Land-to-sea transition in early whales: evolution of Eocene Archaeoceti (Cetacea) in relation to skeletal proportions and locomotion of living semiaquatic mammals

Philip D. Gingerich

Abstract.—Skeletal remains of Eocene Archaeoceti provide the only direct and unequivocal evidence of the evolutionary transition of whales from land to sea. Archaeocete skeletons complete enough to be informative about locomotion are rare (principally *Rodhocetus* and *Dorudon*), and these deserve to be studied in comparison to the full spectrum of semiaquatic mammals. A principal components analysis of 14 trunk and limb measurements for 50 species of living semiaquatic mammals reduces the observed variation to three informative axes. The first principal axis (PC-I) represents overall size (water mice and shrews have the lowest scores on this axis and the hippopotamus has the highest); the second axis (PC-II) represents a spectrum of aquatic adaptation (seals have the lowest scores and tapirs have the highest); and the third principal axis (PC-III) represents a spectrum ranging from hindlimb- to forelimb-dominated locomotion (sea otters have the lowest scores and the platypus the highest).

Dorudon fits poorly into a morphospace defined solely by living semiaquatic mammals; thus a second 53-species set was analyzed, adding an anthracothere to represent an artiodactyl ancestral morphology and two species of archaeocetes to represent successive stages of early whale evolution. This addition has little effect on the first two principal axes but changes the third substantially. PC-III now represents a contrast of lumbus- (and presumably tail-) dominated versus hindlimb-dominated locomotion (*Dorudon* has the lowest score and *Rodhocetus* the highest, whereas the otter shrew has the lowest score among living mammals and the desman the highest). Mammals that are more aquatic have a shorter ilium and femur combined with longer manual and pedal phalanges, whereas the reverse is true for more terrestrial taxa. Lumbus- and tail-dominated swimmers tend to have a longer lumbus combined with shorter pedal elements, whereas the reverse is true for hindlimb-dominated swimmers. Trunk and limb proportions of early middle Eocene *Rodhocetus* are most similar to those of the living, highly aquatic, foot-powered desmans. Trunk and limb proportions of late middle Eocene *Dorudon* indicate that it was a lumbus-and-tail-powered swimmer specialized in the direction of modern whales. Thus it appears that the land-to-sea transition in whale evolution involved at least two distinct phases of locomotor specialization: (1) hindlimb domination for drag-based pelvic paddling in protocetids (*Rodhocetus*), with tail elongation for stability, followed by (2) lumbus domination for lift-based caudal undulation and oscillation in basilosaurids (*Dorudon*). Rates of evolution in both phases of this change of adaptive zone are about an order of magnitude higher than background rates for the timescale involved.

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Introduction

Explorer Samuel Hearne crossed the middle of what is now Manitoba Province in Canada in June of 1774. There he watched black bears in lakes catching insects on the water's surface, ''swimming with their mouths open, in the same manner as the whales do when feeding on the sea-spider'' (Hearne 1795: p. 370). The observation took on new meaning when Charles Darwin cited it in the *Origin of Species* and speculated that a race of bears might have been ''rendered, by natural selection, more and more aquatic in their structure and habits, with larger and larger mouths, till a creature was produced as monstrous as a whale'' (Darwin 1859: p. 184). Darwin had already cited the mink and the otter as transitional in conversion of land carnivores to aquatic habits (Darwin 1859: p. 179). By such logic it is easy to imagine a slightly aquatic mink- or bearlike ancestor giving rise to a more aquatic otterlike stage, followed by a seal-like pinniped stage, until finally whales became fully aquatic as they are today. Such a scenario is appealing because it appears to be simple and direct, and the stages involved are all represented by familiar living animals. But is this really what happened in whale evolution?

TABLE 1. Classification of genera in five families of Archaeoceti (bold). Summary of known skeletal remains is provided in the right-hand column. Skeletons of *Rodhocetus* and *Dorudon* are sufficiently complete and generalized to be included in the analysis presented here.

Genus	Known skeletal remains
Pakicetidae (early to early middle Eocene)	
Ichthyolestes Dehm and Oettingen-Spielberg, 1958	Partial skull, isolated postcranial bones
Pakicetus Gingerich and Russell, 1981	Partial skull, isolated postcranial bones
Nalacetus Thewissen and Hussain, 1998	Dental remains
Himalayacetus Bajpai and Gingerich, 1998	Partial dentary with teeth
Ambulocetidae (early middle Eocene)	
Gandakasia Dehm and Oettingen-Spielberg, 1958	Partial dentary with teeth
Ambulocetus Thewissen et al., 1994	Skull and partial skeleton
Remingtonocetidae (middle Eocene)	
Andrewsiphius Sahni and Mishra, 1975	Maxillae and dentaries, partial skeleton
Remingtonocetus Kumar and Sahni, 1986	Skull and partial skeleton
Dalanistes Gingerich et al., 1995	Skull and partial skeleton
Attockicetus Thewissen and Hussain, 2000	Partial skull
Protocetidae (middle Eocene)	
Protocetus Fraas, 1904	Skull and partial skeleton
Eocetus Fraas, 1904	Partial skull and postcranial remains
Pappocetus Andrews, 1920	Partial dentary with teeth, vertebrae
Indocetus Sahni and Mishra, 1975	Partial skull
Babiacetus Trivedy and Satsangi, 1984	Partial skull
Rodhocetus Gingerich et al., 1994	Skull and partial skeleton
Gaviacetus Gingerich et al., 1995	Skull and partial skeleton
Takracetus Gingerich et al., 1995	Skull and partial skeleton
Georgiacetus Hulbert et al., 1998	Skull and partial skeleton
Natchitochia Uhen, 1998	Vertebrae
Artiocetus Gingerich et al., 2001	Skull and partial skeleton
Qaisracetus Gingerich et al., 2001	Skull and partial skeleton
Basilosauridae (late middle to late Eocene)	
Basilosaurus Harlan, 1834	Virtually complete skeleton
Dorudon Gibbes, 1845	Virtually complete skeleton
Pontogeneus Leidy, 1852	Vertebrae
Zygorhiza True, 1908	Skull and partial skeleton
Saghacetus Gingerich, 1992	Skull and partial skeleton
Ancalecetus Gingerich and Uhen, 1996	Skull and partial skeleton
Basiloterus Gingerich et al., 1997	Vertebrae
Chrysocetus Uhen and Gingerich, 2001	Partial skull and skeleton

The fossil record documenting the land-to-sea transition of early whales includes 30 genera of Eocene Archaeoceti, many of which are represented by skulls and partial postcranial skeletons (Table 1). Predictably, there has been a tendency to compare these to otters and pinnipeds. Fraas (1904) regarded *Protocetus* as related to pinnipeds. Thewissen et al. (1994, 1996), Thewissen and Fish (1997), Thewissen and Williams (2002), and Madar et al. (2002) inferred that *Ambulocetus* swam like otters. Gingerich et al. (2001a) compared *Rodhocetus* to otters, citing Thewissen and Fish (1997). The basis for such comparisons has ranged from general impressions to pairwise ratios of limb bone lengths (Thewissen and Fish 1997;

Madar et al. 2002). But are archaeocetes really like otters and pinnipeds?

Two of the 30 Eocene genera in Table 1, *Rodhocetus* and *Dorudon*, are known from virtually complete skeletons. Others are close to being complete. *Ambulocetus* lacks critical scapula, humerus, and tibia lengths, and lacks the phalangeal lengths included here. *Zygorhiza* lacks some forelimb and all hindlimb elements. *Basilosaurus* is well known, but its vertebrae and vertebral column as a whole are so unusually elongated as to make close relationship to later whales implausible. *Rodhocetus* and *Dorudon*, the two best known archaeocetes with generalized skeletons, represent protocetid and basilosaurid stages regarded as ly-
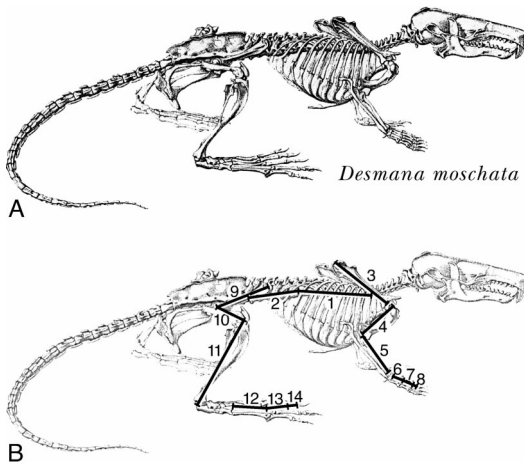
FIGURE 1. Skeleton of the semiaquatic Russian desman or aquatic mole *Desmana moschata*. A, Drawing reproduced from Dobson (1882); note relatively short femur and long hind foot. B, Schematic shows fourteen lengths of trunk and limb segments measured here (see Table 4); measurements were made on original skeletons (see Appendix for list of specimens).

ing in the main line or trend of early cetacean evolution (Fordyce and Barnes 1994; Fordyce and de Muizon 2001; Gingerich et al. 2001a; Heyning and Lento 2002). What does comparison of the trunk and limb skeletons of *Rodhocetus* and *Dorudon* with those of a broad range of living mammals tell us about skeletal proportions, aquatic adaptations, and locomotion in early whale evolution? If we accept that the Eocene forms are on the main line of early cetacean evolution, what does such a comparison tell us about evolution in whales?

Materials and Methods

Semiaquatic Mammals.—Many living mammals fall within a broad spectrum of partially aquatic or ''semiaquatic'' forms that range from being virtually fully terrestrial to fully aquatic. Hearne's black bear is an example of a terrestrial mammal that is partially aquatic at times. The Russian desman (Fig. 1) is another. The full set of living semiaquatic mammalian species studied here is listed in Table 2, including an indication of which authors regarded each as aquatic.

Kükenthal (1890, 1891) initiated comparative study of aquatic adaptations in mammals, listing 46 living species as semiaquatic (including all of the currently recognized species

of pinnipeds, and excluding cetaceans and sirenians). Osburn (1903) mentioned 29 species not listed by Kükenthal, and Howell (1930) added 32 to bring the total identified as semiaquatic at the time of publication of his classic *Aquatic Mammals* to 108 (counting Hearne's black bear). More recently, Hickman (1983) mentioned one species not listed previously, Wolff and Guthrie (1985) added 12 species, Stein (1988) added two, Voss (1988) added three, and Nowak (1999) added one.

Thus some 127 living species of mammals have been identified as being semiaquatic to some degree. These include one species of Monotremata, one species of marsupial Didelphimorphia, 17 species of Insectivora, 17 species of Carnivora (including 13 Lutrinae or otters), 34 species of Pinnipedia, four species of Perissodactyla, two species of Artiodactyla, 49 species of Rodentia, and two species of Lagomorpha (Table 3). Obviously inclusion of some species and exclusion of others could be debated, but in the end the representative set as a whole is not likely to change very much. Living cetaceans and sirenians are not included as ''semiaquatic'' here because they are more fully aquatic, and because they lack hindlimbs necessary for comparison with semiaquatic taxa.

Living semiaquatic mammals represent nine orders and 17 families, and at least one species from each order and family was measured for this study (Table 3). Species not measured are generally small and/or rare, and are rarely represented in museums by good skeletons with hand and foot bones. The reason for sampling the broad diversity of living semiaquatic mammals, rather than focusing narrowly on, say, otters and other Mustelidae, is to enable comparison of early whales with as wide a range of living models as possible. Restricting comparisons to Mustelidae dictates that mustelids are the models of choice without a test. As whales are not closely related to mustelids, there is no phylogenetic justification for such a restriction. Broader comparisons admit other possibilities, while at the same time, permitting mustelids to emerge as models of choice if they prove to be similar to early whales.

Skeletons measured for this study are in the

TABLE 2. Summary classification and common names of living semiaquatic mammals studied here (measurements are listed in the Appendix). Columns He, K, O, Ho, W, and V refer to Hearne (1795), Kükenthal (1890, 1891), Osburn (1903), Howell (1930), Wolff and Guthrie (1985), Voss (1988), respectively, and Xs mark species included by each as semiaquatic. Dashes mark species identified as semiaquatic that are not mentioned by a subsequent author. Column N refers to Nowak (1999) and gives page number of entry in this general reference.

