation in hair diameter across differ-

ent orders of mammals. Taxa were selected randomly from the Louisiana State University Collection of Mammals, except that species with conspicuous spines or quills were avoided and range of body size was maximized as much as possible (Appendix I). Because of difficulty in sampling so many widely divergent taxa, some specimens were not collected from the wild (Appendix I) and season of collection was not standardized.

Guard hairs ($n = 20$ per individual) were removed from the nape region of museum study skins. The nape region was selected to standardize the sampling procedure and reduce the likelihood of damage to hairs from grooming. Hairs were mounted on microscope slides with Permount® and secured with cover slips. Mathiak (1938) determined that the greatest diameter of most mammalian guard hairs was found roughly one-half the distance from the root to the tip. Accordingly, we measured hair diameter about midway between the root and tip using a light microscope fitted with an ocular micrometer scale.

Mass of each mammal in this study was taken directly from the specimen tag or was estimated on the basis of information provided by Nowak (1999).

Fourteen species in the family Geomyidae (Appendix I) were examined to assess variation in hair diameter within a single family of mammals. Guard hairs ($n = 200$ per specimen) were sampled from throughout the gopher pelage and prepared for light microscopy. A single individual from each of 7 species in the genus *Thomomys* (Appendix I) was examined to assess variation in hair diameter within a single genus of pocket gophers. Guard hairs ($n = 200$ per specimen) were sampled from throughout the pelage and prepared for microscopy. Likewise, 8 individuals from a single species, *Thomomys bottae,* were examined to assess variation in hair diameter within a single species of pocket gopher. Guard hairs ($n = 200$ per specimen) were sampled from throughout the gopher pelage and prepared for microscopy.

Width of the rostral groove was measured for adult lice collected from the same individual gophers from which hair diameter was measured and with about equal representation of male and female lice. Louse samples were *Geomydoecus scleritus* ($n = 11$) from *Geomys pinetus, Geomydoecus panamensis* ($n = 11$) from *Orthogeomys cavator, Geomydoecus setzeri* ($n = 8$) from *O. underwoodi, Geomydoecus aurei* ($n = 10$) from *Thomomys bottae, Thomomydoecus minor* ($n = 6$) from *Thomomys bottae,* and *Geomydoecus oregonus* ($n = 11$) from *T. bulbivorus.* Lice were cleared for light microscopy by soaking in the following series of solutions (10–20 min/solution): 50% EtOH, 60% EtOH, 70% EtOH, 10% KOH, 80% EtOH, 90% EtOH, 100% EtOH, and xylene. Lice were mounted on microscope slides, secured with a coverslip, and allowed to dry for 24 h. Rostral groove width was measured with a light microscope fitted with an ocular micrometer.

Because comparisons across species boundaries potentially are confounded by phylogenetic relationships, independent contrasts (Felsenstein 1985; Harvey and Pagel 1991) were used to remove phylogenetic effects from our data. We used the computer program CAIC (Comparative Analysis of Independent Contrasts—Purvis and Rambaut 1995), which uses a phylogenetic hypothesis to generate independent contrasts of data. Those independent contrasts were then an-alyzed statistically. Comparisons among orders of mammals were not transformed using CAIC because most mammalian ordinal relationships are unclear and because such comparisons generally are considered independent because of the large phylogenetic distance between terminal taxa. Hair diameter and body mass measurements for pocket gophers were transformed into independent contrasts using a composite geomyid phylogeny based on phylogenetic studies by Hafner et al. (1994), Smith (1998), and Spradling (1997). No phylogenetic hypotheses were available for taxa below the level of species; therefore, comparisons within *Thomomys bottae* were not transformed into independent contrasts. Model II regression analyses (major axis method) were performed using the SYSTAT statistical analysis software package (SYSTAT, Inc. 1992). Model II regression is appropriate when 2 variables lack a clear dependent–independent relationship and both are measured with error (LaBarbera 1989; Martin and Barbour 1989; Silva 1998). Regressions of independent contrasts were constrained through the origin, as required by CAIC to retain $d.f. = n - 2$ (Garland et al. 1992; Purvis and Rambaut 1995).

