Chewing Rate Allometry Among Mammals

Authors: Gerstner, Geoffrey E., and Gerstein, Jonathan B.

CHEWING RATE ALLOMETRY AMONG MAMMALS

Geoffrey E. Gerstner* and Jonathan B. Gerstein

Department of Biologic and Materials Sciences, School of Dentistry, and Department of Psychology, University of Michigan, Ann Arbor, MI 48109-1078, USA

Mammalian chewing rate scales inversely to body mass (M); however, controversy exists over the value of the scaling exponent. Different mechanisms explain different values of the scaling exponent; hence, a better estimate of the exponent would provide insight into the mechanisms governing chewing rate across mammalian species. We evaluated the relationship between mean chewing cycle duration (CD; i.e., the inverse of mean chewing rate) and M in 132 species and removed phylogenetic effects by using an independent contrast method currently used in evolutionary biology studies. A one-third–power law resulted when independent contrasts were not used; however, a one-third– to one-fourth–power law resulted when independent contrasts were used to remove phylogenetic effects. We hypothesize that variation in the scaling exponent is due to natural selection acting to increase metabolic efficiency; and variation in the complexity of mandibular kinematics, motor control asymmetry, and mandibular biomechanics, which may act to increase CDs above the ''ideal'' one-fourth–power law. Future studies should consider effects due to jaw-movement kinematics, motor control issues, and biomechanics.

Key words: allometry, chewing rate, independent contrasts, mastication, phylogeny, rhythmic movements

Studies of allometry indicate that many biological phenomena, including rhythmic motor behaviors such as locomotion and chewing, scale exponentially to body size. Body size is usually operationally defined as body mass (M), appendage length, or cross-sectional area (e.g., Druzinsky 1993; Turvey et al. 1988; West et al. 1997). This relationship takes the following mathematical form:

$$y = aM^b \qquad (1)$$

or

$$\log_{10}(y) = \log_{10}(a) + b[\log_{10}(M)], \qquad (2)$$

where y is the dependent biological variable under investigation, M is body mass (or appendage length, etc.), a is a constant specific to the system under study, and b is an allometric scaling exponent.

The logarithmic transformation (equation 2) linearizes the relationship between y and M, where $\log_{10}(a)$ is the y-intercept and the scaling exponent (b) is the slope.

The slope or scaling exponent is important for various reasons. First, it describes the relationship between body size and the dependent variable over as many as 10 orders of magnitude in M (e.g., Turvey et al. 1988). Secondly, in comparative studies, the exponent provides insight into or suggests the existence of laws governing morphological (Fox and Wilczynski 1986), physiological (West et al. 1997), or behavioral (Druzinsky 1993; Turvey et al. 1988) variation within taxa. Finally, allometric scaling probably represents the manifestation of general organizing principles of biological systems (Kauffman 1983; Turvey et al. 1988; West et al. 1997). Hence, an understanding of allometric scaling may ultimately lead to a theoretical understanding of many biological relationships.

A theoretical explanation for allometric scaling does not currently exist. Investigators have introduced several hypotheses to explain the observed relationships, including hypotheses based on mathematical–physical principles, metabolic or energetic cost issues, biomechanical principles, physiological findings, or a combination of these factors (Fortelius 1985; Gunther 1975; Heglund and Taylor 1988; McMahon 1975; Platt and Silvert 1981; Turvey et al. 1988; West et al. 1997).

West et al. (1997) make an important distinction between processes that scale to $M^{1/3}$ and those that scale to $M^{1/4}$. They argue that systems manifesting chaotic structure scale to $M^{1/4}$, whereas nonfractal or geometric systems scale to $M^{1/3}$ (West et al. 1997). In other words, there are important mechanistic distinctions between processes manifesting $M^{1/3}$ versus $M^{1/4}$ scaling.

In contrast, Turvey et al. (1988) indicate that the $M^{1/4}$ scaling for time-dependent behaviors is related to (and derivable from) the $M^{1/3}$ scaling for anatomical lengths. That is, during

* Correspondent: geger@umich.edu

a rhythmic behavior, a body part moving at or near its natural resonance frequency is following an $M^{1/4}$ scaling rule. Obviously motor behaviors that move body parts at or near their resonance frequencies would be metabolically efficient, in that such behaviors would not be working against the intrinsic physical properties of the body part.

In the specific case of mastication, a rhythmical oral behavior specific to mammals, Druzinsky (1993) argues for important distinctions between a one-third–power scaling exponent, which would indicate a geometric scaling regime relating to jaw length, and a one-fourth–power scaling exponent relating to elastic scaling. His results provide support for a one-fourth–power scaling across the class Mammalia. In contrast, Druzinsky (1993) cites previous work by Fortelius (1985) performed mainly on ungulates, which provides support for a one-third–power scaling exponent for mammals. However, neither Druzinsky's (1993) nor Fortelius' (1985) data provide a 95% confidence interval that excludes either $M^{1/3}$ or $M^{1/4}$ scaling. Consequently, it remains unclear what the scaling exponent for chewing rate is across mammals.

The discrepancies in scaling between studies could be due to differences in the body-mass ranges of species included in the studies (Turvey et al. 1988), to the manner in which evolutionary history and ecology directly or indirectly affect the scaling law among different taxa (e.g., Gross et al. 1993), or to the phylogenetic relationships among the species (Felsenstein 1985).

Our study addresses these considerations. First, we compared results obtained with and without independent contrasts, the latter of which are designed to remove the effects of phylogenetic relationship among the species, thus rendering each data point statistically independent. Second, we extended the work of Fortelius (1985) and Druzinsky (1993) by assembling chewing-rate and M data from more than 130 mammalian species. The species were chosen to narrow the 95% confidence interval of the scaling exponent. Finally, we compared simple linear regression and reduced major axis analyses to provide a more thorough evaluation of scaling exponent estimation. The results lead to the formulation of a kinematic–motor–biomechanical hypothesis that chewing rates will be slower than predicted by $M^{1/4}$ scaling models, especially in species with relatively complex jaw movements (e.g., herbivores) compared with species with relatively simple jaw movements (e.g., carnivores).