Genus and species	Common name	He	K	O	Ho	W	V	N
Monotremata								
Ornithorhynchidae								
Ornithorhynchus anatinus	Duck-billed platypus		X	X	X	—	—	13
Didelphimorphia								
Didelphidae								
Chironectes minimus	Water opossum		X	X	X	—	—	33
Insectivora								
Tenrecidae								
Potamogale velox	Giant African water shrew			X	X	—	—	187
Limnogale mergulus	Web-footed tenrec			X	X	—	X	192
Soricidae (shrews)								
Neomys fodiens	N. European water shrew		X	X	X	X	X	212
Talpidae (moles)								
Desmana moschata	Russian desman		X	X	X	—	—	230
Galemys pyrenaicus	Pyrenean desman				X	—	X	232
Carnivora								
Ursidae								
Ursus americanus	Black bear	X	—	—	—	—	—	683
Ursus maritimus	Polar bear				X	—	—	688
Mustelidae								
Mustela vison	American mink			X	X	—	—	711
Lutra lutra	European river otter		X	X	X	—	—	737
Lontra canadensis	Canadian river otter				X	—	—	740
Lontra felina	Marine otter				X	—	—	740
Pteronura brasiliensis	Giant otter				X	—	—	742
Aonyx cinerea	Indian clawless otter				X	—	—	743
Enhydra lutris	Sea otter		X	X	X	—	—	745
Pinnipedia								
Otariidae (eared seals and sea lions)								
Callorhinus ursinus	Northern fur seal		X	X	X	—	—	840
Arctocephalus australis	S. American fur seal		X	X	X	—	—	847
Zalophus californianus	California sea lion		X	X	X	—	—	852
Eumetopias jubatus	Steller sea lion		X	X	X	—	—	860
Odobenidae								
Odobenus rosmarus	Walrus		X	X	X	—	—	862
Phocidae (true seals)								
Monachus monachus	Mediterranean monk seal		X	X	X	—	—	870
Lobodon carcinophagus	Crabeater seal		X	X	X	—	—	871
Hydrurga leptonyx	Leopard seal		X	X	X	—	—	873
Leptonychotes weddelli	Weddell seal		X	X	X	—	—	874
Ommatophoca rossi	Ross seal		X	X	X	—	—	875
Mirounga leonina	Southern elephant seal		X	X	X	—	—	880
Erignathus barbatus	Bearded seal		X	X	X	—	—	881
Cystophora cristata	Hooded seal		X	X	X	—	—	882
Halichoerus grypus	Gray seal		X	X	X	—	—	884
Phoca groenlandica	Harp seal		X	X	X	—	—	887
Phoca vitulina	Harbor seal		X	X	X	—	—	892
Perissodactyla								
Tapiridae								
Tapirus terrestris	South American tapir				X	—	—	1025
Tapirus bairdii	Baird's tapir				X	—	—	1025
Tapirus indicus	Malayan tapir				X	—	—	1025

TABLE 2. Continued.

Genus and species	Common name	He	K	O	Ho	W	V	N
Artiodactyla								
Hippopotamidae								
Hippopotamus amphibius	Hippopotamus		X	X	X	—	—	1068
Hexaprotodon liberiensis	Pygmy hippopotamus				X	—	—	1071
Rodentia								
Castoridae								
Castor fiber	European beaver		X	X	X	—	—	1306
Castor canadensis	Canadian beaver			X	X	—	—	1306
Muridae								
Neusticomys monticolus	Andean fish-eating rat					X	X	1414
Ichthyomys hydrobates	Aquatic rat			X	X	X	X	1417
Ichthyomys tweedii	Aquatic rat			X	X	X	X	1417
Rheomys raptor	C. American water mouse				X	X	X	1417
Rheomys underwoodi	C. American water mouse				X	X	X	1417
Arvicola terrestris	European water vole		X	X	X	—	—	1467
Ondatra zibethicus	Muskrat		X	X	X	X	—	1477
Hydrochoeridae								
Hydrochoeris hydrochoeris	Capybara		X	X	X	—	—	1672
Myocastoridae								
Myocastor coypus	Nutria			X	X	—	—	1712
Lagomorpha								
Leporidae								
Sylvilagus aquaticus	Swamp rabbit				X	—	—	1727
Sylvilagus palustris	Marsh rabbit				X	—	—	1727

mammal collection of the Natural History Museum, London; University of Michigan Museum of Zoology division of mammals; and University of Michigan Museum of Paleontology osteology collection. A full list of specimens and measurements analyzed here is provided in the Appendix.

Measurements.—Fourteen measurements were chosen to represent the basic proportions of a semiaquatic mammal skeleton as efficiently as possible. These are listed in Table 4. Thorax and lumbus measurements are total proximal-to-distal centrum lengths made after articulating these vertebrae. Scapula length was measured parallel to the scapular spine. Ilium length was measured from the middle of the acetabulum. Remaining measurements are functional lengths between proximal and distal articular surfaces and not necessarily longest bone dimensions. Head, neck, tail, and manual and pedal phalanx III-3 lengths were not measured because (1) head and neck lengths vary widely in relation to particular feeding modes; (2) tail function is reflected to some degree in lumbus length, and tail length is rarely known in ar-

chaeocetes; (3) distalmost limb elements vary in relation to particular substrates; and (4) distalmost limb elements are often missing both in skeletal preparations of living mammals and in fossils.

Note that all measurements are linear, all are measured in the same units (cm), and all are independently informative in the sense that they represent nonoverlapping segments of the body.

Analysis.—The objective here is a comparison of species of semiaquatic mammals, based on multivariate analysis of all 14 measurements of trunk and limb length simultaneously, to understand both the dimensions and the polarities of observed variability. It is often true that large sets of variates analyzed simultaneously prove to be correlated in ways that yield relatively simple patterns of variation that can be represented on a reduced number of new compound axes, and associated eigenvector coefficients or loadings indicate how these new axes should be interpreted.

Comparison is carried out by using standard

TABLE 3. Nine orders and 17 families of living mammals containing semiaquatic species. Skeletons of 50 out of 124 species were measured, including representatives of all orders and families. Most of the species that were not available for measurement are small shrews (Insectivora) and murids (Rodentia).

Order Family	No. of semiaquatic species	No. of semiaquatic species in study	No. of species not measured
Monotremata			
Ornithorhynchidae	1	1	0
Didelphimorphia			
Didelphidae	1	1	0
Insectivora			
Tenrecidae	4	2	2
Soricidae	10	1	9
Talpidae	2	2	0
Carnivora			
Ursidae	2	2	0
Mustelidae	15	7	8
Pinnipedia			
Otariidae	14	4	10
Odobenidae	1	1	0
Phocidae	19	11	8
Perissodactyla			
Tapiridae	4	3	1
Artiodactyla			
Hippopotamidae	2	2	0
Rodentia			
Castoridae	2	2	0
Muridae	43	7	36
Hydrochoeridae	1	1	0
Myocastoridae	1	1	0
Lagomorpha			
Leporidae	2	2	0
Totals:	124	50	74

TABLE 4. Fourteen measurements representing trunk and limb segments of semiaquatic mammals. Schematic diagram showing measurements is included in Figure 1.

Body segment	Measurement	Abbreviation
Trunk	1. Thorax length (all vertebral centra)	Thorax
	2. Lumbus length (all vertebral centra)	Lumbus
Forelimb	3. Scapula length	Scapula
	4. Humerus length	Humerus
	5. Radius length	Radius
	6. Metacarpal III length	Mcarpiii
	7. Manual phalanx III-1 length	Manpiii1
	8. Manual phalanx III-2 length	Manpiii2
Hindlimb	9. Ilium length	Ilium
	10. Femur length	Femur
	11. Tibia length	Tibia
	12. Metatarsal III length	Mtarsiii
	13. Pedal phalanx III-1 length	Pedpiii1
	14. Pedal phalanx III-2 length	Pedpiii2

principal components analysis of the standardized covariance (correlation) matrix of natural-log (ln, base *e*) transformed measurements. Measurements are log-transformed in recognition that biological variation is geometric-normal or lognormal rather than normal on the scale of arithmetic measurement (Gingerich 2000). Natural logs are used because of their simple relation to the ordinary coefficient of variation (Lewontin 1966). Following standardization to zero mean and unit variance, a covariance matrix becomes a correlation matrix. Analysis was carried out with a program written by the author, following Manly (1994). Eigenvalues and eigenvectors were computed by Jacobi rotation (Press et al. 1989: p. 342).

Fossil Taxa.—Three extinct species relevant to the transition of whales from land to sea are known from skeletons complete enough to compare with those of living semiaquatic mammals: the anthracothere *Elomeryx armatus*, the protocetid *Rodhocetus balochistanensis*, and the basilosaurid *Dorudon atrox* (Fig. 2).

The best specimens of *Elomeryx armatus* were described by Scott (1894; as ''*Ancodus brachyrhynchus?*''), and by Scott (1940; as ''*Elomeryx brachyrhynchus*''). The low-crowned cheek teeth of anthracotheres and their frequent occurrence in paleochannel deposits suggest habits and habitat similar to those of modern hippos (Kron and Manning 1998: p. 381). *Elomeryx armatus* itself is early Oligocene in age, too young geologically to be ancestral to whales, yet anthracotheres plausibly represent the skeletal form of the as yet unknown artiodactyl ancestor of archaeocetes (Gingerich et al. 2001a).

Rodhocetus balochistanensis is the protocetid archaeocete with the best-known postcranial skeleton, including virtually complete fore- and hindlimbs (Gingerich et al. 2001a), however the thorax and lumbus of *R. balochistanensis* are only partially preserved. Thoracic and lumbar vertebrae that are preserved average 87% the length of corresponding elements in *Rodhocetus kasranii* (Gingerich et al. 1994). Thus the thorax and lumbus lengths for *R. balochistanensis* used here are scaled down to 87% of those of *R. kasranii*. The latter was found and excavated with an articulated vertebral column complete from cervical vertebra C2
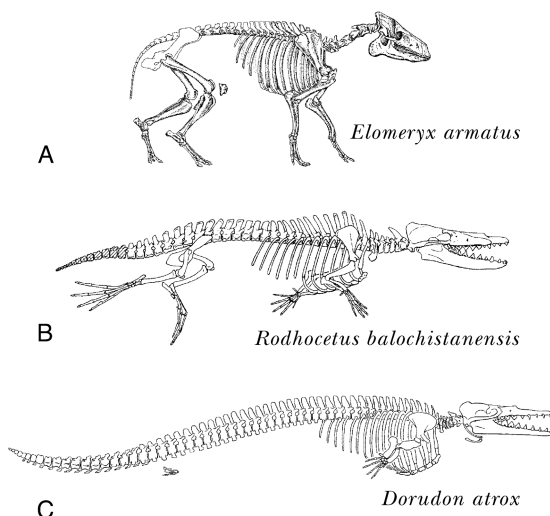

FIGURE 2. Skeletons of semiaquatic mammals transitional from land to sea in the origin of whales. A, Hippo-like early Oligocene anthracothere artiodactyl *Elomeryx armatus* assumed to represent a Paleocene-to-early Eocene stage of cetacean evolution. B, Early middle Eocene archaeocete *Rodhocetus balochistanensis* (tail length not known) representing an early middle Eocene protocetid stage of cetacean evolution. C, Middle-to-late Eocene archaeocete *Dorudon atrox* representing a middle-to-late Eocene basilosaurid stage of cetacean evolution. *Elomeryx* restoration is from Scott (1894), *Rodhocetus* restoration is from Gingerich et al. (2001a), and *Dorudon* restoration is from Gingerich and Uhen (1996). Skeletons are drawn at comparable sizes, not to scale (see Appendix for measurements).

through caudal vertebra Ca4, including a complete trunk series of 13 thoracic and six lumbar vertebrae. Cervical C1 and all distal caudals are missing, which is why the skeleton was conservatively described as being ''partially articulated'' (Gingerich et al. 1994). The length of the scapula in *R. balochistanensis* is assumed to have been the same length as that of contemporary and similar-sized *Artiocetus clavis* (Gingerich et al. 2001a). The length of the ilium in *R. balochistanensis* is scaled up 12% from that of *R. kasranii*, reflecting the difference in femur lengths in the two species (regression of ln ilium length on ln femur length for 50 species of living mammals in the Appendix yields a coefficient of determination $r^2 = 0.96$, meaning femur length is generally a good predictor of ilium length).

Dorudon atrox is known from several good skeletons (Gingerich and Uhen 1996; Uhen 1996, 2003). All trunk and forelimb bones are known for *D. atrox*. In the hindlimb, a partial

femur, patella, and astragalus are known. These are smaller than but closely resemble corresponding parts of the hindlimb and foot of *Basilosaurus isis* (Gingerich et al. 1990). Missing lengths in the hindlimb of *D. atrox* were estimated by scaling down known hindlimb elements of *B. isis*. Femur length in *D. atrox* was scaled to 56% that of *B. isis*, reflecting the ratio of femur widths in the two species. Remaining lengths in *D. atrox* were scaled to 65% those of *B. isis*, reflecting the average ratio of patellar and astragalar dimensions in the two species. *Dorudon atrox* was fully aquatic behaviorally, with a greatly reduced hindlimb that could not possibly have supported its weight on land. It is included here because retention of a hindlimb with feet and toes makes it structurally intermediate, and because later cetaceans have greatly reduced hindlimbs precluding measurement of many lengths that are required for the present quantitative comparison with semiaquatic mammals.