RESULTS

The regression analysis of hair diameter and body mass for 18 species representing 9 orders of mammals (Fig. 2a) revealed a positive relationship ($P < 0.05$; Table 1). The allometric coefficient of this relationship ($\alpha = 0.13 \pm 0.03$) was low, indicating that body mass increased more rapidly than hair diameter among mammals examined, which ranged in body size from a 3.5-g bat (*Pipistrellus*) to a 600-kg bear (*Ursus*).

Regression analysis of independent contrasts of hair diameter and body mass for 14 species of pocket gophers (Fig. 2b) revealed a similar allometric trend ($\alpha = 0.25 \pm 0.05$, $P < 0.05$; Table 1). Thus, when analyzed at the family level (and controlling for phylogenetic relationships within the family), larger species of pocket gophers tended to have thicker guard hairs.

Examination of the relationship between hair diameter and body mass within a single genus of pocket gophers (*Thomomys;* Fig. 2c) showed the same trend evident in the
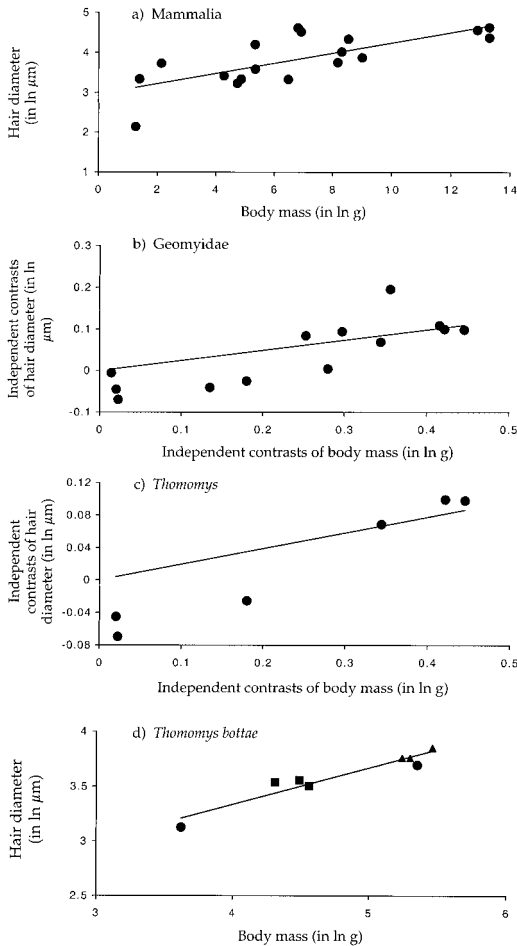
FIG. 2.—a) Major axis regressions performed on ln(mass) and ln(diameter) for 18 species of mammals. b) Major axis regression through the origin of independent contrasts of ln(mass) and ln(diameter) for members of the family Geomyidae. c) Major axis regression through the origin of independent contrasts of ln(mass) and ln(diameter) for pocket gophers in the genus *Thomomys.* d) Regression (major axis method) performed on ln(mass) and ln(diameter) for 8 individuals of *Thomomys bottae.* Individuals designated by squares (collected in native desert–scrub habitat) and triangles (collected in alfalfa fields) are those analyzed by Patton and Brylski (1987) and Smith and Patton (1988). Regression models are in Table 1, and taxa examined are listed in Appendix I.

analyses at higher taxonomic levels. In individuals representing 7 species of *Thomomys,* hair diameter showed a significant allometric relationship with body mass ($\alpha = 0.20 \pm 0.07$, $P < 0.05$; Table 1).

Regression analysis of hair diameter and body mass for 8 individuals of *Thomomys bottae* (Fig. 2d) also showed a significant, positive relationship ($\alpha = 0.33 \pm 0.04$, $P < 0.05$; Table 1). Thus, larger individuals of *T. bottae* tended to have thicker guard hairs than smaller individuals of the same species.