MATERIALS AND METHODS

We used data on chewing cycle duration (CD) and M obtained from animals representing 132 mammalian species (Table 1). The data were collected in a humane manner under guidelines of the American Society of Mammalogists (Gannon et al. 2007) and guidelines established by the University of Michigan Committee on Use and Care of Animals. Methods used to obtain these data were similar to those used by Druzinsky (1993). Specifically, investigators obtained CD data by focally videotaping animals during masticatory behavior. Rhythmic oral movements associated with incising (food

acquisition) were not analyzed. Chewing samples contained 10–30 chews per animal, from which each animal's mean CD was calculated. For about 120 species, a single animal represented a given species. The remaining species were represented by 2–7 animals, from which each species' mean CD was calculated from the mean CD of each animal. In 34 cases, mean CDs were obtained from literature sources as indicated in Table 1.

We used M data from the animals being videotaped when it was available. Where not available, M was estimated from literature sources (Table 1). Data on mean CD and M were log-transformed to meet assumptions for use in linear regression (Gould 1966) as in Fig. 1.

Phylogenetic histories of the species were obtained from literature sources that provided estimates of times of divergence (Table 1, footnotes). The complete phylogenetic tree used in the study appears in Fig. 2, and detailed phylogenies of relatively well-sampled orders appear in Figs. 3–5. Times of divergence were used in independent contrast methods.

Independent contrasts on mean CD and M for each species were obtained using the Contrasts module of Phylip 3.65 (Felsenstein 1985). Figs. 3–5 were constructed by Phylip and served to confirm that the program was correctly reading our phylogenetic data. Least-squares regressions were obtained using Microsoft Excel 2003 (Microsoft Corp., Redmond, Washington). Reduced major axis analyses were obtained using PAST version 1.4 (Hammer et al. 2001).

Sources of animals used in our study included the San Diego Zoo, San Diego Wild Animal Park, the Greater Los Angeles Zoo, the Phoenix Zoo, the Wildlife World Zoo, the Toledo Zoo, the Detroit Zoo, and Belle Isle Zoo. Data on humans and some rodents were obtained from projects in our laboratory and in field studies performed near Ann Arbor, Michigan.

Food sources varied according to each zoo's dietary requirements for the animals. In general, videotaped data contained samples of each species chewing at least 2 different types of food. The food eaten by any given species depended on whether the species was herbivorous, carnivorous, or omnivorous by nature. Examples of different types of food include acacia browse, hay, and fresh vegetables for herbivores; raw meat and commercially available dried pellet feed for carnivores; and vegetables, gruel, or eggs for omnivores.

RESULTS

Table 1 shows M and mean CD for the species used in the study. Paired M and CD values representing 34 species were obtained from Druzinsky (1993—$n = 30$) and Gross et al. (1993—$n = 4$). The remaining 98 CD values were obtained as part of our study, of which 86 were paired with M values representing the individuals whose chewing was videotaped and analyzed. Thus, 120 of 132 cases represent paired M and CD values, whereas only 12 represent estimated M values paired with actual CD values. The results described below were not significantly affected by the presence or absence of these 12 estimates; consequently, results are based on all 132 cases.

Relationships between M and CD based on uncorrected data.—Figure 1 plots $\log_{10}(M)$ against $\log_{10}(CD)$ for the 132

TABLE 1.—Body mass (M) and mean chewing cycle duration (CD) of 132 mammalian species. Superscripts with values of M and CD indicate species for which data were obtained from the literature, and associated references.[a] Superscripts with mammalian orders indicate sources[a] of data on times of phylogenetic divergence. Taxonomy follows Wilson and Reeder (2005), except where indicated by an asterisk (*), and thus may differ slightly from references cited.

