On mammalian sperm dimensions

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Summary. Data on linear sperm dimensions in mammals are presented. There is information on a total of 284 species, representing 6·2% of all species; 17·2% of all genera and 49·2% of all families have some representation, with quantitative information missing only from the orders Dermoptera, Pholidota, Sirenia and Tubulidentata. In general, sperm size is inverse to body mass (except for the Chiroptera), so that the smallest known spermatozoa are amongst those of artiodactyls and the largest are amongst those of marsupials. Most variations are due to differences in the lengths of midpiece and principal piece, with head lengths relatively uniform throughout the mammals.

Introduction

There is increasing interest in comparative studies of gametes both from the phylogenetic viewpoint (Afzelius, 1983) and also in the analysis of the evolution of sexual reproduction and anisogamy (Bell, 1982; Parker, 1982). This work emerged as part of a review of the relationship between sperm size and body mass in mammals (Cummins, 1983), in which lack of space precluded the inclusion of raw data. In publishing this catalogue of sperm dimensions we wish to rectify this defect, and to provide a reference point for, and stimulus to, further quantitative work while obviating the need for laborious compilation of raw data. Some aspects of the material presented previously (Cummins, 1983) have been re-analysed in the light of new data.

Materials and Methods

This catalogue of sperm dimensions has been built up from cited measurements, from personal observations and from communication with other scientists. Where personal measurements are included, they were made on air-dried nigrosin–eosin live/dead sperm smears (Campbell, Dott & Glover, 1956) using a calibrated projection microscope. Some data are based on measurements made from Retzius' series of monographs (1906–1910). Although Retzius did not, unfortunately, give accurate scales for his illustrations, it appears that in most cases all the spermatozoa on a single plate were drawn to the same scale. On many plates, therefore, it was possible to find a reference spermatozoon of known dimensions, and to estimate the total sperm lengths of other species from this. While these measurements can be no more than rough approximations, they have nevertheless proved useful for comparative work. In Table 1, such measurements are only included when more accurate data for an otherwise unknown group are not available. When it subsequently proved possible to double-check such estimates, they were usually accurate to within 5 µm.

The weights and classification of eutherian and monotreme mammals are from Walker (1975); marsupial taxonomy is from Kirsch (1977). Species identification is listed as given by the original source. Where necessary, more modern or more widespread synonyms are shown in parentheses. These were obtained from Ellerman (1940, 1941), Hall & Kelson (1959), Meester & Setzer (1974), Walker (1975) and Haltenorth & Diller (1980).

Results and Discussion

Table 1 gives a complete listing of all the data that we have collected on sperm dimensions. Excepting only those figures keyed by an asterisk, which are probably inaccurate (see Key to Table 1), all figures have been accepted uncritically, and readers are referred to the original source for details of methodology, ranges and standard errors of mean measurements. Figures given in parentheses are estimates from Retzius' monographs (1906, 1909a, b, c, 1910: see 'Material and Methods'). Table 2 summarizes the extent of our data coverage. We now have collected quantitative data on 6.2% of all mammalian species, covering 17.2% of genera and 49.2% of families. We have been unable to find quantitative information for 4 minor orders; the Pholidota (pangolins), the Dermoptera (flying lemurs), the Sirenia (dugongs, manatees) and the Tubulidentata (aardvark). Of the larger orders, as might be expected, the extent of coverage is most comprehensive for those most likely to be used in the laboratory or as domestic species; the Artiodactyla, Perissodactyla, Lagomorpha and Primates. While we have data on more species of rodents (122) than for any other order, because of the enormous diversity and number of species, this represents only 5.3% of the total—slightly less than the average cover for all mammalian species. Marsupials and monotremes are reasonably well represented, reflecting much recent interest in the use of sperm morphology for phylogenetic analysis (see, for example Harding, Woolley, Shorey & Carrick, 1982). Rather surprisingly, there are no sperm dimensions published for American marsupials, even though details of morphology have been known since the beginning of the century. This account deals only with linear measurements, and not with other quantitative aspects such as mass, volume or density; for a detailed bibliography before 1964, together with an exhaustive discussion of sperm mensuration in terms of volume, mass and projected surface area, together with a discussion of the possible sources of error in measurement, see van Duijn (1975) and van Duijn & van Voorst (1971). For a review of the genetics of sperm dimensions in mammals see Beatty (1970, 1972, 1975), Williams, Beatty & Burgoyne (1970) and Burgoyne (1975). For correlating sperm dimensions with those of eggs, see Hartman (1929).