Principal Components Analysis of Living Semiaquatic Mammals

The results of a principal components analysis of trunk and limb measurements of 50 species of extant semiaquatic mammals are shown graphically in Figures 3 and 4. Numerical scores for the first three principal components are listed in Table 5; eigenvalues, and the means, standard deviations, and eigenvectors necessary to calculate scores for additional taxa are listed in Table 6.

PC-I.—The first principal component separates species along an axis spanning some 12 ln units, ranging from the smallest of the species included (water shrew, *Neomys fodiens*) to the largest (hippo, *Hippopotamus amphibius*; walrus, *Odobenus rosmarus;* and elephant seal, *Mirounga leonina*; Fig. 3A). PC-I has an eigenvalue of 13.167, accounting for 94.1% of the total variance in the measurements. Eigenvector coefficients or loadings are all positive, and similar in value (Table 6, Fig. 3B), indicating that PC-I represents overall size.

Regression of PC-I scores on ln body weights, available for 46 of the 50 living species studied here, yields a coefficient of determination $r^2 = 0.97$, confirming that PC-I is a measure of overall size. However, PC-I is not a measure of weight but rather the sum of products of eigenvector coefficients and scaled measurements for all skeletal elements included in a study. Skeletons that deviate most from average proportions, as that of *Dorudon atrox* does here, will have correspondingly distorted sums of products. This means PC-I is not always a good substitute for other measures of size, like body weight for example, and explains the position of *Dorudon atrox* (*D.a.*) among the much smaller Phocidae and Otariidae in Figure 3A.

PC-II.—The second principal component separates species along an orthogonal axis spanning about 2.8 ln units, ranging from the most aquatic species included (Ross seal *Ommatophoca rossi*) to the most terrestrial (Malayan tapir, *Tapirus indicus*; Figs. 3A, 4A). PC-II has an eigenvalue of 0.509, accounting for 3.6% of the total variance in the measurements. Eigenvector coefficients or loadings span a range of values (Table 6, Figs. 3C, 4B), with the strongest contrast being between species with long manual and pedal phalanges (most-negative loadings in Fig. 3C) and those with a long ilium and femur (most positive loadings in Fig. 3C). The loadings indicate that aquatic mammals generally have long manual and pedal phalanges and a short ilium and femur, whereas more terrestrial mammals generally have the reverse. PC-II coefficients identify skeletal characteristics that will be most effective in assessing the degree of aquatic or terrestrial adaptation of a fossil taxon.

PC-III.—The third principal component separates species along a third axis perpendicular to the first two and spanning about 1.7 ln units, ranging from the sea otter, *Enhydra lutris*, to the duck-billed platypus, *Ornithorhynchus anatinus* (Fig. 4A). PC-III has an eigenvalue of 0.102, accounting for 0.7% of the total variance in the measurements. Eigenvector coefficients or loadings span a range of values (Table 6, Fig. 4C), with the strongest contrast being between species with a long lumbus, long metatarsal III, and long pedal phalanx III-1 (most-negative loadings in Fig. 4C) and those with a long metacarpal III and long manual phalanges (most-positive loadings in
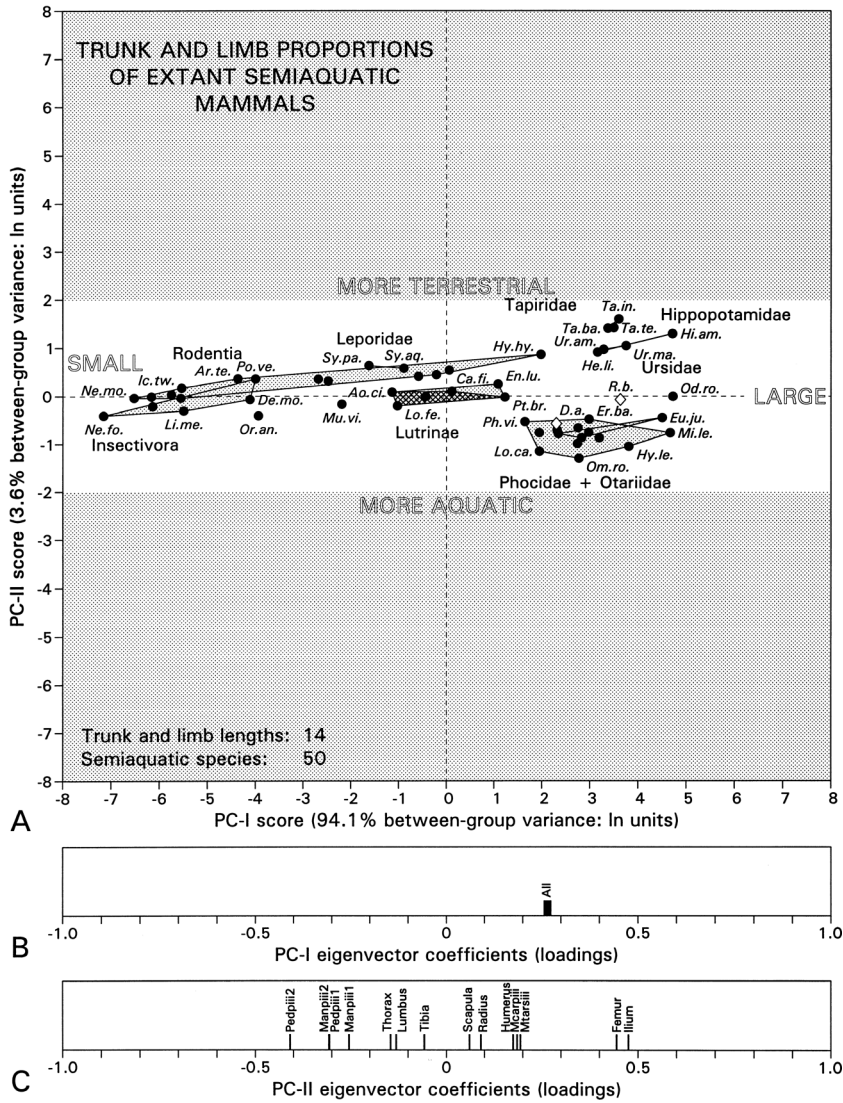
FIGURE 3. Fifty-species principal components analysis of trunk and limb lengths of living semiaquatic mammals. A, Bivariate plot of PC-I versus PC-II, with related taxonomic groups enclosed in shaded convex polygons. B, Univariate plot of eigenvector coefficients or loadings for PC-I. C, Univariate plot of eigenvector coefficients or loadings for PC-II. PC-I is an axis of general size separating species in a spectrum from small (at left) to large (at right). Note that loadings for PC-I are all similar and positive. PC-II is an axis of aquatic adaptation separating mammals that are more aquatic (below) from those that are more terrestrial (above). Note that loadings for PC-II contrast long manual and pedal phalanges (*Pedpiii2, Manpiii2, Pedpiii1, Manpiii1*) in species that are more aquatic versus a long ilium and femur (*Ilium, Femur*) in species that are more terrestrial. Open diamonds labeled *R.b.* and *D.a.* show positions of *Rodhocetus balochistanensis* and *Dorudon atrox*, respectively, projected into this morphometric space based on living semiaquatic mammals. Neither taxon is particularly similar to river otters (cross-hatched) or to the sea otter (*En.lu.*). Remaining abbreviations are listed in Tables 4 and 5.

Fig. 4C). Comparing the loadings and differences between the sea otter and platypus, it is clear that PC-III distinguishes hindlimb-dominated foot swimmers from forelimb-dominated hand swimmers. PC-III coefficients identify skeletal characteristics that are useful in assessing forelimb or hindlimb domination in a semiaquatic fossil taxon.

Positions of Rodhocetus and Dorudon.—*Rodhocetus balochistanensis* and *Dorudon atrox* are the two archaeocetes with complete skeletons sufficiently generalized to be of interest for inter-
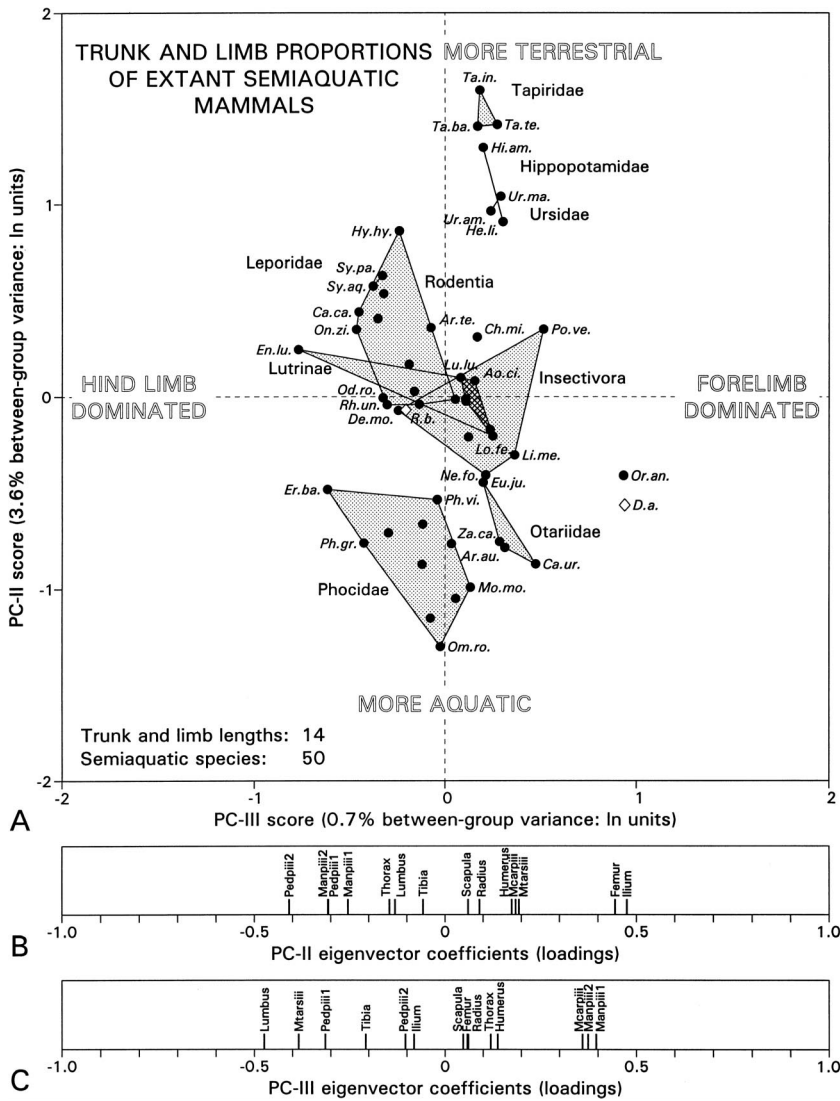
FIGURE 4. Fifty-species principal components analysis of trunk and limb lengths of living semiaquatic mammals. A, Bivariate plot of PC-III versus PC-II, with related taxonomic groups enclosed in shaded convex polygons. B, Univariate plot of eigenvector coefficients or loadings for PC-II. C, Univariate plot of eigenvector coefficients or loadings for PC-III. PC-II is an axis of aquatic adaptation separating mammals that are more aquatic (below) from those that are more terrestrial (above). Note that loadings for PC-II contrast long manual and pedal phalanges (*Pedpiii2, Manpiii2, Pedpiii1, Manpiii1*) in mammals that are more aquatic versus a long ilium and femur (*Ilium, Femur*) in mammals that are more terrestrial. PC-III is an axis of locomotor specialization separating species that are hindlimb dominated (left) from those that are forelimb dominated (right). Note that loadings for PC-III contrast a long lumbus, metatarsal III, and pedal phalanx III-1 (*Lumbus, Mtarsiii, Pedpiii1*) in species that are more hindlimb dominated versus long manual phalanges and metacarpal III (*Manpiii1, Manpiii2, Mcarpiii*) in species that are more forelimb dominated. Open diamonds labeled *R.b.* and *D.a.* show positions of *Rodhocetus balochistanensis* and *Dorudon atrox*, respectively, projected into this morphometric space based on living semiaquatic mammals. Neither taxon is particularly similar to river otters (crosshatched) or to the sea otter (*En.lu.*). Remaining abbreviations are listed in Tables 4 and 5.

preting skeletal proportions and locomotor stages leading to modern whales. These genera can be added to the principal component plots in Figures 3 and 4 by using the eigenvector coefficients in Table 6 to calculate

scores. Scores calculated this way are enclosed in parentheses in Table 5, and their positions in Figures 3 and 4 are indicated with open diamonds.