Common name	Order[18]	Family	Genus	Species	M (g)	CD (ms)
Giraffe	Artiodactyla[31]	Giraffidae	*Giraffa*	*camelopardalis*	1,240,000	976
Okapi	Artiodactyla[31]	Giraffidae	*Okapia*	*johnstoni*	240,000	798
European bison	Artiodactyla[21]	Bovidae	*Bison*	*bonasus*	300,000[8]	793[8]
Domestic cow	Artiodactyla[21]	Bovidae	*Bos*	*taurus*	476,272[8]	690[8]
Yak	Artiodactyla[21]	Bovidae	*Bos*	*grunniens*	250,000[8]	872[8]
Nilgai	Artiodactyla[17]	Bovidae	*Boselaphus*	*tragocamelus*	180,000[22]	550
Sitatunga	Artiodactyla[2]	Bovidae	*Tragelaphus*	*spekii*	88,000	568
Nyala	Artiodactyla[2]	Bovidae	*Tragelaphus*	*angasii*	45,400	534
Greater kudu	Artiodactyla[2]	Bovidae	*Tragelaphus*	*strepsiceros*	252,500	690
Blackbuck	Artiodactyla[12]	Bovidae	*Antilope*	*cervicapra*	36,000	493
Dama gazelle	Artiodactyla[2]	Bovidae	*Nanger*	*dama*	63,000[22]	478
Thomson's gazelle	Artiodactyla[2]	Bovidae	*Eudorcas*	*thomsonii*	24,000	450
Saudi goitered gazelle	Artiodactyla[17]	Bovidae	*Gazella*	*subgutturosa*	20,000	880
Springbok	Artiodactyla[17]	Bovidae	*Antidorcas*	*marsupialis*	37,500	562
Impala	Artiodactyla[2]	Bovidae	*Aepyceros*	*melampus*	62,500[22]	420
Sable antelope	Artiodactyla[2]	Bovidae	*Hippotragus*	*niger*	230,000	737
Arabian oryx	Artiodactyla[17]	Bovidae	*Oryx*	*leucoryx*	70,000[22]	621
Scimitar-horned oryx	Artiodactyla[17]	Bovidae	*Oryx*	*dammah*	204,000	890
Gemsbok	Artiodactyla[2]	Bovidae	*Oryx*	*gazella*	200,000	735
Addax	Artiodactyla[2]	Bovidae	*Addax*	*nasomaculatus*	102,000	1,000
Rocky mountain goat	Artiodactyla[12]	Bovidae	*Oreamnos*	*americanus*	60,000[8]	780[8]
Dall's sheep	Artiodactyla[12]	Bovidae	*Ovis*	*dalli*	10,500[22]	493
Himalayan tahr	Artiodactyla[17]	Bovidae	*Hemitragus*	*jemlahicus*	50,000[8]	471[8]
Alpine ibex	Artiodactyla[23]	Bovidae	*Capra*	*ibex*	40,000[8]	597[8]
Markhor	Artiodactyla[23]	Bovidae	*Capra*	*falconeri*	64,000[8]	581[8]
Goat	Artiodactyla[23]	Bovidae	*Capra*	*hircus*	40,000	600
Barbary sheep	Artiodactyla[17]	Bovidae	*Ammotragus*	*lervia*	66,000[8]	584[8]
Musk ox	Artiodactyla[17]	Bovidae	*Ovibos*	*moschatus*	400,000[8]	1,169[8]
Waterbuck	Artiodactyla[2]	Bovidae	*Kobus*	*ellipsiprymnus*	220,000	519
Lechwe	Artiodactyla[2]	Bovidae	*Kobus*	*leche*	96,000	599
Blue duiker	Artiodactyla[2]	Bovidae	*Philantomba*	*monticola*	4,500	358
Elk	Artiodactyla[31]	Cervidae	*Cervus*	*elaphus*	266,000[15]	536[15]
Chital	Artiodactyla[31]	Cervidae	*Axis*	*axis*	53,000[15]	496[15]
Reeve's muntjac	Artiodactyla[35]	Cervidae	*Muntiacus*	*reevesi*	11,000[22]	413
Indian muntjac deer	Artiodactyla[35]	Cervidae	*Muntiacus*	*muntjak*	18,000	565
Roe deer	Artiodactyla[27]	Cervidae	*Capreolus*	*capreolus*	20,000	612
Moose	Artiodactyla[27]	Cervidae	*Alces*	*alces*	450,000[8]	1,072[8]
White-tailed deer	Artiodactyla[27]	Cervidae	*Odocoileus*	*virginianus*	78,500	660
Reindeer	Artiodactyla[27]	Cervidae	*Rangifer*	*tarandus*	125,000[8]	864[8]
Dromedary camel	Artiodactyla[29]	Camelidae	*Camelus*	*dromedarius*	525,000	990
Bactrian camel	Artiodactyla[29]	Camelidae	*Camelus*	*bactrianus*	500,000[8]	912[8]
Guanaco	Artiodactyla[29]	Camelidae	*Lama*	*guanicoe*	120,000	610
Llama	Artiodactyla[29]	Camelidae	*Lama*	*glama*	140,000	780
Alpaca	Artiodactyla[29]	Camelidae	*Lama*	*pacos*	100,000	460
Hippo	Artiodactyla[25]	Hippopotamidae	*Hippopotamus*	*amphibius*	2,300,000	1,039
Wild boar	Artiodactyla[30]	Suidae	*Sus*	*scrofa*	22,300[8]	330[8]
Warthog	Artiodactyla[30]	Suidae	*Phacochoerus*	*aethiopicus*	90,000	518
Collared peccary	Artiodactyla[30]	Tayassuidae	*Pecari*	*tajacu*	19,000	480
Brazilian tapir	Perissodactyla[33]	Tapiridae	*Tapirus*	*terrestris*	230,000	650
White rhinoceros	Perissodactyla[33]	Rhinocerotidae	*Ceratotherium*	*simum*	2,300,000	1,440
Grant's zebra	Perissodactyla[12]	Equidae	*Equus*	*burchellii*	200,000	720
Przewalski's horse	Perissodactyla[14]	Equidae	*Equus*	*przewalskii**	300,000	813
Domestic horse	Perissodactyla[14]	Equidae	*Equus*	*caballus*	65,0905[8]	785[8]
Asiatic wild ass	Perissodactyla[12]	Equidae	*Equus*	*hemionus*	210,000[8]	797[8]
Indian flying fox	Chiroptera[24]	Pteropodidae	*Pteropus*	*giganteus*	480[8]	581[8]
Little brown bat	Chiroptera[24]	Vespertilionidae	*Myotis*	*lucifugus*	7[8]	250[8]
Domestic dog	Carnivora[7]	Canidae	*Canis*	*familiaris**	63,287[8]	316[8]
Mexican gray wolf	Carnivora[36]	Canidae	*Canis*	*lupus*	32,000	280
Maned wolf	Carnivora[16]	Canidae	*Chrysocyon*	*brachyurus*	23,000[22]	390
Ferret	Carnivora[10]	Mustelidae	*Mustela*	*putorius*	737	244
North American otter	Carnivora[10]	Mustelidae	*Lontra*	*canadensis*	15,000	280

TABLE 1.—Continued.