Table 1. Linear dimensions (μm) of mammalian spermatozoa

Species (common name)	Source	Head		Midpiece		Principal piece length	Total
		Length	Width	Length	Width		
EUTHERIAN MAMMALS							
Order Artiodactyla							
Family Bovidae							
<i>Aepyceros melampus</i> (impala)	1	6.52	4.13	7.63	—	32.00	46.15
<i>Antilope cervicapra</i> (blackbuck)	2	—	—	—	—	—	48.4*
<i>Alcelaphus buselaphus</i> (hartebeeste)	1	4.82	3.06	7.23	—	36.32	48.37
<i>Bos taurus</i> (ox)	1	6.77	4.27	9.83	—	36.93	53.53
	3	—	—	—	—	—	50–80
	4	—	—	—	—	—	25.01*
	61	8.79	4.62	—	—	—	—
		—9.71	—4.72				
	70	10.2	5.4				
<i>Bubalus bubalis</i> (water buffalo)	3	9.45	5.08	14.19	—	33.35	56.99
<i>Capra hircus</i> (goat)	6	8.27	4.25	11.38	0.74	39.75	59.39
<i>Capra ibex</i> (ibex)	7	8.5	4.5	20.0	—	40–45	68–73.5

Table 1, cont.

Species (common name)	Source	Head		Midpiece		Principal piece length	Total
		Length	Width	Length	Width		
<i>Cephalophus abyssinicus</i> (= <i>Sylvicapra grimmia abyssinicus</i>) (common duiker)	5	—	—	—	—	—	[68]
<i>Connochaetes albojubatus</i> (= <i>C. gnou</i>) (black wildebeeste)	5	—	—	—	—	—	[55]
<i>Connochaetes taurinus</i> (blue wildebeeste)	1	5.01	3.56	7.86	—	33.90	46.77
<i>Damaliscus dorcas</i> (blesbok)	1	4.53	2.97	7.7	—	38.59	50.82
<i>Gazella granti</i> (Grant's gazelle)	5	—	—	—	—	—	[48]
<i>Hemitragus jemlahicus</i> (Himalayan tahr)	2	—	—	—	—	—	46.3*
<i>Litocranius walleri</i> (gerenuk)	4	—	—	—	—	—	[35]
<i>Ovis aries</i> (sheep)	1	5.78	—	10.27	—	—	45.69
<i>Ovis musimon</i> (mouflon)	6	8.2	—	14.0	—	40.45	62.2–67.2
<i>Ovis vignei</i> (urial)	2	—	—	—	—	—	31.1*
<i>Tragelaphus strepsiceros</i> (greater kudu)	8	—	—	—	—	—	26.6*
<i>Tragelaphus strepsiceros</i> (greater kudu)	8	—	—	—	—	—	24.3*
<i>Tragelaphus strepsiceros</i> (greater kudu)	1	6.41	3.75	8.99	—	30.14	45.54
Family Camelidae							
<i>Camelus dromedarius</i> (one-humped camel)	9	5.62	2.92	7.34	—	34.23	47.21
Family Cervidae							
<i>Alces alces</i> (moose)	10	8.8	5.2	—	—	54.7	60–65
<i>Axis axis</i> (chital)	2	—	—	—	—	—	40.6*
<i>Cervus elaphus</i> (red deer)	5	—	—	—	—	—	[57]
<i>Odocoileus virginianus</i> (white-tailed deer)	11	10.0	6.0	7.0	—	35.0	52
<i>Rangifer tarandus</i> (reindeer)	8	—	—	—	—	—	18.9*
<i>Rangifer tarandus</i> (reindeer)	12	7.636	5.027	10.38	—	38.48	56.496
Family Giraffidae							
<i>Giraffa camelopardalis</i> (giraffe)	13	5.77	3.77	—	—	—	47.77
Family Hippopotamidae							
<i>Choeropsis liberiensis</i> (pygmy hippopotamus)	2	—	—	—	—	—	31.5*
<i>Hippopotamus amphibius</i> (hippopotamus)	1	3.77	2.65	7.85	—	21.87	33.49
Family Suidae							
<i>Sus scrofa</i> (pig)	14	8.5	4.2	10.0	—	36.1	54.6
	1	6.55	3.47	11.88	—	21.53	39.96
	71	8.4	4.3	—	—	—	—
		9.4	5.5	—	—	—	—
Family Tayassuidae							
<i>Tayassu tajacu</i> (collared peccary)	2	—	—	—	—	—	[40]
		—	—	—	—	—	23.4*

Table 1, cont.