The size and shape scores on PC-I, II, and

TABLE 5. Principal components scores by species for PC-I, PC-II, and PC-III in (1) an analysis of 50 species of living semiaquatic mammals excluding fossil taxa; and (2) an analysis of all 53 semiaquatic species considered here (50 species of living mammals plus three fossil taxa *Elomeryx armatus*, *Rodhocetus balochistanensis*, and *Dorudon atrox*). PC scores for fossil taxa added to 50-species analysis are enclosed in parentheses.

Genus and species	Abbr.	Extant species only			Extant species plus three fossil taxa		
		PC-I (94.1%)	PC-II (3.6%)	PC-III (0.7%)	PC-I (92.5%)	PC-II (3.7%)	PC-III (1.9%)
Ornithorhynchus anatinus	Or.an.	−3.935	−0.411	0.933	−4.096	−0.367	0.341
Chironectes minimus	Ch.mi.	−2.479	0.311	0.168	−2.651	0.308	−0.086
Potamogale velox	Po.ve.	−3.996	0.352	0.516	−4.167	0.280	−0.640
Limnogale mergulus	Li.me.	−5.493	−0.305	0.364	−5.667	−0.272	0.165
Neomys fodiens	Ne.fo.	−7.157	−0.409	0.212	−7.337	−0.433	−0.327
Desmana moschata	De.mo.	−4.115	−0.073	−0.245	−4.288	−0.013	0.534
Galemys pyrenaicus	Ga.py.	−6.138	−0.212	0.123	−6.306	−0.181	0.244
Ursus americanus	Ur.am.	3.286	0.965	0.240	3.122	0.923	−0.270
Ursus maritimus	Ur.ma.	3.753	1.041	0.292	3.592	1.033	0.021
Mustela vison	Mu.vi	−2.192	−0.172	0.237	−2.370	−0.213	−0.342
Lutra lutra	Lu.lu.	0.115	0.099	0.082	−0.060	0.075	−0.151
Lontra canadensis	Lo.ca.	−0.431	−0.012	0.108	−0.607	−0.040	−0.156
Lontra felina	Lo.fe.	−1.028	−0.206	0.251	−1.203	−0.223	−0.079
Pteronura brasiliensis	Pt.br.	1.225	−0.024	0.109	1.051	−0.036	0.020
Aonyx cinerea	Ao.ci.	−1.137	0.082	0.155	−1.310	0.059	−0.155
Enhydra lutris	En.lu.	1.080	0.246	−0.770	0.904	0.285	0.516
Callorhinus ursinus	Ca.ur.	2.827	−0.870	0.474	2.657	−0.872	0.134
Arctocephalus australis	Ar.au.	2.339	−0.786	0.313	2.171	−0.769	0.314
Zalophus californianus	Za.ca.	2.974	−0.754	0.286	2.803	−0.765	0.100
Eumetopias jubatus	Eu.ju.	4.502	−0.446	0.200	4.334	−0.455	0.176
Odobenus rosmarus	Od.ro.	4.725	−0.007	−0.326	4.555	0.013	0.442
Monachus monachus	Mo.mo.	2.741	−0.991	0.133	2.565	−1.031	−0.073
Lobodon carcinophagus	Lo.ca.	1.949	−1.154	−0.077	1.774	−1.144	0.279
Hydrurga leptonyx	Hy.le.	3.809	−1.050	0.056	3.633	−1.077	−0.012
Leptonychotes weddelli	Le.we.	3.194	−0.873	−0.121	3.019	−0.885	0.117
Ommatophoca rossi	Om.ro.	2.770	−1.302	−0.025	2.595	−1.301	0.240
Mirounga leonina	Mi.le.	4.667	−0.765	0.032	4.495	−0.797	−0.006
Erignathus barbatus	Er.ba.	2.981	−0.483	−0.618	2.802	−0.464	0.358
Cystophora cristata	Cy.cr.	2.754	−0.665	−0.118	2.585	−0.651	0.344
Halichoerus grypus	Ha.gr.	2.317	−0.709	−0.298	2.144	−0.695	0.305
Phoca groenlandica	Ph.gr.	1.943	−0.762	−0.426	1.769	−0.736	0.376
Phoca vitulina	Ph.vi.	1.644	−0.537	−0.041	1.473	−0.578	−0.135
Tapirus terrestris	Ta.te.	3.500	1.418	0.274	3.336	1.392	−0.147
Tapirus bairdii	Ta.ba.	3.375	1.408	0.171	3.213	1.397	−0.036
Tapirus indicus	Ta.in.	3.602	1.598	0.182	3.440	1.565	−0.177
Hippopotamus amphibius	Hi.am.	4.717	1.296	0.200	4.550	1.248	−0.201
Hexaprotodon liberiensis	He.li.	3.162	0.909	0.304	2.994	0.871	−0.159
Castor fiber	Ca.fi.	0.057	0.535	−0.322	−0.114	0.574	0.415
Castor canadensis	Ca.ca.	−0.210	0.441	−0.453	−0.381	0.482	0.474
Neusticomys monticolus	Ne.mo.	−6.525	−0.041	−0.135	−6.703	−0.037	−0.083
Ichthyomys hydrobates	Ic.hy.	−5.750	0.027	−0.161	−5.928	0.053	0.120
Ichthyomys tweedii	Ic.tw.	−5.535	0.169	−0.189	−5.713	0.166	−0.046
Rheomys raptor	Rh.ra.	−6.163	−0.014	0.053	−6.342	−0.014	−0.107
Rheomys underwoodi	Rh.un.	−5.556	−0.043	−0.304	−5.733	0.006	0.320
Arvicola terrestris	Ar.te.	−4.364	0.359	−0.075	−4.542	0.332	−0.253
Ondatra zibethicus	On.zi.	−2.685	0.349	−0.465	−2.861	0.374	0.241
Hydrochoeris hydrochoeris	Hy.hy.	1.979	0.861	−0.241	1.804	0.825	−0.201
Myocastor coypus	My.co.	−0.583	0.406	−0.353	−0.756	0.439	0.348
Sylvilagus aquaticus	Sy.aq.	−0.890	0.575	−0.378	−1.066	0.563	−0.152
Sylvilagus palustris	Sy.pa.	−1.624	0.629	−0.329	−1.800	0.603	−0.274
Elomeryx armatus	E.a.	(3.203)	(1.205)	(0.103)	3.458	−0.017	0.617
Rodhocetus balochistanensis	R.b.	(3.635)	(−0.068)	(−0.205)	3.035	1.189	−0.137
Dorudon atrox	D.a.	(2.304)	(−0.563)	(0.940)	2.128	−0.990	−3.153

TABLE 6. Eigenvalues and eigenvector coefficients associated with each principal component (PC) based on 50 living semiaquatic mammals. Scores for an additional species like *Rodhocetus balochistanensis* are determined by summing products of the appropriate eigenvector coefficient here multiplied by $(x_i - m_i)/s_i$, over all $i = 14$ measurements, where x_i is the vector of ln-transformed measurements, m_i is the corresponding 50-species mean from the bottom of the table, and s_i is the corresponding 50-species standard deviation from the bottom of the table. Results for principal components I, II, and III are shown graphically in Figures 3 and 4.

PC	Eigen-value	Thorax	Lumbus	Scapula	Humerus	Radius	Mcarpiii	Manpiii1	Manpiii2	Ilium	Femur	Tibia	Mtarsiii	Pedpiii1	Pedpiii2
I	13.167	0.271	0.265	0.273	0.272	0.273	0.269	0.268	0.266	0.257	0.260	0.273	0.268	0.266	0.261
II	0.509	-0.146	-0.131	0.060	0.175	0.090	0.194	-0.255	-0.306	0.475	0.445	-0.058	0.185	-0.307	-0.409
III	0.102	0.120	-0.474	0.047	0.138	0.058	0.360	0.395	0.375	-0.081	0.061	-0.208	-0.384	-0.314	-0.104
IV	0.079	-0.118	-0.737	0.285	-0.075	0.156	-0.223	-0.095	-0.053	0.258	-0.140	0.102	0.071	0.346	0.222
V	0.037	-0.262	-0.066	-0.234	-0.174	-0.244	0.199	0.293	0.211	0.137	-0.150	-0.393	0.628	0.140	-0.063
VI	0.030	-0.565	-0.054	-0.101	0.066	0.524	0.136	-0.048	0.105	-0.478	0.035	0.286	0.191	-0.078	-0.050
VII	0.023	-0.177	-0.035	-0.571	0.153	0.018	-0.211	-0.151	0.245	0.185	0.434	-0.162	-0.191	0.059	0.449
VIII	0.019	0.418	-0.254	-0.068	0.152	-0.130	0.234	-0.381	-0.114	-0.356	0.013	-0.049	0.402	-0.262	0.378
IX	0.012	0.122	-0.146	-0.360	-0.536	-0.115	0.432	0.077	-0.199	0.019	0.210	0.444	-0.123	0.212	-0.026
X	0.009	0.357	-0.214	-0.329	0.258	0.025	-0.464	0.264	-0.006	-0.189	0.163	0.185	0.230	0.145	-0.444
XI	0.006	0.317	0.053	-0.326	-0.210	0.538	-0.004	-0.218	0.221	0.337	-0.443	-0.013	0.041	-0.196	-0.103
XII	0.003	0.039	0.022	-0.213	0.301	0.322	0.234	0.211	-0.606	-0.045	-0.171	-0.365	-0.142	0.314	0.093
XIII	0.002	-0.002	0.015	0.045	-0.304	0.173	-0.301	0.506	-0.318	0.064	0.124	0.027	0.148	-0.514	0.349
XIV	0.002	-0.198	-0.039	-0.229	0.457	-0.319	0.081	0.139	-0.084	0.266	-0.433	0.488	-0.024	-0.229	0.119
50-species mean:		3.087	2.404	2.067	2.074	1.969	0.941	0.546	0.114	1.749	2.093	2.403	1.373	0.868	0.407
50-species std. dev.:		1.264	1.088	1.078	1.031	1.000	1.060	1.074	1.178	0.906	0.960	0.910	0.812	1.039	1.172

III axes can be used to calculate distances of *Rodhocetus* and *Dorudon* from all of the extant species. When scores on all three axes are used, *R. balochistanensis* is closest to the bearded seal, *Erignathus barbatus* (a phocid; 0.877 ln units) and *D. atrox* is closest to the southern fur seal, *Arctocephalus australis* (an otariid; 0.666 ln units). When PC-I is excluded and we focus on shape, *R. balochistanensis* is closest to the desman, *Desmana moschata* (0.040 ln units) and *D. atrox* is closest to the platypus, *Ornithorhynchus anatinus* (0.152 ln units). Such a surprising result, implying that *Dorudon* and *Ornithorhynchus* are similar, makes little sense because the two differ so greatly in thorax and lumbus proportions: *Dorudon* is lumbus dominated and the platypus is thorax dominated.

Rodhocetus balochistanensis and *Dorudon atrox* are proportioned differently, which is indicated immediately by their relative positions on the PC-I size axis (Fig. 3A; open diamonds *R.b.* and *D.a.*, respectively): *R. balochistanensis* has a higher PC-I score than *D. atrox*, even though *D. atrox* is the larger species (body weights estimated from vertebrae are 450 and 1140 kg, respectively; Gingerich 1998; Gingerich et al. 2001a). Lumbus length of *D. atrox* contributes more than expected to its PC-I score, but all of the hindlimb measurements contribute much less than expected, and the net effect is underestimation of overall size relative to more normally proportioned *R. balochistanensis*.

Dorudon atrox has a lower and hence more aquatic PC-II score than *Rodhocetus balochistanensis* (Fig. 4A), and *R. balochistanensis* has a lower and hence more hindlimb-dominated PC-III score. However, the higher PC-III score of *D. atrox* is surprising in implying that *D. atrox* was forelimb dominated. If we look at the contribution of each *D. atrox* skeletal measurement to its PC-III score, we see that its longer lumbus contributes negatively to the overall score, but this is offset by more positive than expected hindlimb contributions. These results raise questions about whether archaeocetes are adequately represented in a principal component space based on living semiaquatic mammals alone. One way to test this is to rerun the analysis with archaeocetes included.

Principal Components Analysis Including Archaeocetes

A second principal components analysis of trunk and limb measurements was run for 53 species, the original 50 species of extant semi-aquatic mammals used in the first analysis plus the three fossil taxa of interest here: *Elomeryx armatus*, *Rodhocetus balochistanensis*, and *Dorudon atrox* (all described above). Results are shown graphically in Figures 5 and 6. Numerical scores for the first three principal components are listed in Table 5; eigenvalues and means, standard deviations, and eigenvectors necessary to calculate scores for additional taxa are listed in Table 7.

PC-I.—Here again, the first principal component separates species along an axis spanning some 12 ln units. PC-I has an eigenvalue of 12.963, accounting for 92.5% of the total variance in the measurements. Eigenvector coefficients or loadings are all positive, and similar in value (Table 7, Fig. 5B), indicating that PC-I again represents overall size.