Common name	Order[18]	Family	Genus	Species	M (g)	CD (ms)
Coati	Carnivora[10]	Procyonidae	*Nasua*	*nasua*	4,800	258
Raccoon	Carnivora[10]	Procyonidae	*Procyon*	*lotor*	4,288	292
Red panda	Carnivora[36]	Ailuridae	*Ailurus*	*fulgens*	4,000	345
Himalayan black bear	Carnivora[34]	Ursidae	*Ursus*	*thibetanus*	70,000	400
American black bear	Carnivora[34]	Ursidae	*Ursus*	*americanus*	70,000	390
Polar bear	Carnivora[34]	Ursidae	*Ursus*	*maritimus*	390,000	490
Grizzly bear	Carnivora[34]	Ursidae	*Ursus*	*arctos*	143,000[15]	585[15]
Spectacled bear	Carnivora[34]	Ursidae	*Tremarctos*	*ornatus*	90,000	470
California sea lion	Carnivora[10]	Otariidae	*Zalophus*	*californianus*	91,000	310
Domestic cat	Carnivora[16]	Felidae	*Felis*	*catus*	2,500[8]	308[8]
Snow leopard	Carnivora[16]	Felidae	*Uncia*	*uncia*	43,200	660
Leopard	Carnivora[16]	Felidae	*Panthera*	*pardus*	43,000	580
Lion	Carnivora[12]	Felidae	*Panthera*	*leo*	130,000	690
Tiger	Carnivora[12]	Felidae	*Panthera*	*tigris*	150,000	390
Meerkat	Carnivora[36]	Herpestidae	*Suricata*	*suricatta*	1,100	180
Two-toed sloth	Pilosa[3]	Megalonychidae	*Choloepus*	*hoffmanni*	4,000	660
African elephant	Proboscidea[3]	Elephantidae	*Loxodonta*	*africana*	2,812,273	1,530
Domestic rabbit	Lagomorpha[5]	Leporidae	*Oryctolagus*	*cuniculus*	2,500	180
Thick-tailed bush baby (= brown greater galago)	Primates[26]	Galagidae	*Otolemur*	*crassicaudatus*	1,500[8]	314[8]
Ring-tailed lemur	Primates[26]	Lemuridae	*Lemur*	*catta*	2,500	270
Spider monkey	Primates[26]	Atelidae	*Ateles*		6,000[8]	326[8]
Squirrel monkey	Primates[26]	Cebidae	*Saimiri*	*sciureus*	550[8]	357[8]
Common marmoset	Primates[26]	Cebidae	*Callithrix*	*jacchus*	315[22]	262
Pygmy marmoset	Primates[26]	Cebidae	*Callithrix*	*pygmaea*	120	237
Golden lion tamarin	Primates[26]	Cebidae	*Leontopithecus*	*rosalia*	600	339
Red-handed tamarin	Primates[26]	Cebidae	*Saguinus*	*midas*	320[22]	274
Cotton-top tamarin	Primates[26]	Cebidae	*Saguinus*	*oedipus*	320	293
Japanese macaque	Primates[26]	Cercopithecidae	*Macaca*	*fuscata*	15,000	420
Rhesus macaque	Primates[26]	Cercopithecidae	*Macaca*	*mulatta*	3,500[8]	334[8]
Mandrill	Primates[26]	Cercopithecidae	*Mandrillus*	*sphinx*	18,000	556
Sykes monkey	Primates[26]	Cercopithecidae	*Cercopithecus*	*mitis*	5,650	310
De Brazza's monkey	Primates[26]	Cercopithecidae	*Cercopithecus*	*neglectus*	5,850[22]	328
Patas monkey	Primates[26]	Cercopithecidae	*Erythrocebus*	*patas*	8,500[22]	405
Guereza	Primates[26]	Cercopithecidae	*Colobus*	*guereza*	9,900	560
Hanuman langur	Primates[26]	Cercopithecidae	*Semnopithecus*	*entellus*	16,000	415
White-handed gibbon	Primates[26]	Hylobatidae	*Hylobates*	*lar*	6,000	374
Siamang	Primates[26]	Hylobatidae	*Symphalangus*	*syndactylus*	10,400	353
Human	Primates[26]	Hominidae	*Homo*	*sapiens*	67,900	1,102
Chimpanzee	Primates[26]	Hominidae	*Pan*	*troglodytes*	40,000	540
Gorilla	Primates[26]	Hominidae	*Gorilla*	*gorilla*	92,500	690
Orangutan	Primates[26]	Hominidae	*Pongo*	*pygmaeus*	37,000	660
Tree shrew	Scandentia[3]	Tupaiidae	*Tupaia*	*glis*	150[8]	238[8]
Naked mole rat	Rodentia[20]	Bathyergidae	*Heterocephalus*	*glaber*	45	300
Agouti	Rodentia[20]	Dasyproctidae	*Dasyprocta*		2,700[9]	212
Capybara	Rodentia[20]	Caviidae	*Hydrochoerus*	*hydrochaeris*	45,000	1,249
Guinea pig	Rodentia[31]	Caviidae	*Cavia*	*porcellus*	900	162
Patagonian cavy	Rodentia[20]	Caviidae	*Dolichotis*	*patagonum*	7,800	309
Chinchilla	Rodentia[5]	Chinchillidae	*Chinchilla*	*lanigera*	500	260
Springhare	Rodentia[5]	Pedetidae	*Pedetes*	*capensis*	2,300[8]	317[8]
Spiny mouse	Rodentia[11]	Muridae	*Acomys*	*dimidiatus*	50	282
Norway rat	Rodentia[11]	Muridae	*Rattus*	*norvegicus*	200[8]	192[8]
Collared lemming	Rodentia[1]	Cricetidae	*Dicrostonyx*	*groenlandicus*	50[15]	127[15]
Valley pocket gopher	Rodentia[28]	Geomyidae	*Thomomys*	*bottae*	473	309
Mountain beaver	Rodentia[28]	Aplodontiidae	*Aplodontia*	*rufa*	583[8]	207[8]
Prevost's squirrel	Rodentia[21]	Sciuridae	*Callosciurus*	*prevostii*	325	177
Black-tailed prairie dog	Rodentia[21]	Sciuridae	*Cynomys*	*ludovicianus*	750	217
Fox squirrel	Rodentia[21]	Sciuridae	*Sciurus*	*niger*	900	220
Woodchuck	Rodentia[32]	Sciuridae	*Marmota*	*monax*	3,790[8]	583[8]
Oriental musk shrew	Soricomorpha[25]	Soricidae	*Suncus*	*murinus*	41[8]	183[8]
Lesser hedgehog tenrec	Afrosoricida[6]	Tenrecidae	*Echinops*	*telfairi*	180	400
Common tenrec	Afrosoricida[6]	Tenrecidae	*Tenrec*	*ecaudatus*	210	489
Wallaroo	Diprotodontia[4]	Macropodidae	*Macropus*	*robustus*	24,900	455
Red kangaroo	Diprotodontia[4]	Macropodidae	*Macropus*	*rufus*	35,000	538
Agile wallaby	Diprotodontia[4]	Macropodidae	*Macropus*	*agilis*	11,300	355

TABLE 1.—Continued.

Common name	Order[18]	Family	Genus	Species	M (g)	CD (ms)
Gray kangaroo	Diprotodontia[4]	Macropodidae	*Macropus*	*giganteus*	30,000	499
Bennett's wallaby	Diprotodontia[4]	Macropodidae	*Macropus*	*rufogriseus*	18,000	460
Tammar wallaby	Diprotodontia[4]	Macropodidae	*Macropus*	*eugenii*	7,700	467
Matschie's tree kangaroo	Diprotodontia[4]	Macropodidae	*Dendrolagus*	*matschiei*	10,700	402
Sugar glider	Diprotodontia[13]	Petauridae	*Petaurus*	*breviceps*	110	236
Koala	Diprotodontia[19]	Phascolarctidae	*Phascolarctos*	*cinereus*	7,800	410
Opossum	Didelphimorphia[3]	Didelphidae	*Didelphis*	*marsupialis*	2,500[8]	390[8]