Species (common name)	Source	Head		Midpiece		Principal piece length	Total
		Length	Width	Length	Width		
Order Carnivora							
Family Canidae							
<i>Canis familiaris</i> (dog)	15	5.6	—	—	—	—	55.3
	4	—	—	—	—	—	14.54*
	67	5.9	3.9	10.6	—	45.8	62.7
<i>Vulpes fulva</i> (American red fox)	16	8.0	5.0	—	—	—	60.0
Family Felidae							
<i>Felis catus</i> (cat)	6	4.76	2.56	8.34	0.77	46.25	59.35
	4	—	—	—	—	—	12.92*
<i>Panthera tigris</i> (= <i>Leo tigris</i>) (tiger)	17	5.80	3.59	—	—	—	43.63
Family Mustelidae							
<i>Meles meles</i> (badger)	5	—	—	—	—	—	[80]
<i>Mustela vison</i> (mink)	11	7.0	6.1	6.0	—	30.0	43.0
Family Ursidae							
<i>Thalarctos maritimus</i> (polar bear)	8	—	—	—	—	—	36.3*
<i>Ursus arctos</i> (brown bear)	2	—	—	—	—	—	30.7*
Family Viverridae							
<i>Cryptoprocta ferox</i> (fossa)	5	—	—	—	—	—	[69]
<i>Eupleres goudotii</i> (small-toothed mongoose)	5	—	—	—	—	—	[45]
<i>Paradoxurus jerdoni</i> (Indian palm civet)	2	—	—	—	—	—	42.4*
Family Procyonidae							
<i>Ailuropoda melanoleuca</i> (giant panda)	18	5.0	4.2	7.2	0.8	39.0	51.2
Order Cetacea							
Family Balaenopteridae							
<i>Megaptera nodosa</i> (= <i>M. novaeangliae</i>) (humpback whale)	19	—	—	—	—	—	52.5–61.4
Family Delphinidae							
<i>Globicephala melas</i> (= <i>G. melaena</i>) (pilot whale)	5	—	—	—	—	—	[67]
<i>Phocoena communis</i> (= <i>P. phocoena</i>) (common porpoise)	20	—	—	—	—	—	73.8
<i>Tursiops truncatus</i> (Atlantic bottle-nosed dolphin)	21	4.5	2.0	4.0	—	56.0	64.5
Family Physeteridae							
<i>Physeter catodon</i> (sperm whale)	22	—	—	—	—	—	45.5

Table 1, cont.

Species (common name)	Source	Head		Midpiece		Principal piece length	Total
		Length	Width	Length	Width		
Order Chiroptera							
Family Molossidae							
<i>Mormopterus planiceps</i> (= <i>Tadarida planiceps</i>) (little mastiff-bat)	43	6.0	—	8.0	—	52.0	66.0
Family Phyllostomidae							
<i>Anoura cultrata</i> (long-nosed bat)	23	5.01	4.35	7.78	0.76	50.69	62.58
<i>Artibeus jamaicensis</i> (Jamaican fruit-eating bat)	23	3.80	3.41	8.28	0.62	—	—
<i>Artibeus lituratus</i> (big fruit-eating bat)	23	4.50	3.45	9.38	0.96	71.87	85.75
<i>Carollia castanea</i> (Allen's short-tailed bat)	23	4.79	3.95	9.9	0.88	49.5	64.19
<i>Glossophaga soricina</i> (Pallas' long-tongued bat)	23	4.0	3.52	7.9	0.96	—	—
<i>Phyllostomus discolor</i> (pale spear-nosed bat)	23	5.36	4.18	9.06	0.61	—	—
<i>Sturnira lilium</i> (yellow-shouldered bat)	23	4.24	3.81	9.21	0.82	—	—
<i>Sturnira ludovici</i> (Anthony's bat)	23	4.56	3.75	10.46	0.99	—	—
Family Pteropodidae							
<i>Pteropus alecto</i> (black flying-fox)	73	6.4	4.8	19.2	—	40.0	65.6
<i>Pteropus conspiculatus</i> (spectacled flying-fox)	73	7.2	4.8	21.8	—	74.0	103.0
<i>Pteropus poliocephalus</i> (grey flying-fox)	73	5.1	4.3	23.0	—	32.0	60.1
<i>Pteropus scapulatus</i> (little red flying-fox)	6 73	7.89 8.0	5.06 4.8	22.5 22.4	1.0 —	70.8 76.0	101.24 106.4
<i>Pteropus edwardsi</i> (flying fox)	24	9.0	—	—	—	—	108.9
<i>Syconycteris australis</i> (blossom bat)	73	6.2	4.8	22.4	—	52.0	80.6
Family Vespertilionidae							
<i>Antrozous pallidus</i> (pallid bat)	23	3.59	2.54	11.95	2.15	43.0	58.54
<i>Chalinolobus morio</i> (chocolate wattled bat)	43	4.0	—	6.5	—	32–37	42.5–47.5
<i>Chalinolobus goudii</i> (Gould's wattled bat)	43	4.0	—	8–10	—	45.0	57–59
<i>Eptesicus fuscus</i> (big brown bat)	25 23	5.0 6.59	2.0 2.71	9.0 9.89	0.8 0.92	58.0 —	72.0 —
<i>Lasionycteris noctivagans</i> (silver haired bat)	23	5.5	2.0	8.9	0.8	59.0	73.4
<i>Lasiurus borealis</i> (red bat)	25	5.3	2.0	11.2	0.8	50.6	67.1
<i>Miniopterus schreibersii</i> (common bent-wing bat)	43	9.0	—	6.0	—	50.0	65.0
<i>Myotis keeni</i> (keen myotis)	25 23	4.4 4.9	1.9 2.16	15.4 18.55	1.1 1.41	42.2 65.0	62.0 88.45
<i>Myotis lucifugus</i> (little brown myotis)	25	4.3	1.8	12.7	1.1	34.0	51.0
<i>Myotis sodalis</i> (Indiana myotis)	25 23	4.9 5.60	1.8 2.15	13.7 —	1.0 —	46.9 —	65.5 —