PC-II.—Again, the second principal component separates species along an orthogonal axis spanning about 2.8 ln units, ranging from the most aquatic species included (Ross seal, *Ommatophoca rossi*) to the most terrestrial (Malayan tapir, *Tapirus indicus*; Figs. 5A, 6A). PC-II has an eigenvalue of 0.500, accounting for 3.7% of the total variance in the measurements. Eigenvector coefficients or loadings span a range of values (Table 7, Figs. 5C, 6B), with the strongest contrast being between species with long manual and pedal phalanges (most-negative loadings in Fig. 5C) and those with a long ilium and femur (most-positive loadings in Fig. 5C). As before, the loadings indicate that aquatic mammals generally have long manual and pedal phalanges and a short ilium and femur, whereas more terrestrial mammals generally have short manual and pedal phalanges and a long ilium and femur.

PC-III.—The big difference between the two analyses shows up in the third principal component, which now spans more than 3.5 ln units, ranging from the archaeocete *Dorudon atrox* to the desman *Desmana moschata* (Fig. 6A). PC-III has an eigenvalue of 0.265, ac-
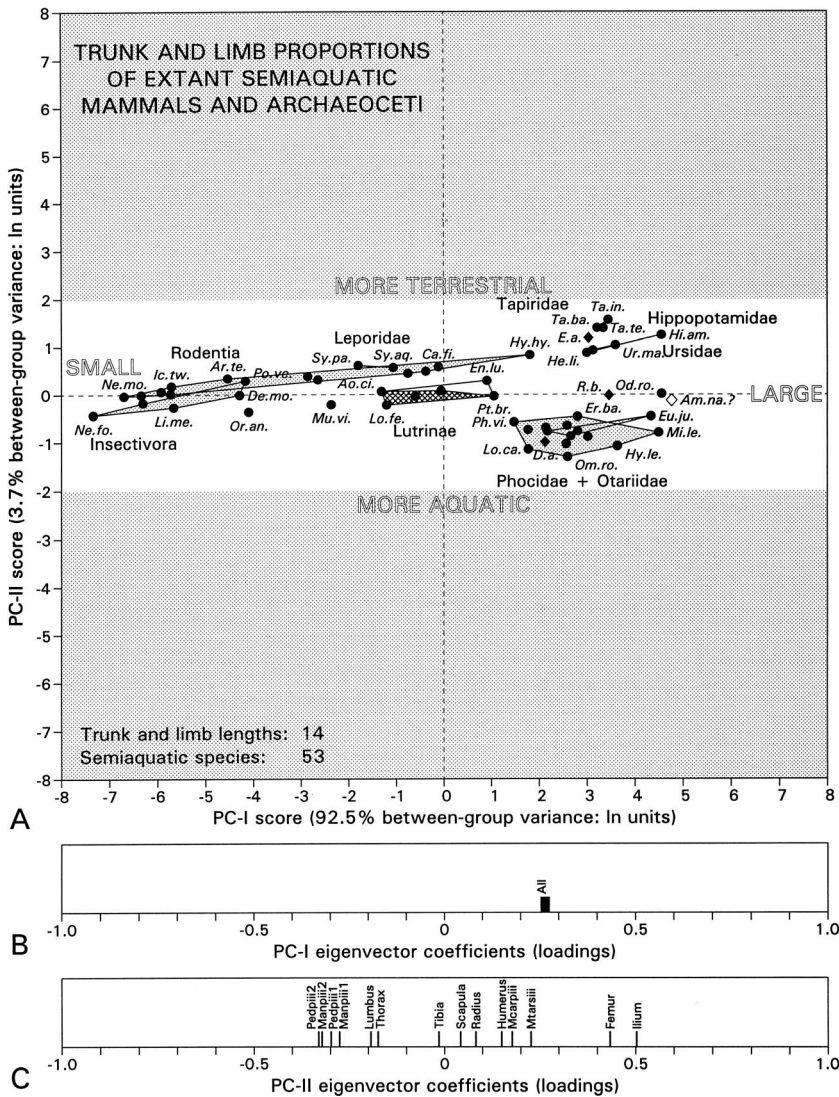
FIGURE 5. Fifty-three-species principal components analysis of trunk and limb lengths of living semiaquatic mammals plus three fossil taxa: *Elomeryx armatus* (*E.a.*), *Rodhocetus balochistanensis* (*R.b.*), and *Dorudon atrox* (*D.a.*). A, Bivariate plot of PC-I versus PC-II, with related taxonomic groups enclosed in shaded convex polygons. B, Univariate plot of eigenvector coefficients or loadings for PC-I. C, Univariate plot of eigenvector coefficients or loadings for PC-II. PC-I is an axis of general size separating species in a spectrum from small (at left) to large (at right). Note that loadings for PC-I are all similar and positive. PC-II is an axis of aquatic adaptation separating mammals that are more aquatic (below) from those that are more terrestrial (above). Note that loadings for PC-II contrast long manual and pedal phalanges (*Manpiii2, Pedpiii2, Pedpiii1, Manpiii1*) in species that are more aquatic versus a long ilium and femur (*Ilium, Femur*) in species that are more terrestrial. None of the fossil taxa (diamonds) is particularly similar to river otters (cross-hatched) or to the sea otter (*En.lu.*). Remaining abbreviations are listed in Tables 4 and 5. Eigenvector coefficients differ slightly from those in 50-species analysis, and the position of *Dorudon atrox* is different (diamond *D.a.*), but otherwise this figure is little changed from Figure 3. Possible position of *Ambulocetus natans* is shown by an open diamond (*Am.na.?*; see text).

counting for 1.9% of the total variance in the measurements. Eigenvector coefficients or loadings span a range of values (Table 7, Fig. 6C), with the strongest contrast being between species with a long lumbus (most-negative loading in Fig. 6C) and those with long pedal phalanges, especially III-2 (most positive loadings in Fig. 6C). Now PC-III distinguishes lumbus-driven tail swimmers, represented by *D. atrox*, from hindlimb-dominated foot swim-
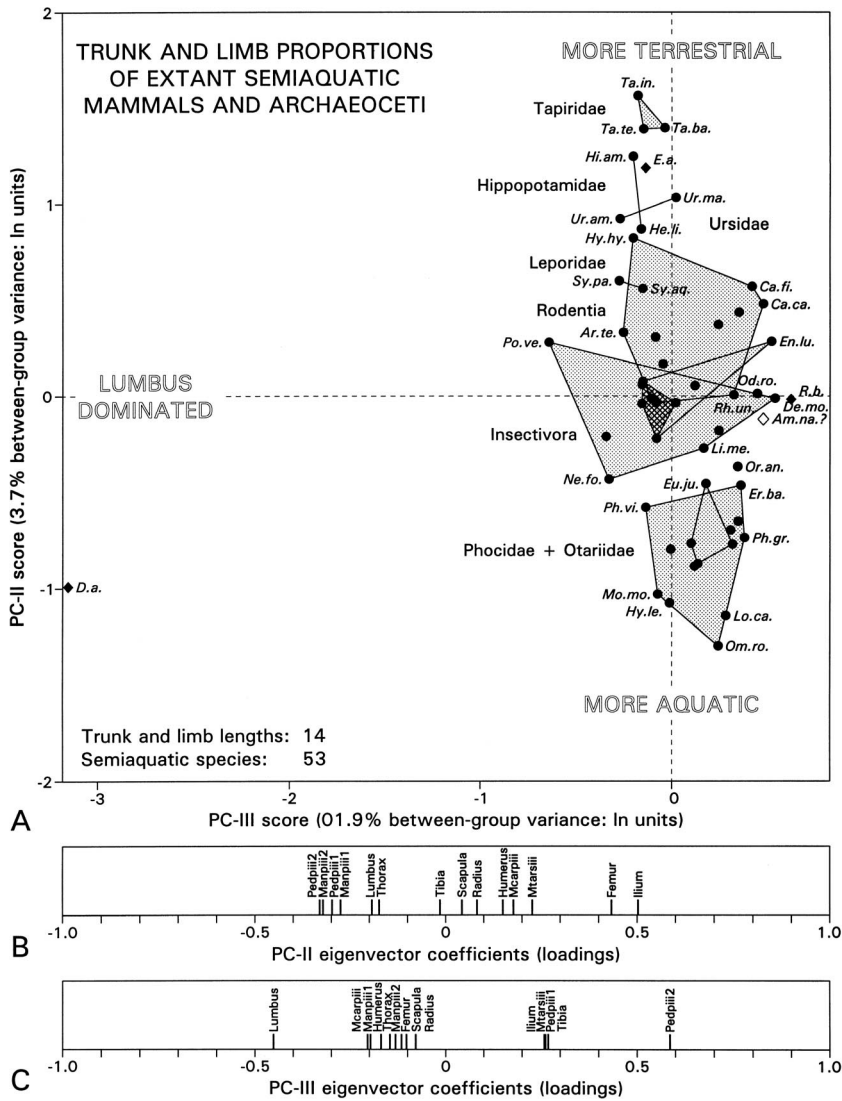
FIGURE 6. Fifty-three-species principal components analysis of trunk and limb lengths of living semiaquatic mammals plus three fossil taxa: *Elomeryx armatus* (*E.a.*), *Rodhocetus balochistanensis* (*R.b.*), and *Dorudon atrox* (*D.a.*). A, Bivariate plot of PC-III versus PC-II, with related taxonomic groups enclosed in shaded convex polygons. B, Univariate plot of eigenvector coefficients or loadings for PC-II. C, Univariate plot of eigenvector coefficients or loadings for PC-III. PC-II is an axis of aquatic adaptation separating mammals that are more aquatic (below) from those that are more terrestrial (above). Note that loadings for PC-II contrast long manual and pedal phalanges (*Manpiii2, Pedpiii2, Pedpiii1, Manpiii1*) in mammals that are more aquatic versus a long ilium and femur (*Ilium, Femur*) in mammals that are more terrestrial. PC-III is an axis of locomotor specialization separating species that are lumbus dominated (left) from those that are hindlimb dominated (right). Note that loadings for PC-III contrast a long lumbus (*Lumbus*) in species that are more lumbus dominated versus a long pedal phalanx III-2 (*Pedpiii2*) in species that are more hindlimb dominated. None of the fossil taxa (diamonds) is particularly similar to river otters (cross-hatched) or to the sea otter (*En.lu.*). Remaining abbreviations are listed in Tables 4 and 5. The vertical aquatic versus terrestrial axis is little changed from that of the 50-species analysis shown in Figure 4, but the horizontal locomotor axis was substantially reorganized when the fossil taxa, particularly *Dorudon atrox* (diamond *D.a.*), were added. Possible position of *Ambulocetus natans* is shown by an open diamond (*Am.na.?*; see text).

TABLE 7. Eigenvalues and eigenvector coefficients associated with each principal component based on 50 living semiaquatic mammals plus three extinct taxa, *Elomeryx armatus*, *Rodhocetus balochistanensis*, and *Dorudon atrox*. Scores for an additional species would be determined by summing products of the appropriate eigenvector coefficient here multiplied by $(x_i - m_i)/s_i$, over all $i = 14$ measurements, where x_i is the vector of ln-transformed measurements, m_i is the corresponding 53-species mean from the bottom of the table, and s_i is the corresponding 53-species standard deviation from the bottom of the table. Results for principal components I, II, and III are shown graphically in Figures 5 and 6.