The regression analysis of louse groove width and gopher hair diameter (Fig. 3) revealed a positive relationship between those variables ($P < 0.05$). The regression coefficient ($\alpha = 1.09 \pm 0.09$) suggested a near-isometric relationship between groove width and hair diameter, indicating that the 2 structures varied proportionately. Importantly, the Y-intercept of the regression (Fig. 3) was close to zero ($\beta = -3.9$ μm), indicating that width of the rostral groove of a chewing louse was very similar in actual dimensions to maximum width of the guard hairs of its host.

DISCUSSION

Hair diameter and body size.—Our analyses document a consistent negative allometric relationship between hair diameter and body mass in mammals, regardless of the taxonomic level examined. The low allometric coefficient of this relationship (ranging from $\alpha = 0.13$ to 0.33; Table 1) indicates that larger mammals tend to have guard hairs that are larger in absolute diameter but proportionately smaller than guard hairs of smaller mammalian species. This consistent relationship between hair diameter and body size in mammals is reminiscent of the negative allometric relationship observed for many other mammalian features that scale with body size (e.g., brain size, longevity, and metabolism) and suggests that in most species of mammals hair diameter may be constrained within certain boundaries by simple growth laws. This is not to suggest that hair lacks im-

TABLE 1.—Model II regression analyses (major axis method) of the relationship between hair diameter (Diam) and body mass at 4 taxonomic levels in mammals (depicted graphically in Fig. 2; taxa examined are listed in Appendix I).

Taxon (n)	Regression model	Slope	SE	95% CI	P
Nongeomyid Mammalia (18)	ln(Diam) = A + B * ln(Mass)	0.13	0.03	0.06–0.19	<0.05
Geomyidae (14)	ln(Diam) = B * ln(Mass)	0.25	0.05	0.13–0.36	<0.05
Thomomys (7)	ln(Diam) = B * ln(Mass)	0.20	0.07	0.02–0.37	<0.05
Thomomys bottae (8)	ln(Diam) = A + B * ln(Mass)	0.33	0.04	0.24–0.43	<0.05

portant functional significance in most mammalian species or that adaptation has not played an important role in evolution of specialized hairs, such as spines or quills (specifically excluded from this analysis). Although hair diameter, per se, may be rigidly constrained in many (or most) species of mammals, other aspects of mammalian pelage, including detailed microstructure of the hair, hair length, shape, color, and density (number of hairs per follicle and follicle density), are less likely to scale with body size and, thus, may have evolutionary flexibility to serve in a wide variety of adaptive contexts.