Table 1, cont.

Species (common name)	Source	Head		Midpiece		Principal piece length	Total
		Length	Width	Length	Width		
<i>Myotis austroriparius</i> (Mississippi myotis)	25	4.6	1.9	12.8	1.2	31.6	49.0
<i>Myotis evotis</i> (long-eared myotis)	23	4.85	2.08	15.05	1.33	—	—
<i>Myotis grisescens</i> (grey myotis)	23	5.81	2.53	18.6	1.83	48.14	72.55
<i>Myotis nigricans</i> (black myotis)	23	4.67	2.22	17.62	1.34	—	—
<i>Myotis velifer</i> (cave myotis)	23	3.95	1.84	16.55	1.70	—	—
<i>Myotis volans</i> (long-legged myotis)	23	5.30	2.02	15.89	1.12	—	—
<i>Nycticeius humeralis</i> (evening bat)	25	5.2	2.1	10.8	2.1	61.3	77.3
<i>Nyctophilus geoffroyi</i> (lesser long-eared bat)	43	4.0	—	6.0	—	43.0	53.0
<i>Nyctophilus timoriensis</i> (greater long-eared bat)	43	4.0	—	8.0	—	40.0	52.0
<i>Pipistrellus subflavus</i> (eastern pipistrelle)	25	5.4	2.0	—	0.8	—	72.0
<i>Pipistrellus tasmaniensis</i> (great pipistrelle)	23	5.81	2.50	10.35	0.82	70.0	86.16
<i>Pipistrellus tasmaniensis</i> (great pipistrelle)	43	6.0	—	8.0	—	52.0	66.0
<i>Plecotus rafinesquii</i> (eastern big-eared bat)	23	4.74	2.25	9.59	1.41	45.0	59.33
<i>Plecotus townsendii</i> (western big-eared bat)	25	3.8	1.9	8.9	1.1	37.3	50.0
<i>Plecotus townsendii</i> (western big-eared bat)	23	5.56	2.79	12.60	1.52	—	—
Order Edentata							
Family Bradypodidae							
<i>Bradypus cuculliger</i> (= <i>B. tridactylus</i>) (three-toed sloth)	5	—	—	—	—	—	[31]
Family Dasypodidae							
<i>Dasypus novemcinctus</i> (nine-banded armadillo)	11	9.0	6.0	14.5	—	45.0	68.0
Order Hyracoidea							
Family Procaviidae							
<i>Procavia capensis</i> (Cape rock hyrax)	62	11.5	5.5	12.0	1.5	—	—
Order Insectivora							
Family Erinaceidae							
<i>Erinaceus</i> sp. (hedgehog)	5	—	—	—	—	—	[88]
Family Soricidae							
<i>Suncus murinus</i> (Asiatic musk shrew)	26	21.5	17.5	~20	—	~80	121.5
Family Talpidae							
<i>Talpa europaea</i> (mole)	5	—	—	—	—	—	[116]
Family Tenrecidae							
<i>Tenrec eucaudatus</i> (tenrec)	5	—	—	—	—	—	[64]

Table 1, cont.