PC	Eigen-value	Thorax	Lumbus	Scapula	Humerus	Radius	Mcarpiii	Manpiii1	Manpiii2	Ilium	Femur	Tibia	Mtarsiii	Pedpiii1	Pedpiii2
I	12.946	0.272	0.260	0.274	0.274	0.274	0.271	0.268	0.267	0.255	0.262	0.273	0.268	0.267	0.255
II	0.518	−0.174	−0.193	0.042	0.150	0.082	0.177	−0.276	−0.322	0.503	0.433	−0.015	0.227	−0.298	−0.331
III	0.268	−0.146	−0.451	−0.103	−0.170	−0.079	−0.205	−0.197	−0.132	0.258	−0.116	0.269	0.260	0.262	0.585
IV	0.090	0.061	−0.730	0.094	0.086	0.095	0.264	0.314	0.332	0.031	0.012	−0.129	−0.316	−0.198	0.057
V	0.050	−0.196	0.094	−0.335	−0.080	−0.454	0.271	0.332	0.192	0.145	−0.009	−0.432	0.443	0.006	0.064
VI	0.036	−0.111	−0.149	0.544	−0.091	0.016	−0.198	0.185	−0.068	0.198	−0.315	−0.231	0.161	0.446	−0.408
VII	0.031	−0.562	−0.078	−0.044	−0.036	0.454	0.177	0.039	0.127	−0.444	−0.094	0.223	0.381	−0.058	−0.122
VIII	0.021	−0.488	0.127	−0.268	0.127	0.214	−0.359	0.100	0.249	0.258	0.305	−0.141	−0.387	0.286	0.015
IX	0.013	−0.105	0.092	−0.112	−0.553	−0.103	0.317	0.317	−0.145	0.229	−0.013	0.495	−0.288	0.083	−0.204
X	0.009	0.482	−0.233	−0.542	−0.076	0.210	−0.249	0.068	0.118	−0.019	0.080	0.090	0.258	0.203	−0.409
XI	0.007	−0.074	−0.200	0.056	0.264	−0.391	0.007	0.208	−0.328	−0.451	0.480	0.139	−0.022	0.348	−0.057
XII	0.006	0.086	−0.027	−0.086	−0.233	0.240	0.519	−0.406	−0.097	−0.111	0.099	−0.388	−0.146	0.480	0.071
XIII	0.003	−0.010	−0.032	0.287	−0.402	−0.287	−0.121	−0.351	0.590	−0.100	0.381	0.100	0.089	−0.023	−0.115
XIV	0.002	0.099	0.029	0.153	−0.487	0.312	−0.253	0.350	−0.279	−0.113	0.370	−0.305	0.113	−0.220	0.252
53-species mean:		3.143	2.484	2.127	2.131	2.011	1.005	0.614	0.175	1.779	2.142	2.424	1.409	0.905	0.419
53-species std. dev.:		1.251	1.125	1.076	1.029	0.988	1.063	1.083	1.173	0.910	0.956	0.896	0.817	1.027	1.173

mers like *D. moschata*. The PC-III spectrum is now no longer one from hindlimb-dominated locomotion to forelimb-dominated locomotion (Fig. 4), but rather a spectrum from lumbus-dominated locomotion to hindlimb-dominated locomotion (Fig. 6).

Position of Rodhocetus and Dorudon.—*Rodhocetus balochistanensis* and *Dorudon atrox* are integral parts of the principal component plots in Figures 5 and 6 (solid diamonds) because they are part of the 53-species analysis. Principal component scores are shown in the right-hand columns at the bottom of Table 5. If we again use the size and shape scores on PC-I, II, and III axes to calculate distances from all other species in the analysis, *R. balochistanensis* is closest to the bearded seal, *Erignathus barbatus* (a phocid; 0.840 ln units), as before, and *D. atrox* is closest to the monk seal, *Monachus monachus* (an otariid; 3.075 ln units). If PC-I is excluded and we focus on shape, *R. balochistanensis* is again closest to the desman, *Desmana moschata* (0.082 ln units) and *D. atrox* is closest to the otter shrew, *Potamogale velox* (2.803 ln units). *Rodhocetus* occupies virtually the same position it did in the 50-species analysis, but *Dorudon* is now relatively far from all of the other semiaquatic taxa, reflecting the unique proportions of its trunk and limb skeleton.

Dorudon is a good model for later Cetacea, which can be demonstrated by using simulation to estimate principal component scores for living whales. Finite lengths must be assumed for all of the missing hindlimb elements, which have a true length of zero. The assumed lengths can then be made arbitrarily small, approaching their true length of zero. Measurements of the pygmy killer whale, *Feresa attenuata* (Yamada 1954), Bering Sea beaked whale, *Mesoplodon stejnegeri* (Nishiwaki and Kamiya 1959), and male and female southern minke whale, *Balaenoptera acutorostrata bonaerensis* (Omura 1975) were used for estimation. When missing hindlimb lengths are arbitrarily set at 1 cm, the four living whales plot just below and to the left and right of *Dorudon atrox* in Figure 6. As the simulation proceeds and hindlimb lengths are reduced, again arbitrarily, to 0.1 cm, and then 0.01 cm, the living whales move to the left of *D. atrox* about 3 ln

units for each order-of-magnitude limb-length reduction, moving farther from *Rodhocetus balochistanensis* and the other semiaquatic mammals. *Dorudon* and all of the fully aquatic Cetacea it can be taken to represent are too different to force into a principal component space defined by living semiaquatic mammals alone.

Evolutionary Transition of Whales from Land to Sea

The origin of whales and their evolutionary transition from land to sea together constitute one of the most tangible examples of a shift of adaptive zone documented in the fossil record. We can use this example both to examine the simplicity or directness of such a shift and to quantify the associated rates of change. Simpson (1944: p. 193) implied that shifts of adaptive zone would be more or less simple and direct, and he expected such transitions to involve unusually high or ''tachytelic'' rates of evolution.

Any attempt to characterize an evolutionary transition or calculate evolutionary rates necessarily relies on available evidence, which in this case is represented by *Elomeryx armatus*, *Rodhocetus balochistanensis*, and *Dorudon atrox*. It is a commonly accepted working hypothesis that whales evolved from an *E. armatus*-like land mammal ancestor, passing through an aquatic stage that was first protocetid and semiaquatic (represented by *Rodhocetus balochistanensis*) and then basilosaurid and fully aquatic (represented by *Dorudon atrox*). This is illustrated in Figure 7, which is a simplified version of the principal component plot of Figure 6, with arrows added to indicate the hypothesized path that archaic whales followed through the morphospace. The arrows are linear, but dashed to emphasize that this is a representation of present evidence: the true paths are not known and new discoveries are almost certain to show that there was additional complexity.

Protocetids have been regarded as ancestral to later basilosaurids since *Protocetus* itself was described by Fraas (1904). This placement was based initially on the greater geological age of protocetids (early middle Eocene versus late middle Eocene to late Eocene) and their inter-
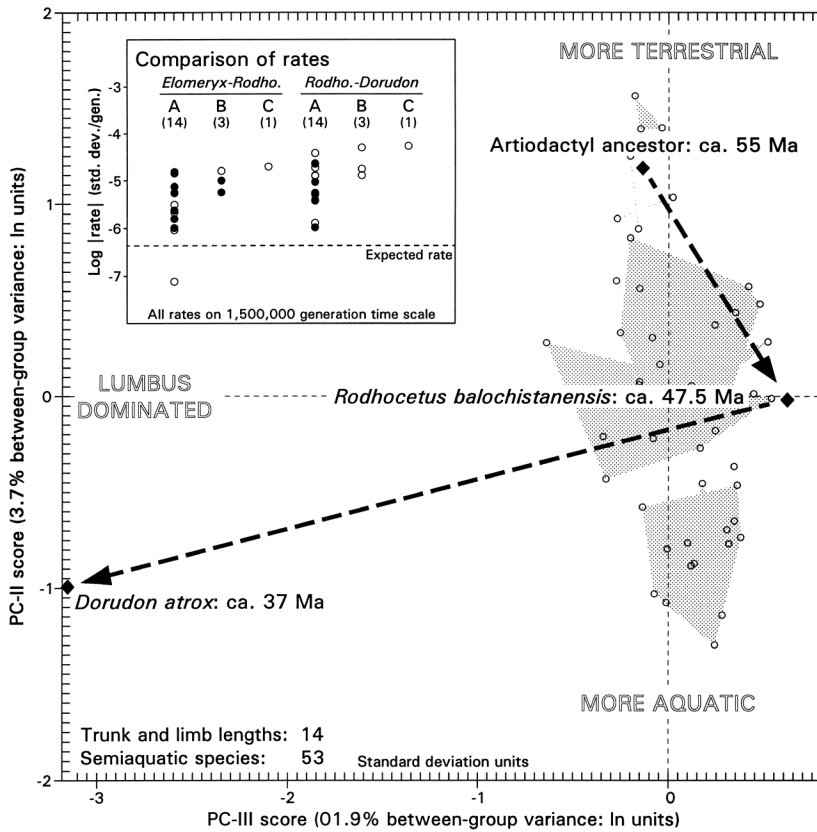
FIGURE 7. Evolutionary trajectory of early whale evolution from an artiodactyl land-mammal ancestor at ca. 55 Ma, represented morphologically by *Elomeryx armatus*, to semiaquatic *Rodhocetus balochistanensis* at ca. 47.5 Ma, to fully-aquatic *Dorudon atrox* retaining hindlimbs and feet at 37 Ma. Trajectory is graphed on the bivariate plot of PC-III versus PC-II in the 53-species analysis of Figure 6. Note that the successive fossil taxa show a progression of increasing aquatic adaptation moving from the top to the bottom of the diagram. However, they simultaneously show an abrupt reversal on the locomotor axis, moving first to extreme hindlimb domination (right) and then to extreme lumbus domination (left). Axes are calibrated in natural log (ln) units externally and corresponding standard deviation units internally (employing generally observed 5% coefficient of variation for linear measurements; see text). Inset box shows rates of evolution calculated for the first or *Elomeryx* to *Rodhocetus* transition and for the second or *Rodhocetus* to *Dorudon* transition, based on 14 measurements of each (A), based on PC-I, PC-II, and PC-III individually (B), and based on PC-I, PC-II, and PC-III simultaneously (C). Sample sizes are given in parentheses. All rates are calculated in standard deviation units on a 1,500,000 or $10^{6.18}$ generation timescale. Solid circles represent positive rates and open circles negative rates. All but one of the rates calculated here exceeds the rate of $10^{-6.36}$ (dashed line) expected for paleontological rates calculated on such long time scales (Gingerich 2001: p. 139). Note that multivariate rates here are higher than the average for univariate rates, and rates for the second or *Rodhocetus* to *Dorudon* transition are higher than corresponding rates for the first or *Elomeryx* to *Rodhocetus* transition.

mediacy between land mammals and basilosaurids, and today is supported by a large number of morphological characteristics summarized cladistically by Uhen (1998) and Luo and Gingerich (1999).

Simplicity and Directness.—The artiodactyl ancestor of whales was possibly semiaquatic in the sense that hippos, tapirs, and bears are semiaquatic, but the first transition, from land mammals to semiaquatic protocetids represented by *Rodhocetus*, clearly started near the terrestrial pole of aquatic adaptation. The first stage of aquatic adaptation, represented by *Rodhocetus*, is otterlike in terms of its intermediacy on the terrestrial-aquatic axis, as are many other mammals, but *Rodhocetus* is not otterlike in terms of its skeletal proportions. It is more desmanlike, and the first transition ended at the hindlimb-dominated pole of aquatic locomotor adaptation.

The second transition, from protocetids represented by *Rodhocetus* to basilosaurids

represented by *Dorudon*, started among hind-limb-dominated semiaquatic mammals and crossed to establish an opposite lumbus-dominated pole that has no representation among living semiaquatic mammals. The best living models for archaic whales at this third stage are fully aquatic Cetacea, which plot off the left side of the chart, more lumbus dominated than *Dorudon* (see above). This second transition appears more profound than the first in that the distance traveled was greater and the full spectrum of semiaquatic locomotor morphologies was crossed.

Clearly the transition from land to sea in whale evolution, taken as a whole, was not simple or direct. This involved first the evolution of a protocetid semiaquatic stage that was intermediate in time and intermediate in degree of aquatic adaptation, but specialized in terms of hindlimb-dominated locomotion (Fig. 2B). The transition then involved subsequent evolution of a basilosaurid fully aquatic stage with reversal and reduction of hindlimbs while gaining a new lumbus and tail domination (Fig. 2C).

Rates of Change.—The time of origin of Archaeoceti and hence Cetacea is thought to be about 54–55 Ma (Gingerich and Uhen 1998; Bajpai and Gingerich 1998), which probably represents their time of divergence from an anthracothere-like artiodactyl ancestor (Gingerich et al. 2001a). *Rodhocetus balochistanensis* lived about 47.5 Ma (Gingerich et al. 2001a). *Dorudon atrox* lived at the time of the Bartonian-Priabonian middle-to-late Eocene transition (Gingerich 1992), which is calibrated at 37 Ma (all numerical ages on the timescale of Berggren et al. 1995). Thus the first transition in Figure 7, from an artiodactyl ancestor to *R. balochistanensis*, took about 7.5 Myr; and the second transition, from *R. balochistanensis* to *D. atrox*, took about 10.5 Myr.

The most general units for calculating evolutionary rates are haldanes, or within-group standard deviations per generation (Gingerich 2001). One generation for a mammal intermediate in size between *Elomeryx* and *Rodhocetus* is equivalent to about five years, and one generation for a mammal intermediate in size between *Rodhocetus* and *Dorudon* is about seven years (combining data on body weight, age

of first reproduction, and generation time in appendices 2 and 4 of Eisenberg 1981). Thus the 7.5-Myr duration of the initial artiodactyl-to-*Rodhocetus* transition is equivalent to about 1,500,000 or $10^{6.18}$ generations, and the 10.5 Myr duration of the second *Rodhocetus*-to-*Dorudon* transition is also equivalent to about $10^{6.18}$ generations.