The analysis of hair diameter and body-mass relationships within a single species of pocket gopher (*T. bottae*; Fig. 2d) emphasizes the tight linkage between these 2 variables in this species. This leads us to predict that a change in mean body mass within a lineage of pocket gophers over time (e.g., in response to climate change or an increase or decrease in food resources)
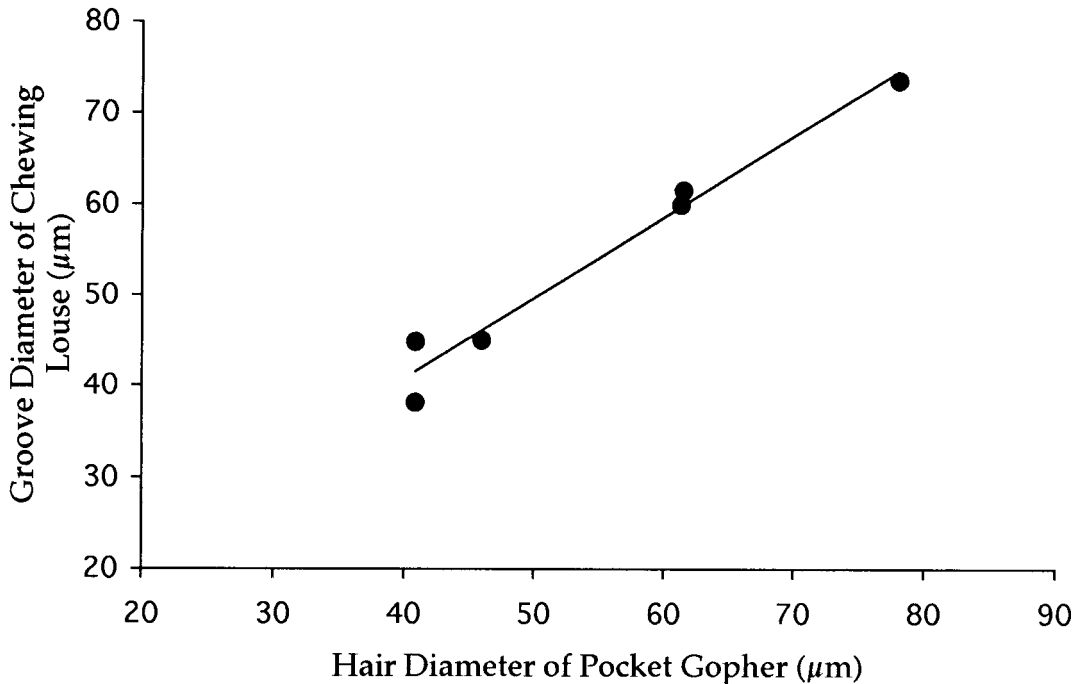

FIG. 3.—Linear regression (general linear model) performed on chewing louse groove width and pocket gopher hair diameter for 6 species of lice collected from 5 species of pocket gophers (*Geomys pinetus, Orthogeomys cavator, O. underwoodi, Thomomys bottae,* and *T. bulbivorus*). Regression models are shown in Table 1, and taxa examined are listed in Appendix I.

will be accompanied by a corresponding change in hair diameter. To test this, we included in our analysis 6 individuals of *T. bottae* that also were examined by Patton and Brylski (1987) and Smith and Patton (1988). Those studies compared body-size relationships between gophers collected from native desert–scrub habitat in 1937–1971 (indicated by squares in Fig. 2d) to those collected from the same geographic region in 1984–1985, many years after the native vegetation had been converted to irrigated alfalfa fields (indicated by triangles in Fig. 2d). Smith and Patton (1988) showed that the pocket gophers collected in the alfalfa fields (presumably direct descendants of the populations sampled decades earlier in native habitat) were significantly larger than their ancestors in overall body mass and other body dimensions. This increase in body mass is evident in our analysis (Fig. 2d), and it is clear that the increase in overall body size in these pocket gophers was accompanied by an increase in hair diameter.

Hair diameter and parasite size.—Larger pocket gophers host larger chewing lice (Harvey and Keymer 1991; Morand et al. 2000), and the previous analyses corroborate the preliminary evidence presented by Morand et al. (2000), showing that larger pocket gophers also have thicker guard hairs. To establish a meaningful connection between hair diameter and louse body size, it is important to focus on some aspect of the body of the louse that interacts directly with the hair of the gopher. For this, we chose the rostral groove of the chewing louse, which is used to grasp the hair of the gopher (Fig. 1). Given that the rostral groove is a rather rigid structure (D. L. Reed et al., in litt.), we predicted a close fit between rostral groove width in chewing lice and hair diameter in pocket gophers under the assumption that a louse with a very narrow rostral groove would be unable to grasp a thick hair, whereas a louse with a very wide groove may slip from a narrow hair. Murray's (1957) studies of chewing

lice (*Damalinia*) on sheep (*Ovis*) showed that lice kept in laboratory colonies in which thin glass fibers were used as artificial hairs were extremely sensitive to width of the glass fibers. If fibers were too thick, lice were unable to grasp them between the gonopod and abdomen and could not lay eggs. Similarly, differences in hair shape (and perhaps diameter) between humans of African descent and those of European descent have been used to explain reduced susceptibility of Africans to head lice (*Pediculus humanus*) from Europe and reduced susceptibility of Europeans to head lice of the same species from Africa (United States Centers for Disease Control 1984). Presumably, lice in the 2 regions have evolved differential abilities to grasp flat hairs typical of humans of African descent versus round hairs typical of humans of European descent.