Species (common name)	Source	Head		Midpiece		Principal piece length	Total
		Length	Width	Length	Width		
<i>Setifer setosus</i> (large Madagascar 'hedgehog')	5	—	—	—	—	—	[64]
Order Lagomorpha							
Family Leporidae							
<i>Bunolagus monticularis</i> (bushman hare)	30	6.6	3.6	—	—	—	—
<i>Lepus capensis</i> (brown hare)	30	6.5	4.0	—	—	—	—
<i>Lepus saxatilis</i> (scrub hare)	30	6.7	3.7	—	—	—	—
<i>Lepus</i> sp. (hare)	2	—	—	—	—	—	29.57*
<i>Pronolagus crassicaudatus</i> (= <i>P. randensis</i>)	30	6.7	3.8	—	—	—	—
(Natal red hare)	30	6.4	3.6	—	—	—	—
<i>Pronolagus rupestris</i> (Smith's red hare)	30	6.8	3.7	—	—	—	—
<i>Oryctolagus cuniculus</i> (rabbit)	27	8.4	—	8.0	—	38.0	55.0
	6	8.51	4.98	8.81	0.73	40.7	58.02
	51	8.06– 8.42	4.59– 4.86	—	—	—	—
Order Perissodactyla							
Family Equidae							
<i>Equus asinus</i> (donkey)	28	6.9	3.96	9.9	—	47.3	64.1
	69	5.74	3.17	—	—	—	—
<i>Equus caballus</i> (horse)	28	7.0	3.9	9.8	—	43.8	60.6
	69	6.41	3.00	—	—	—	—
<i>Equus asinus</i> × <i>E. caballus</i> (hinny)	69	5.63	2.88	—	—	—	—
<i>Equus grevyi</i> (Grevy's zebra)	5	—	—	—	—	—	[50]
Order Pinnipedia							
Family Phocidae							
<i>Mirounga leonina</i> (southern elephant seal)	6	4.8	3.02	5.3	0.5	63.6	73.7
<i>Halichoerus grypus</i> (grey seal)	5	—	—	—	—	—	[53]
Order Primates							
Family Callitrichidae							
<i>Callithrix jacchus</i> (short-tusked marmoset)	64	5.0	3.0	—	—	—	50
Family Cebidae							
<i>Lagothrix</i> sp. (woolly monkey)	2	—	—	—	—	—	21.0*
<i>Saimiri sciureus</i> (squirrel monkey)	32	5.11	3.51	9.03	—	55.34	69.24
Family Cercopithecidae							
<i>Cercocebus</i> sp. (mangabey)	5	—	—	—	—	—	[70]
<i>Cercopithecus aethiops</i> (vervet monkey)	32	5.22	3.36	10.18	—	51.87	66.73

Table 1, cont.

Species (common name)	Source	Head		Midpiece		Principal piece length	Total
		Length	Width	Length	Width		
<i>Cercopithecus fuliginosus</i> (= <i>Colobus badius temminckii</i>) (red colobus)	5	—	—	—	—	—	[84]
<i>Cercopithecus pygerythrus</i> (vervet monkey)	5	—	—	—	—	—	[88]
<i>Chaeropithecus cynocephalus</i> (= <i>Papio cynocephalus</i>) (yellow baboon)	32	4.62	3.98	10.30	—	61.06	76.19
<i>Erythrocebus patas</i> (patas monkey)	2	—	—	—	—	—	38.7*
<i>Macaca mulatta</i> (rhesus monkey)	32	5.31	3.16	11.06	—	57.73	73.83
<i>Macaca arctoides</i> (stump-tailed macaque)	32	5.57	3.38	10.53	—	61.46	77.61
<i>Macaca fascicularis</i> (= <i>Macaca irus</i>) (crab-eating macaque)	32 5	5.53 —	3.45 —	11.06 —	— —	57.04 —	73.63 [91]
<i>Macaca sinicus</i> (= <i>M. sinica</i>) (toque macaque)	5	—	—	—	—	—	[68–70]
<i>Mandrillus sphinx</i> (= <i>Papio sphinx</i>) (mandrill)	5	—	—	—	—	—	[67.5]
Family Daubentoniidae							
<i>Chiromys madagascariensis</i> (= <i>Daubentonia madagascariensis</i>) (aye-aye)	24	6.3	—	—	—	—	55.8
Family Hominidae							
<i>Homo sapiens</i> (man)	32 66 72 74	6.11 — 4.5 4.5	3.45 — 3.2 3.0	4.70 4.18 4.0 5.7	— 0.88 1.0 —	47.13 56.16 46–50 50.0	58.39 — 54.5 58.5 59.5 61.5
Family Lemuridae							
<i>Lemur anjonanensis</i> (= <i>L. mongoz</i>) (mongoose lemur)	24	5.8	—	—	—	—	55.3
<i>Lemur catta</i> (ring-tailed lemur)	5	—	—	—	—	—	[52]
<i>Microcebus myoxinus</i> (= <i>M. murinus</i>) (lesser mouse-lemur)	24	8.1	—	—	—	—	93.6
<i>Lepilemur</i> sp. (lemur)	5	—	—	—	—	—	[52]
Family Pongidae							
<i>Gorilla gorilla</i> (gorilla)	32	4.78	7.11	11.74	—	40.97	61.17
<i>Pan troglodytes</i> (= <i>Chimpanzee troglodytes</i>) (chimpanzee)	32	4.68	2.90	6.34	—	46.42	57.36
<i>Pongo pygmaeus</i> (orangutan)	32	5.31	3.80	9.01	—	52.27	66.58