[a] 1, Adkins et al. 2001; 2, Brashares et al. 2000; 3, Browham et al. 1999; 4, Burk and Springer 2000; 5, De Jong 1985; 6, Douady et al. 2002; 7, Douzery and Randi 1997; 8, Druzinsky 1993; 9, Eisenberg 1981; 10, Ferguson et al. 1996; 11, Fraguedakis-Tsolis et al. 1993; 12, Garland et al. 1993; 13, Geiser 1994; 14, George and Ryder 1986; 15, Gross et al. 1993; 16, Harris and Steudel 1997; 17, Hassanin and Douzery 1999; 18, Hedges et al. 1996; 19, Houlden et al. 1996; 20, Huchon and Douzery 2001; 21, Janecek et al. 1996; 22, Macdonald 1987; 23, Manceau et al. 1999; 24, Nikaido et al. 2000; 25, Nikaido et al. 2001; 26, Purvis 1995; 27, Randi et al. 1998; 28, Sarich 1985; 29, Stanley et al. 1994; 30, Theimer and Keim 1998; 31, Thenius and Hofer 1960; 32, Thomas and Martin 1993; 33, Tougard et al. 2001; 34, Waits et al. 1999; 35, Wang and Hong 2000; 36, Wayne 1993.

mammalian species. $\log_{10}(M)$ was significantly correlated with $\log_{10}(CD)$ ($r = 0.80$, $P < 0.001$), with $\log_{10}(M)$ accounting for about 65% of the variance in $\log_{10}(CD)$. Regression analysis found the following relationship: $\log_{10}(CD) = 2.024 + 0.1521[\log_{10}(M)]$. The 95% confidence interval for the scaling exponent ranged from 0.133 to 0.171. In other words, CD was proportional to $M^{1/6}$, and the 95% confidence interval did not include either $M^{1/8}$ or $M^{1/4}$.

A reduced major axis analysis also found a significant relationship between $\log_{10}(M)$ and $\log_{10}(CD)$ ($r = 0.80$, $P < 0.001$; results based on 132 bootstraps). The relationship between $\log_{10}(CD)$ and $\log_{10}(M)$ was: $\log_{10}(CD) = 1.862 + 0.1893[\log_{10}(M)]$. The 95% confidence interval for the scaling exponent was 0.168–0.212, which did not include $M^{1/8}$, $M^{1/6}$, $M^{1/4}$, or $M^{1/3}$; however, the scaling exponent and confidence interval were closer to $M^{1/6}$ than to $M^{1/8}$, $M^{1/4}$, or $M^{1/3}$.

Relationships between M and CD using independent contrasts.—Phylogenetic relationships can influence the results of linear regressions (Felsenstein 1985). To remove these effects, independent contrasts were generated on the $\log_{10}(M)$ and $\log_{10}(CD)$ data using divergence times taken from the literature (Table 1). Divergence times are depicted diagrammatically in the phylogenetic trees shown in Figs. 2–5. The relationship between $\log_{10}(M)$ and $\log_{10}(CD)$ using independent contrasts was significant ($r = 0.493$, $P < 0.001$, $n = 66$), and accounted for 24% of the variation in CD. Regression analysis found the following relationship: $\log_{10}(CR) = 0.138[\log_{10}(M)]$. (The contrast method standardized the data so that the regression passed through the origin.) The 95% confidence interval for the scaling exponent was 0.0784–0.198, which included both $M^{1/8}$ and $M^{1/6}$ in the confidence interval estimate.

A reduced major axis analysis found a significant correlation between the independent contrast data for $\log_{10}(M)$ and $\log_{10}(CD)$ ($r = 0.493$, $P < 0.001$, based on 66 bootstraps). The relationship was $\log_{10}(CR) = -0.008 + 0.280[\log_{10}(M)]$. The 95% confidence interval for the scaling exponent was 0.219–0.346, which included both $M^{1/4}$ and $M^{1/3}$ in the confidence interval.

Regressions of selected mammalian orders.—Allometric relationships and comparisons may vary among mammalian species subgroups based on shared functional and evolutionary historical characters. Therefore, simple linear regressions were run on log-transformed data representing 4 mammalian orders for which we had sufficient samples: Rodentia, Artiodactyla, Primates, and Carnivora (Table 2). For all 4 orders, $M^{1/6}$ is included in the 95% confidence interval of the scaling exponent. $M^{1/4}$ and $M^{1/8}$ also are included in the 95% confidence interval of the scaling exponent for rodents, and $M^{1/8}$ is included in the 95% confidence interval of the scaling exponent for carnivores, artiodactyls, and primates.

DISCUSSION

Allometric scaling between chewing rate and M suggests the existence of underlying principles governing the evolution and perhaps the development of chewing rate. It is possible that general biological principles or "unifying theories" may ultimately emerge from allometric studies (see Calder 1996: chapter 1). No widely accepted theoretical framework yet exists
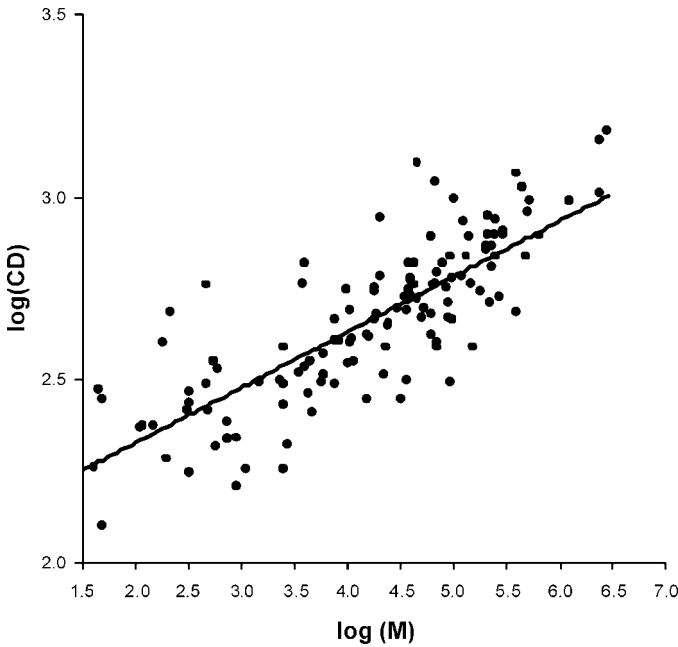