There are not enough specimens available for the living or fossil taxa discussed here to be able to calculate within-group standard deviations individually, but we can take advantage of the generalization that coefficients of variation of linear measurements like those used here average about 0.05 or 5% of the mean (rounded mean of coefficients of variation in table 72 of Yablokov 1974). This is equivalent to 0.05 units on a base-*e* natural log (ln) scale (Lewontin 1966). One can log (base *e*) the measurements for *Elomeryx armatus* and *Rodhocetus balochistanensis* in the Appendix (as was done for the principal components analysis), calculate the difference in ln values for each corresponding pair, and express these differences in standard deviation units. Dividing each difference by $10^{6.18}$ generations yields 14 rates, in haldanes, for the artiodactyl ancestor to *R. balochistanensis* transition, which are plotted in the first or left-hand column A in the inset graph in Figure 7. The same calculation can be done for corresponding pairs of measurements representing *R. balochistanensis* and *Dorudon atrox*, and these rates are plotted in the second or right-hand column A in the inset graph in Figure 7.

Both sets of rates calculated for individual measurements are similar, but those for *Elomeryx* to *Rodhocetus* average $10^{-5.57}$ standard deviations per generation (median), whereas those for *Rodhocetus* to *Dorudon* average $10^{-5.14}$ (median). Paleontological rates on a 1,500,000 or $10^{6.18}$-generation timescale are expected to average about $10^{-6.36}$ (Gingerich 2001: p. 139). Thirteen of 14 rates for the *Elomeryx* to *Rodhocetus* transition are above this, and all rates for the *Rodhocetus* to *Dorudon* transition are above this. It is also possible to calculate multivariate rates of evolution from the principal component scores given in Table 5. These scores are expressed in ln units, and for linear measurements like those used here a standard

deviation is equivalent to about 0.05 ln units (see above). PC-I for *Elomeryx armatus* (2.933) and *Rodhocetus balochistanensis* (3.348) differ by 8.3 standard deviation units. Dividing by 1,500,000 or $10^{6.18}$ generations yields a rate of $10^{-5.26}$. Rates can be calculated similarly from PC-II and PC-III scores, and rates for all three axes for the *Elomeryx*-to-*Rodhocetus* transition are plotted in the left-hand column B in the inset graph in Figure 7. Rates for the *Rodhocetus*-to-*Dorudon* transition are plotted in the right-hand column B in the inset graph. A single rate for the three principal component axes can be calculated as the Euclidean distance between taxa of interest, divided by the $10^{6.18}$-generation interval, and these rates ($10^{-4.70}$ and $10^{-4.26}$, respectively) are plotted in left- and right-hand columns C for the two transitions. Note that in each case the single rate based three principal components is higher than the highest of the three individual components, and higher than the highest of the 14 rates based on individual measurements.

Discussion

This study is quantitative in an explicitly statistical sense. It is an attempt to compare the sizes and proportions of different skeletal parts in many semiaquatic taxa simultaneously, with an emphasis on overall patterns rather than details. Principal components analysis performs well here in separating small from large mammals on one axis (PC-I: separating water shrews, *Ne.fo.*, from hippos, *Hi.am.*; Figs. 3 and 5), and more terrestrial from more aquatic mammals on a second axis (PC-II: separating tapirs, *Ti.in.*, from Ross seals, *Om.ro.*; Figs. 3 and 5). Principal components analysis performs well too in separating hind-dominated mammals from forelimb-dominated mammals on PC-III in Figure 4 (separating sea otters, *En.lu.*, from platypuses, *Or.an.*), or in separating lumbus-dominated mammals from hindlimb-dominated mammals on PC-III in Figure 6 (separating *Dorudon atrox*, *D.a.*, and giant African water shrews, *Po.ve.*, from desmans, *De.mo.*, and *Rodhocetus balochistanensis*, *R.b.*).

Principal axes I, II, and III are interpreted to reflect size, terrestrial versus aquatic, and hind versus forelimb (Fig. 4) or lumbus versus hind-limb domination (Fig. 6), but it is important to remember that in each case the axes are combinations of trunk and limb lengths computed to maximize variance orthogonal to any previous axis. The overall patterns are clear, but some of the details are surprising. *Dorudon atrox* (*D.a.*) was larger than the phocids it plots with in Figures 3 and 5, but it falls where it does because it has a different body form with much reduced hindlimbs (hence such overall scores are not always the best numbers to use in predicting body size for an individual taxon). The sea otter (*En.lu.*) appears to be more terrestrial than other otters (cross-hatched) on PC-II in Figures 4 and 6, but it is also more hindlimb dominated on PC-III, which affects its position on PC-II (detailed interpretation of variance on any one axis must control for variance expressed on other axes). A statistical summary inevitably compromises some details in the interest of overall patterns.

Elomeryx, *Rodhocetus*, and *Dorudon* studied here are very different from each other. *Elomeryx*, serving as a model for the ancestral artiodactyl, is thought to have been semiaquatic and to have lived more or less like a hippopotamus (Kron and Manning 1998: p. 381; and it may be related to the origin of hippos). *Rodhocetus* is a seal-sized archaeocete more closely resembling a desman in terms of trunk and limb proportions, and comparison with the full diversity of semiaquatic mammals here weakens the idea that *Rodhocetus* was otterlike (Gingerich et al. 2001a: p. 2241). Desmans are foot-powered swimmers using their tails as rudders and to damp oscillations caused by alternate strokes of the hind feet (Palmeirim and Hoffmann 1983), which deserves consideration for *Rodhocetus* as well. *Dorudon* is a larger archaeocete similar in proportions to fully aquatic cetaceans and hence somewhat different from living semiaquatic mammals.

Thewissen and Fish (1997: p. 489) argued that ''lutrines are the best extant functional models for early cetacean locomotion'' and ''the locomotor morphology of *Ambulocetus* may have been most similar to that of *Lutra* or (less likely) *Pteronura*''—without really considering alternatives. Lutrines (otters) are not good models unless early cetaceans look like

them, and neither of the two early cetacean taxa studied here resembles a lutrine in trunk and limb proportions. At the same time, the heuristic functional and physiological model of Fish (1996, 2000, 2001) illustrating the sequence of stages to be expected in any transition from a terrestrial to a high performance marine mammal is as valuable as ever. Fish's model was developed in part from study of lutrines, and they illustrate important stages of the model, but other semiaquatic mammals were studied and are included too.

Discovery that *Rodhocetus* has trunk and limb proportions like a desman implies, in the context of Fish's model, that it was at an alternate-pelvic-paddling stage of drag-based propulsion, swimming mostly at the surface, insulated and buoyed by non-wettable fur, and incapable of deep diving. *Dorudon*, with its trunk and limb proportions more like modern cetaceans, was probably at or approaching a more advanced and efficient caudal oscillation stage of lift-based propulsion, swimming submerged more than at the surface, possibly insulated by blubber rather than fur, and capable of deeper diving (Fish 1996, 2000, 2001).

Flower (1883a,b) hypothesized that whales evolved from mammals with long tails used in swimming. This is inconsistent with his idea that whales evolved from ungulates, which generally have short tails. It now appears from the fossil record that archaeocetes evolved from *Elomeryx*-like ungulates with short tails. The first stage of aquatic locomotor specialization, well developed in *Rodhocetus* and other early protocetids, involved development of drag-based alternate pelvic paddling like that seen in desmans, muskrats, and many other semiaquatic mammals. Concomitant development of a long tail would be important to damp lateral oscillation and control yaw associated with pelvic paddling (Fish 1982; Palmeirim and Hoffmann 1983). Then, in a second stage of locomotor specialization illustrated by *Dorudon*, later archaeocetes developed the lift-based propulsion of modern whales using dorsoventral undulation and eventually oscillation of these long tails. *Basilosaurus*, with its exaggerated serpentine elongation of the posterior thorax, lumbus, and tail, is very differently proportioned from con-

temporary *Dorudon* and later whales, and it may represent a group of archaeocetes divergently specialized for lateral rather than dorsoventral undulation.

It is undoubtedly simplistic to treat the evolution of Eocene archaeocetes and the whole land-to-sea transition of early whales in two major steps, but this reflects the state of our knowledge. Only two of the 30 genera of archaeocetes in Table 1 are known from sufficiently complete skeletal remains to enable them to be integrated into a multivariate study of skeletal proportions of living semiaquatic mammals. It is not easy to find and collect associated trunk and fore- and hindlimb elements necessary for such comparisons, and perhaps the sizes of the gaps that separate artiodactyls from *Rodhocetus*, and *Rodhocetus* from *Dorudon*, will serve as encouragement to search for and study better specimens of additional genera.

Pakicetus, classified as a protocetid or in a separate family Pakicetidae, and *Ambulocetus*, classified in its own family (Ambulocetidae), are the best-known archaeocetes intermediate in age between the ancestral artiodactyl and *Rodhocetus* analyzed here. *Pakicetus* is about 48 Ma in age (Gingerich 2003: Fig. 6), slightly older than *Rodhocetus* studied here at 47.5 Ma. *Ambulocetus* is bracketed between the two stratigraphically and is thus intermediate in age.

Pakicetus has long been known to have cranial characteristics of both land and aquatic mammals (Gingerich and Russell 1981; Gingerich et al. 1983; Thewissen and Hussain 1993), but little has been known of the postcranial skeleton. Isolated postcranial elements attributed to *Pakicetus attocki* have recently been described and compared with *Dorudon* and other basilosaurids (but not with protocetids), leading to the the conclusion that "pakicetids were terrestrial mammals, no more amphibious than a tapir" (Thewissen et al. 2001: p. 278). The 14 pakicetid postcranial elements illustrated in detail (Thewissen et al. 2001: Fig. 1) are all plausibly archaeocete because they differ little from comparable elements of *Rodhocetus* and other early protocetids (Gingerich et al. 1994, 2001a). Most interesting are two partial innominates that to-

gether show the ilium to have been shorter than the ischium (Thewissen et al. 2001: p. 277 and Fig. 1n). Length of the ilium is the most important determinant of the PC-II score reflecting aquatic adaptation (Tables 6, 7, Figs. 3–6), and an innominate with a short ilium implies that *Pakicetus* was much more aquatic than a tapir. *Rodhocetus* has an ilium about 0.9 times as long as the ischium. Tapirs, at the terrestrial end of the terrestrial-aquatic spectrum of semiaquatic mammals, have an ilium that is 1.38 to 1.46 times as long as the ischium.

Ambulocetus natans is known from a good partial skeleton described by Thewissen et al. (1994, 1996) and Madar et al. (2002). It cannot be included properly in the analysis here because it lacks the scapula, humerus, manual phalanx III-1, tibia, and pedal phalanges III-1 and III-2. Lengths of the missing elements can be estimated by scaling them up from *Rodhocetus balochistanensis*, using the average proportion of measured elements present in both species (1.45) as a multiplier, and in this way *A. natans* can be added—very tentatively—to the graphs of Figures 5 and 6. In Figure 6, *A. natans* (*Am.na.?*) plots close to *Desmana moschata* (*De.mo.*) and *R. balochistanensis* (*Ro.ba.*). It is plausible that *Ambulocetus* belongs on the hindlimb-dominated side of the locomotor spectrum as shown, but this remains to be tested by finding the missing skeletal elements. *Ambulocetus* is cited as showing that spinal undulation evolved in whales before development of a tail fluke (e.g., Thewissen et al. 1994: p. 212; Fish 2001: p. 637), but that claim was made when only one lumbar and one caudal vertebra were known (Thewissen et al. 1994: p. 210).

Some archaeocetes known from good but incomplete skeletons, like *Artiocetus* (Gingerich et al. 2001a), *Qaisracetus* (Gingerich et al. 2001b), and *Remingtonocetus* (Gingerich et al. unpublished data) for example, appear basically similar in skeletal proportions to *Rodhocetus* analyzed here. Others, like *Zygorhiza* (Kellogg 1936), appear basically similar to *Dorudon*. Two genera that appear particularly interesting in being different are *Georgiacetus* (Hulbert et al. 1998) and *Eocetus* (Uhen 1999). *Georgiacetus* is intermediate in age and could well be intermediate in morphology between *Rodhocetus* and *Dorudon*, providing insight into the transition from hindlimb-dominated swimming to lumbus-dominated swimming. *Eocetus* appears to have been divergently specialized in its own way, developing osteosclerotic ribs and vertebrae, and a greatly reduced innominate. *Basilosaurus*, mentioned above, is another divergently specialized genus showing that archaeocetes were much more diverse than Figure 7 indicates. Nevertheless, as better skeletons of these and other genera are discovered, the principal axes of Figure 7, enabling separation of aquatic adaptation and locomotor specialization based on skeletal proportions in semiaquatic mammals, will continue to provide a framework for their interpretation.