Our results corroborate preliminary findings of Morand et al. (2000), which show a close fit between hair diameter in pocket gophers and rostral groove width of chewing lice when analyzed at interspecific and intergeneric levels (Fig. 3). This finding, coupled with Morand et al.'s (2000) discovery of a relationship between body size and groove width in chewing lice, suggests that interspecific variation in body size of lice may be determined largely by interspecific variation in diameter of gopher hair. If small species of lice (with narrow rostral grooves) are unable to grasp thick hairs of large pocket gophers and if large lice tend to avoid hosts with thin hairs, this could help explain the high level of host specificity observed in chewing lice at zones of contact between gopher species of very different body sizes (M. S. Hafner, in litt.). This potentially obligate relationship between groove size and hair diameter also may explain why certain species of lice are unable to survive on certain species of hosts in laboratory transfer experiments. For example, experiments by Reed and Hafner (1997) have shown that chewing lice transferred between species of pocket gophers of

similar body size often are able to establish successful breeding colonies on foreign (nonnative) hosts. Lice that occur naturally on a large species of host occasionally are able to survive and reproduce on a smaller species of host, but the reverse does not seem to be true. This suggests that the rostral groove of lice from the smaller hosts may be too narrow to grasp thick hairs of the larger host species. A similar study of body-size relationships between bird lice and their hosts has shown that feather size is a crucial factor in determining success of lice experimentally introduced onto new host taxa (D. Clayton, pers. comm.).

Preliminary analyses of individual, sexual, and ontogenetic variation in hair diameter in pocket gophers (Reed et al., in press.) suggests that variation at these levels may be within the normal range of tolerance for louse rostral grooves. This would explain why a young pocket gopher does not "outgrow" its parasites as the gopher increases in body size (and, thus, hair diameter) ontogenetically. It also would explain why male and female pocket gophers, which often show marked sexual dimorphism in size (Patton and Brylski 1987), nevertheless host the same species of chewing louse.

Our analyses demonstrate a negative allometric relationship between hair diameter and body mass among mammals when analyzed at multiple taxonomic levels. This relationship is evident in the family Geomyidae, even at the intraspecific level. Our data also reveal a significant positive relationship between hair diameter of pocket gophers and rostral groove width of their chewing lice. In fact, we show a nearly exact fit between hair diameter and groove width for host–parasite pairs. Given that lice eventually die if removed from their host, it seems likely that groove width would be under strong selective pressure to conform to host hair diameter. If groove width in lice scales with overall body size, then selection for optimal groove width could indirectly constrain body size in lice.

However, the causal mechanism driving the positive relationship between host and parasite body size (as originally documented by Harvey and Keymer 1991) remains untested. Further studies involving direct observation of chewing lice transferred to nonnative hosts may elucidate the causal mechanism underlying the empirical observation that larger species of pocket gophers tend to host larger species of chewing lice.

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APPENDIX I

Specimens examined and deposited in the Museum of Natural Science, Louisiana State University (LSUMZ), and the Museum of Vertebrate Zoology, University of California, Berkeley (MVZ).