FIG. 1.—Scatterplot and regression of $\log_{10}$ mass (M) against $\log_{10}$ chewing cycle duration (CD) for the 132 species listed in Table 1.
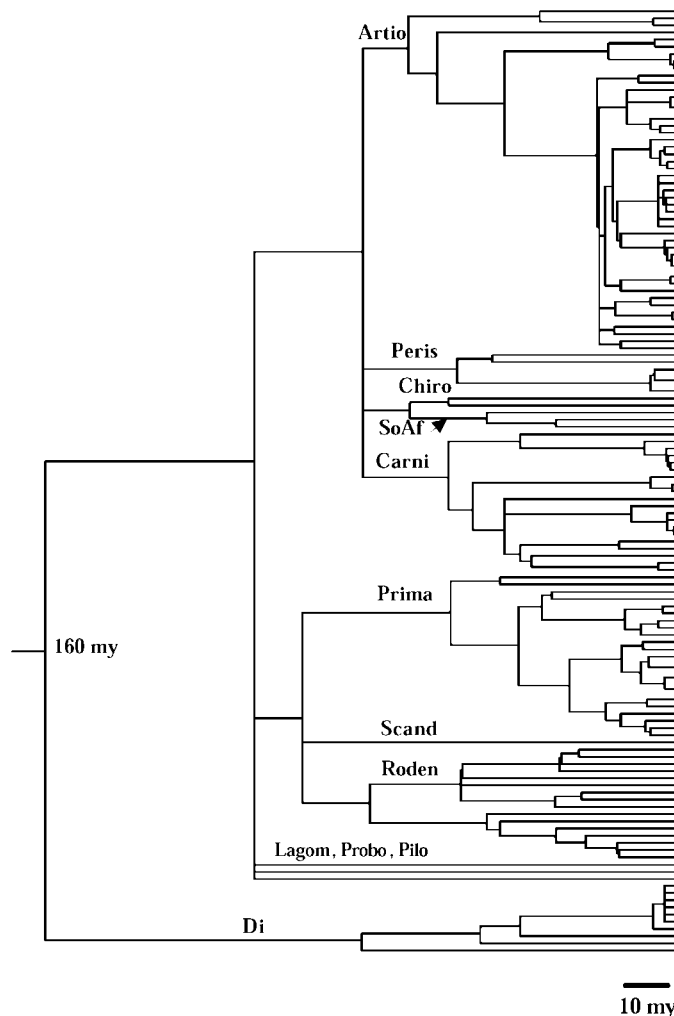
Fig. 2.—Phylogeny of 132 mammalian species used in this study. Branch lengths correspond to divergence times (bar, lower right = 10 million years). Abbreviations: Artio = Artiodactyla; Peris = Perissodactyla; Chiro = Chiroptera; SoAf = Soricomorpha and Afrosoricida; Carni = Carnivora; Prima = Primates; Scand = Scandentia; Roden = Rodentia; Lagom = Lagomorpha; Probo = Proboscidea; Pilo = Pilosa; Di = Didelphimorphia and Diprotodontia.

Fig. 3.—Details of the Artiodactyla phylogeny from Fig. 2.

for understanding allometric relationships, especially for biologically ensconced dynamical regimes like chewing rate (cf. Iberall 1995; Rapp 1987). Several models have been proposed; however, most, including those proposed for chewing timing (Druzinsky 1993), rely critically on the value of the scaling exponent.

In our study, the simple linear regression analysis of the raw data representing all 132 mammalian species showed that CD (which is the reciprocal of chewing rate) scaled to $M^{1/6}$. Importantly, the 95% confidence interval for the scaling exponent in this analysis excluded both $M^{1/4}$ and $M^{1/8}$. Likewise, the scaling exponent was closer to $M^{1/6}$ than to $M^{1/8}$ for all 4 of the within-order analyses (Table 2), and for the reduced major axis analysis of the raw data representing all 132 species. These results suggest that an $M^{1/6}$-power law governs mammalian chewing rate allometry.
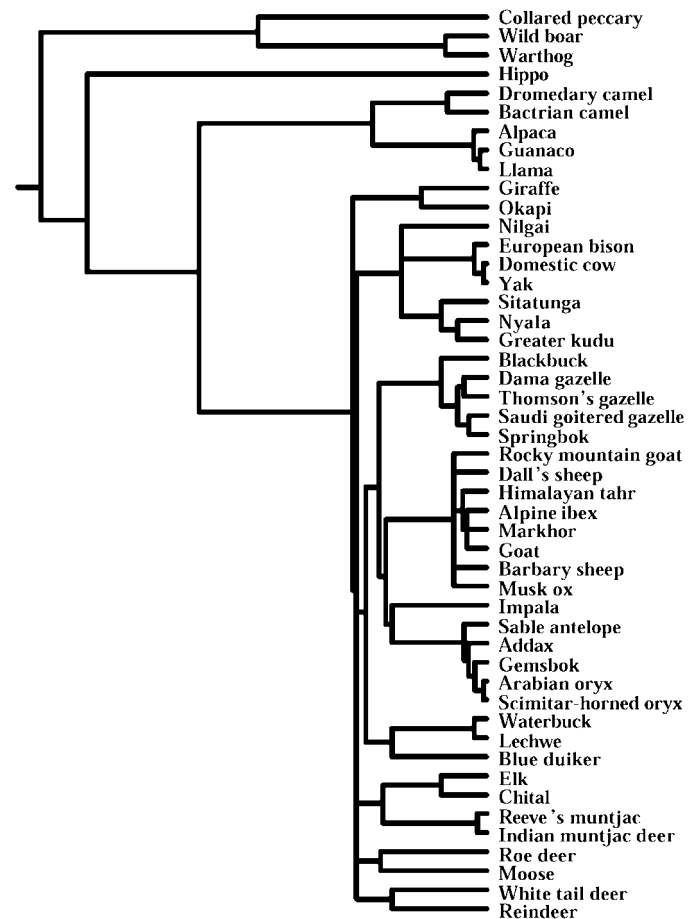
According to Turvey et al. (1988), the $M^{1/6}$ scaling is likely a one-third–power law operating in a unique geometric setting. West et al. (1997) have argued that one-third–power scaling represents the operation of a nonfractal or geometric system. If this is the case, then a geometric dynamical regime, as opposed to a fractal dynamical regime, appears to govern CD among mammals. It has been argued that motor activity dynamics in individual organisms are fractal (Cole 1995); however, results of our study appear to refute this argument.