Table 1, cont.

Species (common name)	Source	Head		Midpiece		Principal piece length	Total
		Length	Width	Length	Width		
Order Proboscidea							
Family Elephantidae							
<i>Elephas maximus</i>	29	8.3	—	—	—	42.0	50.3
(Indian elephant)	33	—	—	—	—	—	58.5
	65	7.5	3.0	10.6	—	40.0	58–60
<i>Loxodonta africana</i>							
(African elephant)	34	—	—	—	—	—	61.6
Order Rodentia							
Family Aplodontidae							
<i>Aplodontia rufa</i>							
(mountain beaver)	35	—	—	—	—	—	~100
Family Capromyidae							
<i>Myocastor coypus</i>							
(coypu)	36	3.28	4.11	4.46	—	—	34.64
Family Caviidae							
<i>Cavia porcellus</i>	6	10.87	9.45	11.1	1.0	92.1	114.07
(guinea-pig)	36	9.19	10.05	8.75	—	—	99.15
<i>Galea musteloides</i>							
(cuis)	36	5.45	5.68	5.89	—	32.91	44.25
Family Chinchillidae							
<i>Chinchilla laniger</i>							
(chinchilla)	36	3.76	5.50	4.73	—	38.34	46.83
<i>Lagidium boxi</i>							
(mountain viscacha)	36	3.50	5.08	5.23	—	—	41.02
Family Cricetidae							
<i>Clethrionomys glareolus</i>							
(bank vole)	37	6.85	—	19.5	—	59.0	86.7
<i>Cricetulus griseus</i>	38	13.2	—	105.6	—	132.2	~250
(Chinese hamster)	6	12.66	—	103.06	—	142.61	258.32
<i>Mesocricetus auratus</i>							
(golden (Syrian) hamster)	5	15.2	2.51	50.5	1.0	126.3	186.8
<i>Microtus agrestis</i>							
(field vole)	39	6.9	—	27.4	—	70.0	103.5
<i>Microtus hirtus</i>							
(= <i>M. agrestis hirtus</i>)							
(field vole)	37	7.6	—	30.0	—	80.0	117.0
<i>Microtus ochrogaster</i>							
(prairie vole)	25	7.9	4.9	21.8	0.8	64.7	94.4
<i>Neofiber alleni</i>							
(eastern wood rat)	25	4.9	3.0	21.0	0.8	49.0	74.9
<i>Neotoma floridana</i>							
(Florida water-rat)	25	8.1	1.5	—	0.9	—	138.1
<i>Ondatra zibethicus</i>							
(musk rat)	37	5.39	—	16.25	—	46.06	67.7
<i>Oryzomys palustris</i>							
(rice rat)	25	5.5	2.1	—	0.9	—	79.4
<i>Peromyscus banderanus</i>							
(Michoacan deer mouse)	40	5.6	2.7	18.0	—	56.0	79.6
<i>Peromyscus boylei</i>							
(brush mouse)	40	5.5	2.4	17.0	—	55.1	77.6
<i>Peromyscus californicus</i>	40	5.3	3.4	15.2	—	51.5	72.0
(California mouse)	25	5.5	3.2	—	0.8	—	78.5
<i>Peromyscus crinitus</i>							
(canyon mouse)	40	5.2	2.8	19.0	—	54.6	78.8

Table 1, cont.