Order	Family	Species	Specimen number	Sex	Mass (g)
Interordinal comparisons					
Insectivora	Soricidae	*Cryptotis parva*	LSUMZ 23789	U	4.0
	Talpidae	*Scalopus aquaticus*	LSUMZ 6981	M	113.4
Chiroptera	Pteropodidae	*Pteropus*	LSUMZ 17726	M	900[a]
	Vespertilionidae	*Pipistrellus hesperus*	LSUMZ 22041	M	3.5
Primates	Cercopithecidae	*Colobus guereza*	LSUMZ 26271[b]	F	8,000[a]
	Lorisidae	*Nycticebus*	LSUMZ 28897[b]	M	650[a]
Lagomorpha	Leporidae	*Lepus alleni*	LSUMZ 13465	M	3,500[a]
	Ochotonidae	*Ochotona princeps*	LSUMZ 35909	F	129.9
Rodentia	Heteromyidae	*Dipodomys ordii*	LSUMZ 25321	M	72
	Muridae	*Baiomys taylori*	LSUMZ 4629	F	8.4
	Sciuridae	*Sciurus niger*	LSUMZ 28476	F	1,000
Artiodactyla	Bovidae	*Taurotragus oryx*	LSUMZ 36155[b]	U	600,000[a]
	Bovidae	*Madoqua*	LSUMZ 36156[b]	M	5,000[a]
Hyracoidea	Procaviidae	*Procavia capensis*	LSUMZ 34649[b]	M	4,000[a]
Perissodactyla	Tapiridae	*Tapirus bairdii*	LSUMZ 6977	M	250,000[a]
	Equidae	*Equus*	LSUMZ 36157[b]	U	400,000[a]
Carnivora	Mustelidae	*Mustela frenata*	LSUMZ 28014	M	207
	Ursidae	*Ursus arctos*	LSUMZ 36158[b]	U	600,000[a]

APPENDIX I.—Continued.

Order	Family	Species	Specimen number	Sex	Mass (g)
Intrafamilial comparisons					
Rodentia	Geomyidae	*Geomys breviceps*	LSUMZ 31451	M	180
	Geomyidae	*G. pinetus*	LSUMZ 23655	M	360
	Geomyidae	*G. tropicalis*	LSUMZ 34345	M	235
	Geomyidae	*Orthogeomys cavator*	LSUMZ 29253	M	875
	Geomyidae	*O. cherriei*	LSUMZ 29539	M	455
	Geomyidae	*O. heterodus*	LSUMZ 29265	M	620
	Geomyidae	*O. underwoodi*	LSUMZ 28368	M	260
	Geomyidae	*Thomomys bottae*	LSUMZ 35992	M	210
	Geomyidae	*T. bulbivorus*	LSUMZ 31313	M	410
	Geomyidae	*T. mazama*	LSUMZ 31398	F	87
	Geomyidae	*T. monticola*	LSUMZ 31411	M	94
	Geomyidae	*T. talpoides*	LSUMZ 34387	F	91
	Geomyidae	*T. townsendii*	LSUMZ 31264	M	300
	Geomyidae	*T. umbrinus*	LSUMZ 34362	M	115
Intrageneric comparisons					
Rodentia	Geomyidae	*Thomomys bottae*	LSUMZ 35992	M	210
	Geomyidae	*T. bulbivorus*	LSUMZ 31313	M	410
	Geomyidae	*T. mazama*	LSUMZ 31398	F	87
	Geomyidae	*T. monticola*	LSUMZ 31411	M	94
	Geomyidae	*T. talpoides*	LSUMZ 34387	F	91
	Geomyidae	*T. townsendii*	LSUMZ 31264	M	300
	Geomyidae	*T. umbrinus*	LSUMZ 34362	M	115
Intraspecific comparisons					
Rodentia	Geomyidae	*Thomomys bottae*	LSUMZ 35992	M	210
	Geomyidae	*T. bottae* (juvenile)	LSUMZ 20936	M	37.5
	Geomyidae	*T. b. perpes*	MVZ 166402	M	236
	Geomyidae	*T. b. perpes*	MVZ 140497	M	96
	Geomyidae	*T. b. perpallidus*	MVZ 170521	M	189
	Geomyidae	*T. b. perpallidus*	MVZ 170565	M	200
	Geomyidae	*T. b. perpallidus*	MVZ 80595	M	74.2
	Geomyidae	*T. b. perpallidus*	MVZ 80606	M	89.0

[a] Specimens not collected from the wild.
[b] Body mass estimated from Nowak (1999).