On the other hand, our estimates of the scaling exponent that were relatively close to $M^{1/6}$ stemmed from results performed on raw data. By contrast, estimates of the scaling exponent were relatively close to $M^{1/8}$ or $M^{1/4}$ when independent contrasts were used. This variation in scaling exponent estimates may be due to statistical error, to biological effects, or both. In terms of potential biological effects, we hypothesize that the leading candidates include jaw kinematics, motor control issues, and biomechanics, or more general processes such as canalization, grade shifts, phylogenetic inertia, or a combination of factors.

Jaw kinematics, motor control, and biomechanics.—When phylogenetic effects were removed with independent contrasts, the $M^{1/6}$ scaling exponent appeared to move toward a one-fourth–power law. The $M^{1/4}$ scaling proposed by Turvey et al.
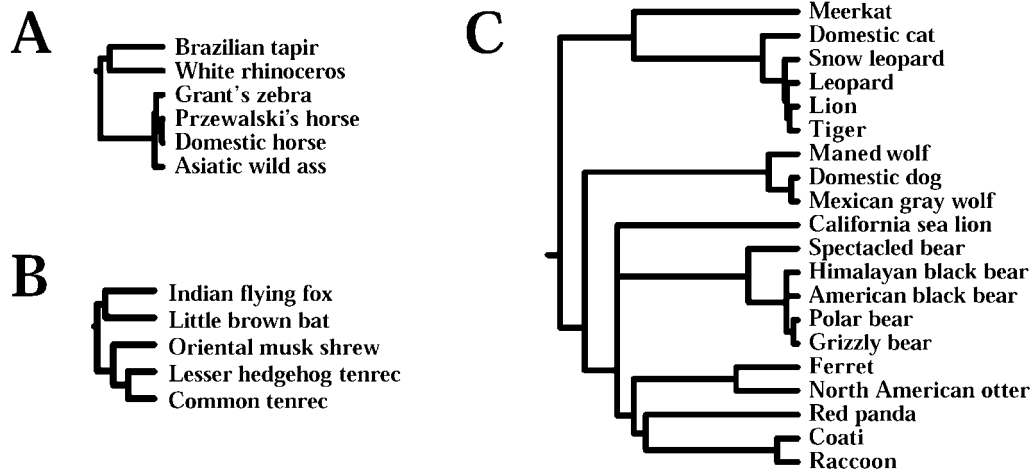
Fig. 4.—Details of the phylogenies of A) Perissodactyla; B) Chiroptera, Soricomorpha, and Afrosoricida; and C) Carnivora from Fig. 2.

(1988) assumes a relatively simple, 1 degree-of-freedom movement, which would be a reasonable approximation if mammalian species were characterized by simple, vertically directed jaw opening and closing movements. However, the rodents, primates, ungulates, and some of the marsupials sampled in our study have been shown to possess relatively complex jaw movements with considerable lateral movements of the jaw during a chewing cycle (Byrd 1981; Gerstner and Goldberg 1994; Luschei and Goodwin 1974). About three-fourths of the species involved in our study probably have significant lateral jaw movements associated with chewing.

To determine whether a lateral movement component could influence chewing rate, we performed a simple experiment with a mass-spring system, a system upon which some one-fourth–power law models are based (Turvey et al. 1988). We determined that the oscillatory rate was up to 30% slower when the mass was forced to have a lateral movement component than when it had a simple vertical trajectory. This provided support for the hypothesis that lateral movements may be associated with relatively slow chewing rates.

Additionally, mastication with a lateral jaw movement component would require asymmetrical muscle activity patterns as well as complex (rotational and translational) movements of the mandibular condyles. Hence, lateral movements of the jaw increase the complexity of motor coordination and of condylar biomechanics. Therefore, we hypothesize that chewing strokes with complex (lateral movement) kinematics, motor control, and biomechanics will occur in conjunction with chewing rates that are slower than the one-fourth–scaling law would predict. This would translate to CD moving away from the "ideal" scaling exponent of $M^{1/4}$ and toward the $M^{1/3}$ scaling exponent in studies involving species with relatively complex jaw movements. Complexities in the anteroposterior dimension of jaw movements also could play a role in moving the scaling exponent away from the "ideal." Given that chewing is a complex 3-dimensional movement, further studies will be required to
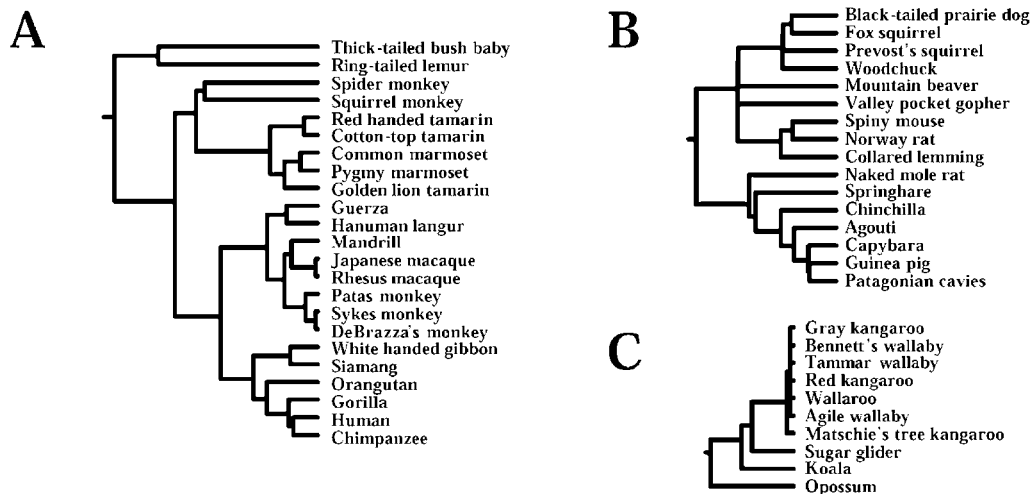

Fig. 5.—Details of the phylogenies of A) Primates, B) Rodentia, and C) Diprotodontia and Didelphimorphia from Fig. 2.

TABLE 2.—Correlations between chewing cycle duration and body mass for 4 mammalian orders.

Group	n	Scaling exponent	95% CI for exponent	Intercept	r	P
Rodents	16	0.188	0.0752−0.301	1.891	0.658	<0.010
Artiodactyls	48	0.170	0.122−0.217	1.958	0.719	<0.001
Primates	23	0.164	0.116−0.212	1.997	0.826	<0.001
Carnivores	20	0.147	0.0832−0.210	1.924	0.730	<0.001

evaluate fully our proposed kinematic–motor–biomechanical hypothesis.