Species (common name)	Source	Head		Midpiece		Principal piece length	Total
		Length	Width	Length	Width		
<i>Peromyscus difficilis</i> (rock mouse)	40	5.4	2.6	17.0	—	56.4	78.8
<i>Peromyscus eremicus</i> (cactus mouse)	40	5.9	3.5	16.6	—	53.5	76.0
<i>Peromyscus flavidus</i> (yellow deer mouse)	40	5.9	3.0	16.8	—	61.3	84.0
<i>Peromyscus floridanus</i> (Florida mouse)	40	5.2	2.9	15.9	—	53.9	75.0
	25	5.4	2.7	—	0.8	—	79.9
<i>Peromyscus fuvus</i> (blackish deer mouse)	40	5.3	2.5	17.1	—	54.8	77.2
<i>Peromyscus gossypinus</i> (cotton mouse)	40	5.4	2.9	17.3	—	63.4	86.1
<i>Peromyscus grandis</i> (big deer mouse)	40	5.3	2.5	17.8	—	56.7	79.8
<i>Peromyscus guatemalensis</i> (Guatemalan deer mouse)	40	5.5	2.6	18.2	—	58.5	82.2
<i>Peromyscus lepturus</i> (slender-tailed deer mouse)	40	6.0	4.1	19.3	—	51.8	77.1
<i>Peromyscus leucopus</i> (white-footed mouse)	40	5.3	3.4	16.8	—	52.7	74.8
	25	5.5	3.0	—	0.9	—	79.8
<i>Peromyscus lophurus</i> (crested-tailed mouse)	40	6.2	4.9	19.7	—	50.8	76.7
<i>Peromyscus maniculatus</i> (deer mouse)	40	5.2	3.0	16.7	—	53.1	75.0
<i>Peromyscus megalops</i> (brown deer mouse)	40	5.1	2.6	19.5	—	69.3	93.9
<i>Peromyscus melanotis</i> (black-eared mouse)	40	5.3	3.1	16.7	—	51.3	73.3
<i>Peromyscus mexicanus</i> (Mexican deer mouse)	40	5.5	2.6	17.4	—	49.3	72.2
<i>Peromyscus nudipes</i> (naked-footed deer mouse)	40	5.5	2.6	17.1	—	56.6	79.2
<i>Peromyscus nuttalli</i> (golden mouse)	25	4.2	3.0	—	2.0	—	67.7
<i>Peromyscus pirrensis</i> (Mt. Pirri deer mouse)	40	5.8	2.9	16.9	—	62.2	84.9
<i>Peromyscus polionotus</i> (old field mouse)	40	5.4	3.0	15.2	—	54.2	74.8
	25	5.4	3.1	—	1.4	—	77.4
<i>Peromyscus thomasi</i> (Thomas' deer mouse)	40	5.7	3.1	21.4	—	62.9	90.0
<i>Peromyscus truei</i> (piñon mouse)	40	5.4	2.6	16.2	—	56.8	78.4
<i>Peromyscus zarhynchus</i> (Chiapan deer mouse)	40	5.2	2.5	17.7	—	52.5	75.4
<i>Sigmodon hispidus</i> (hispid cotton rat)	25	6.1	3.2	17.2	0.9	63.1	87.0
	27	7.0	—	19.0	—	60.0	87.0
<i>Synaptomys cooperi</i> (southern bog lemming)	25	7.7	4.0	—	0.7	—	99.7
<i>Tylomys gymnurus</i> (naked-tailed climbing rat)	41	4.86	1.6	37.52	—	—	~87
<i>Tylomys panamensis</i> (Panama climbing rat)	41	5.47	1.6	33.89	—	—	~87
<i>Ototylomys phyllotis</i> (big-eared climbing rat)	41	5.47	2.4	94.20	—	—	~137
Family Ctenomyidae							
<i>Ctenomys fulvus</i>	68	7.30	3.55	6.68	—	—	—
<i>Ctenomys magellanicus</i>	68	9.13	5.22	8.12	—	—	—

Table 1, cont.