The fossils we know well support the idea of a unidirectional trend of increasing aquatic adaptation through *Rodhocetus* and *Dorudon* stages of whale evolution (PC-II component of the heavy dashed lines in Fig. 7). However, superimposed on this is simultaneous change in locomotor adaptation involving a distinct reversal of specialization, from hindlimb-dominated swimming in *Rodhocetus*, to lumbus- and tail-dominated swimming in *Dorudon* (PC-III component of the heavy dashed lines in Fig. 7). Thus the overall pattern is neither simple nor direct. It is common to see microevolutionary histories zig-zag back and forth through time as they reverse themselves to track changing opportunities, and the land-to-sea transition of early whales provides a macroevolutionary example.

Before quantifying the rates of evolution documented here, I expected that rates associated with changes of an adaptive zone would be more or less the same as background rates calculated on comparable timescales in other settings (Gingerich 2001). This expectation was based on the repeated observation that change documented in the fossil record is almost always diluted by the passage of so much time that such very long time series are effectively stationary, and long-term rates scale as the simple inverse of interval length. Rates calculated here, univariate and multivariate, seem instead to confirm Simpson's (1944) expectation that unusually high rates are associated with changes of adaptive zone.

Acknowledgments

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Appendix

Measurements of trunk and limb lengths for 50 species of living semiaquatic mammals and three species known from fossils, including archaeocetes *Rodhocetus balochistanensis* and *Dorudon atrox*, documenting the transition from land to sea in early whale evolution. Male (M) and female (F) specimens were averaged (geometric mean) when both (B) were available. Abbreviations: MCZ, Museum of Comparative Zoology, Harvard University, Cambridge; L-, Natural History Museum, London; UMMP, University of Michigan Museum of Paleontology, Ann Arbor; UMMZ, University of Michigan Museum of Zoology, Ann Arbor.

Genus and species	Sex	Reference	Measurements (cm)													
			Thorax	Lum-bus	Scap-ula	Hu-merus	Radius	Mcarp-iii	Man-piii1	Man-piii2	Ilium	Femur	Tibia	Mtars-iii	Ped-piii1	Ped-piii2
Ornithorhynchus anatinus	—	UMMZ uncat.	8.45	1.30	3.07	2.74	2.74	0.89	0.66	0.47	2.05	3.10	4.70	0.90	0.78	0.80
Chironectes minimus	F	UMMZ 134024	7.69	4.72	3.15	4.25	4.77	1.37	0.94	0.53	3.42	5.02	5.76	2.58	1.00	0.55
Potamogale velox	—	L-.75.1829	9.20	3.60	2.92	3.67	2.40	1.05	0.60	0.27	2.19	3.57	3.88	1.20	0.48	0.30
Limnogale mergulus	F	L-1897.9.1.161	3.30	1.57	1.41	1.64	1.46	0.63	0.46	0.29	1.46	1.66	2.58	1.29	0.54	0.34
Neomys fodiens	F	L-1919.7.7.1855	2.50	1.85	0.92	0.94	0.98	0.40	0.26	0.15	0.83	1.12	1.79	0.71	0.29	0.18
Desmana moschata	M	L-1919.7.7.2313	4.15	2.50	3.45	2.24	2.42	0.62	0.50	0.25	2.68	2.40	4.40	1.63	1.10	0.52
Galemys pyrenaicus	F	L-1962.4.5.19	2.56	1.20	1.96	1.28	1.54	0.38	0.32	0.18	1.35	1.40	2.63	0.96	0.60	0.22
Ursus americanus	M	UMMZ 103537	42.50	25.30	19.80	30.00	25.50	7.30	3.53	2.78	15.50	34.80	26.00	7.22	3.76	2.52
Ursus maritimus	F	UMMZ 102200	57.00	20.00	21.50	32.00	26.50	8.92	3.80	3.20	19.00	40.00	28.50	9.30	4.60	3.20
Mustela vison	M	UMMZ 168144	13.50	8.00	3.12	4.78	3.26	1.67	0.98	0.74	2.84	5.10	5.22	2.22	1.03	0.85
Lutra lutra	M	L-1955.2.19.1	23.70	13.00	6.80	9.30	6.20	3.10	1.85	1.25	5.50	9.50	9.90	4.50	2.13	1.45
Lontra canadensis	M	UMMZ 78545	22.00	11.50	6.32	7.33	4.92	2.55	1.60	1.18	5.28	7.41	8.30	3.72	1.90	1.25
Lontra felina	F	L-1880.7.28.15	18.80	8.20	4.62	6.20	4.55	2.15	1.69	0.93	4.08	6.37	6.70	3.10	1.80	1.25
Pteronura brasiliensis	M	L-1939.3.4.1	37.50	16.00	9.00	10.90	8.00	4.10	2.80	1.90	8.20	11.20	12.70	5.60	3.30	2.20
Aonyx cinerea	F	L-1962.3.28.1	14.50	8.20	4.82	6.40	5.19	2.15	1.43	0.80	4.20	6.64	7.61	3.10	1.65	0.92
Enhydra lutris	M	UMMZ 156623	35.50	18.00	11.00	11.70	8.50	2.36	1.30	1.05	9.50	11.50	13.50	6.83	3.88	2.68
Callorhinus ursinus	B	L-1893.1.28.2/1960.5.2.2	49.86	20.12	17.94	15.68	16.33	6.09	6.18	5.20	7.29	10.84	19.30	6.48	6.20	5.45
Arctocephalus australis	B	L-1950.11.14.3/1950.11.14.4	49.52	16.21	15.93	14.12	15.14	4.84	4.24	3.80	7.28	9.34	17.86	5.87	5.72	5.10
Zalophus californianus	B	MCZ 6159/L-1965.10.29.1	65.97	23.74	20.35	17.16	17.39	6.20	5.65	3.98	8.07	10.39	21.16	6.71	6.36	5.18
Eumetopias jubatus	M	MCZ 2920 (Allen, 1880)	105.00	34.00	38.00	30.00	26.00	8.50	7.00	6.00	14.00	17.00	32.00	9.50	9.00	7.50
Odobenus rosmarus	M	UMMZ 100780 (')	117.00	38.00	42.00	33.00	24.00	6.80	5.70	3.90	18.50	24.50	35.00	13.00	10.20	7.80
Monachus monachus	M	L-1894.7.27.1	78.50	36.00	15.50	14.40	13.20	4.50	5.40	4.10	8.20	11.20	22.50	4.50	6.40	5.00
Lobodon carcinophagus	—	L-1908.2.20.57	49.00	23.00	11.80	9.50	10.50	3.80	5.00	2.60	5.50	8.50	19.00	5.50	6.80	4.60
Hydrurga leptonyx	B	L-1966.10.17.3/1959.12.17.4	82.55	49.44	20.71	17.89	18.55	6.80	7.55	6.00	8.25	15.25	28.20	7.25	8.75	7.54
Leptonychotes weddelli	M	MCZ 51874 (Piérard, 1971)	82.00	38.50	16.40	15.20	16.60	5.20	5.40	4.10	8.58	12.20	28.70	6.80	7.40	5.40
Ommatophoca rossi	B	L-1965.12.20.1/1965.8.2.1	68.95	31.46	16.49	11.40	12.45	4.56	5.60	4.50	6.45	9.85	24.75	5.89	7.91	6.24
Mirounga leonina	—	L-1912.9.28.1	126.00	53.00	28.00	30.00	26.00	7.00	9.00	7.00	11.50	18.50	37.50	9.80	9.80	7.50
Erignathus barbatus	—	L-1887.9.28.1	68.50	42.00	18.30	14.80	13.50	4.50	3.30	2.60	10.00	13.50	27.50	8.20	6.60	5.70
Cystophora cristata	—	L-1956.11.7.1	81.50	23.50	17.50	15.00	13.60	4.50	4.00	2.80	8.20	12.50	27.50	6.30	6.90	5.00

Appendix. Continued.

Genus and species	Sex	Reference	Measurements (cm)													
			Thorax	Lum-bus	Scap-ula	Hu-merus	Radius	Mcarp-iii	Man-piii1	Man-piii2	Ilium	Femur	Tibia	Mtars-iii	Ped-piii1	Ped-piii2
Halichoerus grypus	B	L-1962.3.6.1/1938.3.12.1	59.25	25.50	16.64	13.22	13.24	3.86	3.09	2.46	6.53	10.74	23.65	6.33	5.94	4.67
Phoca groenlandica	B	L-1951.11.28.2/1938.12.10.1	50.74	23.99	13.25	11.99	11.99	3.49	2.89	1.90	5.60	9.22	24.39	6.28	5.53	4.30
Phoca vitulina	M	UMMZ 102482	46.00	22.00	14.50	11.50	10.30	3.50	3.65	2.10	6.00	9.30	20.00	5.05	4.85	2.05
Tapirus terrestris	M	UMMZ 160907	65.00	19.50	28.80	24.50	20.50	11.25	3.77	2.16	23.50	31.00	23.50	11.35	3.40	2.06
Tapirus bairdii	—	UMMZ 81051	50.00	18.00	25.50	25.00	21.50	10.90	3.44	1.92	20.50	32.50	24.50	11.30	3.85	2.10
Tapirus indicus	—	L-85.808	67.00	20.50	28.00	25.50	22.50	12.00	3.40	2.10	26.50	32.70	26.00	11.80	3.70	1.70
Hippopotamus amphibius	—	UMMZ 84041	110.00	36.00	37.00	35.00	24.50	12.50	5.70	3.30	37.00	46.50	28.00	11.50	5.50	3.30
Hexaprotodon liberiensis	B	L-1952.4.1.4/1914.6.21.1	54.05	21.85	23.00	21.65	15.25	8.65	4.30	2.50	20.15	27.75	19.00	7.83	4.45	2.42
Castor fiber	M	L-1897.10.14.1	17.50	9.50	7.40	8.00	8.10	2.40	1.26	0.84	9.00	10.20	12.40	4.46	2.70	1.42
Castor canadensis	—	UMMP 2543	19.00	9.00	6.78	7.17	7.40	2.05	1.10	0.71	8.00	9.30	11.50	4.35	2.88	1.35
Neusticomys monticolus	—	UMMZ 155604	2.50	2.05	1.16	1.23	1.27	0.40	0.24	0.14	1.14	1.51	2.26	1.01	0.37	0.20
Ichthyomys hydrobates	—	UMMZ 156375	1.93	2.23	1.35	1.61	1.39	0.47	0.35	0.20	1.57	1.98	2.73	1.30	0.56	0.25
Ichthyomys tweedii	—	UMMZ 126300	3.65	2.60	1.57	1.70	1.39	0.49	0.33	0.17	1.84	2.16	2.68	1.26	0.55	0.23
Rheomys raptor	—	UMMZ 111985	2.64	2.05	1.29	1.42	1.23	0.40	0.34	0.18	1.38	1.81	2.28	1.06	0.38	0.22
Rheomys underwoodi	—	UMMZ 115389	2.68	2.10	1.53	1.50	1.53	0.44	0.34	0.19	1.60	1.90	2.80	1.61	0.61	0.30
Arvicola terrestris	M	L-1991.157	4.76	4.19	2.34	2.74	2.54	0.64	0.42	0.25	2.60	3.27	3.68	1.27	0.57	0.32
Ondatra zibethicus	—	UMMP 1695	7.00	5.70	3.50	3.56	3.75	1.02	0.65	0.34	4.15	4.44	6.06	2.61	1.33	0.57
Hydrochoeris hydrochoeris	—	UMMZ 168362	32.00	28.00	14.50	15.50	11.80	5.75	2.37	1.28	14.00	19.00	18.50	6.10	3.16	1.78
Myocastor coypus	—	UMMZ 95735	14.50	9.00	6.00	6.60	6.95	1.91	1.06	0.75	7.07	8.22	9.70	4.04	2.20	1.25
Sylvilagus aquaticus	F	UMMZ 76781	11.30	12.80	6.04	6.82	6.50	2.47	0.89	0.57	4.55	8.76	10.16	3.86	1.41	0.92
Sylvilagus palustris	F	UMMZ 59048	10.30	10.50	4.95	5.59	5.35	2.08	0.71	0.44	3.78	7.48	8.50	3.20	1.10	0.65
Elomeryx armatus	—	Scott (1894, 1940)	42.50	23.10	22.50	22.50	19.20	9.60	3.60	2.20	17.60	28.90	24.70	11.30	3.10	2.20
Rodho. balochistanensis	—	Gingerich et al. (2001a)	47.80	27.60	20.00	21.00	11.00	7.60	6.30	3.30	17.50	19.00	21.00	12.20	9.00	7.00
Dorudon atrox	—	Uhen (1996, 2003)	96.80	148.20	26.50	22.70	16.45	6.90	8.43	5.00	3.00	13.00	8.00	3.00	3.50	0.40