The independent contrasts removed phylogenetic effects, which essentially reduced the contribution from closely related, that is, within-order species. Because large numbers of species of ungulates, rodents, and primates were sampled, the independent contrast methods would have reduced the weighting due to repeated measures of the many related species with significant lateral jaw movement components. Consequently, scaling estimates would move toward the ''ideal'' $M^{1/4}$ scaling exponent. Indeed, this was the case, suggesting that the kinematic–motor–biomechanical hypothesis may explain the discrepancies in results obtained with raw data compared to data processed with independent contrasts.

There are several other possible explanations for why one-third–power estimates were observed with data where phylogenetic effects were preserved, versus why one-fourth–power estimates were observed with data where phylogenetic effects were removed. Martin et al. (2005) and Nunn and Barton (2000) discuss effects due to grade shifts and phylogenetic inertia. Table 1 shows that our sample of rodents and artiodactyls represented different ranges of M; hence, body-size inertia is certainly an important consideration. What specific roles any grade or inertial effects may be playing will be an issue for future studies. Studies involving larger, carefully selected samples will allow for rigorous testing and evaluation of the biological factors.

Sensitivity of scaling exponent estimates to study design.— The fact that the one-fourth–power scaling was excluded in the 95% confidence interval of the analyses involving all 132 species, but that it was included in all other analyses, could be due to the widening of the confidence interval as a result of reduced sample sizes for these comparisons (e.g., $n = 16$–48, Table 2; and $n = 66$ in the analyses involving independent contrasts). Future investigations should include carefully selected additional species of rodents, artiodactyls, carnivores, and primates in order to fine-tune the 95% confidence intervals for within-order comparisons. We anticipate that the scaling exponent will continue to lie between $M^{1/4}$ and $M^{1/6}$ in accordance with predictions of the kinematic–motor–biomechanical hypothesis; however, it should be possible to ascertain the precise roles that specific factors such as grade, inertia, jaw kinematics, and biomechanics play in modifying the scaling exponent.

As the results of our study demonstrated, selection of analytic methods, such as simple linear regression, reduced major axis, or independent contrasts, as well as selection of taxa, can have a significant impact on the estimate of the scaling exponent. Because estimation of the scaling exponent is sensitive to statistical design issues (Nunn and Barton 2000; Symonds and Elgar 2002), results that support specific models should be interpreted in light of the analytic methods used.

It would be useful if a set of standardized methods and approaches existed for allometric studies. The advantages, problems, and challenges inherent in existing approaches have been discussed at length in various papers (Fortelius 1985; Garland et al. 1992; LaBarbera 1989; Martin et al. 2005; Riska 1991), and a discussion of this topic goes beyond the scope of this paper. Because these issues remain unresolved, our study used several presently accepted methods to study the relationship between M and chewing timing. Similar multimethod approaches are common in allometric studies (Nunn and Barton 2000; Symonds and Elgar 2002).

Two common criticisms of allometric studies are their reliance on small samples representing each data point, that is, each species is often represented by 1 or a few individual animals; and not accounting for confounding factors such as sexual dimorphism, age, or social status. Calder (1996) argues that what is most important in allometric study designs is the range of body sizes studied. In our study, size ranged from 7 g (little brown bat) to 2,812,273 g (African elephant), that is, over 5 orders of magnitude. Calder (1996:41) argues that ''a 25% 'error' displacement from true M will have only negligible effect on the overall relationship'' in studies that cover such a size range. Likewise, factors that would introduce an error in size equal to 25%, for example, selecting a female animal to represent a species that manifests sexual dimorphism, would have negligible effect on the overall relationship. Of course, this assumes that these biologically based ''errors'' will be randomly distributed across the data set, and hence only the degree of scatter will be slightly affected and not the estimate of the scaling exponent. In practice, such an assumption is difficult if not impossible to demonstrate definitively.

Moreover, although such sources of error may not affect the estimate of the scaling exponent, they may influence the 95% confidence interval. This could be another important reason why it was not possible to isolate the one-third–power versus one-fourth–power scaling exponent in several of our tests. Future study designs should take this issue into consideration.

Neurobiological considerations in CD production.—Models of rhythmic chewing need to consider important neurobiological aspects of chewing rate generation. Chewing rate is controlled by central timing networks, also called central rhythm generators, located in the brain stem (for review, see Goldberg and Chandler [1990] and Nakamura and Katakura [1995]). For models to be biologically meaningful, they would

have to account for how peripheral feedback containing information about jaw mass would act to entrain the central timing network to produce a rhythm that matches the mass properties of the jaw. In this way, CD and M would come to be allometrically related.

Turvey et al. (1988) showed that rhythmic movements of human subjects adapted to the experimental paradigm. In other words, under the given experimental conditions, rhythmicity responded to peripheral feedback that contained information about mass. In contrast, our unpublished studies of chewing rate and M among breeds of dogs indicates that chewing rate and M do not scale as predicted. Likewise, other studies indicate that the rhythmicity of jaw movements is not modified by experimentally increasing jaw mass in individual animals (Carvalho and Gerstner 2004; Chandler et al. 1985). This suggests that for chewing rate and M to scale among wild mammals, as it clearly does in our study, there is a key role for natural selection in the scaling.

In summary, results of our study showed that CD scaled according to a one-fourth–power law when phylogenetic effects were removed and to a one-third–power law when phylogenetic effects were not removed. Moreover, the one-third–power law appeared to hold for comparisons across the class Mammalia as well as for comparisons within 4 mammalian orders. Consequently, there appear to be many evolutionary (ultimate causality) and neurobiological (proximate causality) issues for future studies to address regarding the sources of variation in mammalian chewing rates. Work will need to focus on ecological and morphological issues, to evaluate the scaling exponent at the family and genus levels, and to understand the influences of jaw movement kinematics, motor control, and biomechanics on chewing rate. The sensitivity of results to statistical and study design features also will need to be evaluated. Mastication, as a behavior in which most mammalian species engage, and which is a vital interface between mammals and their environments, provides a subject to develop new ways of thinking that are simultaneously compatible with neurophysiologic, motor control, biomechanical, ontogenetic, evolutionary, and ecological traditions (Gerstner and Goldberg 1999).

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