Species (common name)	Source	Head		Midpiece		Principal piece length	Total
		Length	Width	Length	Width		
<i>Ctenomys maulinus</i>	42	10.5	5.5	—	—	—	85.7
	68	10.35	5.64	8.38	—	—	—
<i>Ctenomys opimus</i>	68	7.70	3.90	6.13	—	—	—
<i>Ctenomys robustus</i>	68	7.10	3.79	6.14	—	—	—
<i>Ctenomys talarum</i> (all known as tuco-tucos)	36	4.27	6.83	6.18	—	38.83	49.28
Family Dasypodidae							
<i>Myoprocta pratti</i> (acouchi)	36	3.05	5.17	5.62	—	31.52	40.19
Family Dipodidae							
<i>Dipus aegyptius</i> (= <i>Jaculus orientalis</i>) (desert jerboa)	5	—	—	—	—	—	[52]
Family Echimyidae							
<i>Proechimys guairae</i> (casiragua)	36	3.21	5.08	4.21	—	29.97	37.38
Family Geomyidae							
<i>Geomys pinetus</i> (south-eastern pocket gopher)	25	4.5	2.2	—	1.1	—	110.5
Family Gliridae (= Myoxidae)							
<i>Glis glis</i> (= <i>Myoxus glis</i>) (fat dormouse)	5	—	—	—	—	—	[87]
Family Heteromyidae							
<i>Liomys adspersus</i> (Panama spiny pocket mouse)	63	3.17	2.80	—	—	—	—
<i>Liomys irroratus</i> (Mexican pocket mouse)	63	5.35	1.97	—	—	—	—
<i>Liomys pictus</i> (painted spiny pocket mouse)	63	5.22	1.81	—	—	—	—
<i>Liomys salvini</i> (Salvin's spiny pocket mouse)	63	3.22	2.97	—	—	—	—
<i>Liomys spectabilis</i> (spectacled spiny pocket mouse)	63	5.56	2.07	—	—	—	—
Family Muridae							
<i>Aethomys chrysophilus</i> (red veldt rat)	43	7.0	—	15.0	—	35.0	57.0
<i>Apodemus flavicollis</i> (yellow-necked mouse)	37	8.8	—	23.0	—	93.0	125.4
<i>Apodemus sylvaticus</i> (wood mouse)	37	9.8	—	24.0	—	100.0	133.8
<i>Berylmys bowersii</i> (= <i>Rattus bowersii</i>) (Bower's rat)	43	12.5	—	55.0	—	117.0	172.0
<i>Chiropodomys gliroides</i> (brush-tailed rabbit rat)	43	10.0	—	22.0	—	80.0	102.0
<i>Conilurus penicillatus</i> (pencil-tailed tree mouse)	44	7.0	—	20–22	—	96.0	123–125
<i>Haplolomys longicaudatus</i> (marmoset mouse)	43	12.5	—	37.0	—	72.0	109.0
<i>Hydromys chrysogaster</i> (water rat)	44	7.0	—	20.0	—	88.0	115.0

Table 1, cont.

Species (common name)	Source	Head		Midpiece		Principal piece length	Total
		Length	Width	Length	Width		
<i>Leggadina forresti</i> (Forrest's mouse)	45	7.0	—	26.0	—	95.0	128.0
<i>Leopoldamys sabanus</i> (= <i>Rattus sabanus</i>) (long-tailed giant rat)	43	11.5	—	67.0	—	103.0	170.0
<i>Leopoldamys edwardsi</i> (= <i>Rattus edwardsi</i>) (Edward's long-tailed giant rat)	43	12.5	—	—	—	—	172.0
<i>Leporillus conditor</i> (greater stick-nest rat)	44	9.0	—	23.0	—	78.0	110.0
<i>Mastomys coucha</i> (= <i>Rattus/Praomys coucha</i>) (multimammate mouse)	43	10.0	—	42.0	—	105.0	157.0
<i>Mastomys natalensis</i> (= <i>Rattus/Praomys natalensis</i>) (multimammate mouse)	43	11.0	—	50.0	—	107.0	168.0
<i>Maxomys inas</i> (= <i>Rattus inas</i>) (Malayan mountain spiny rat)	43	13.0	—	13.0	—	107.0	139.0
<i>Maxomys surifer</i> (= <i>Rattus surifer</i>) (spiny rat)	43	10.0	—	35.0	—	70.0	115.0
<i>Maxomys whiteheadi</i> (= <i>Rattus whiteheadi</i>) (Whitehead's spiny rat)	43	12.0	—	22.0	—	97.0	119.0
<i>Melomys littoralis</i> (= <i>M. burtoni</i>) (grassland melomys)	44	8.0	—	22.0	—	80.0	110.0
<i>Micromys minutus</i> (harvest mouse)	37	5.7	—	13.0	—	45.0	63.7
<i>Mus musculus</i> (house mouse)	37	8.3	—	21.0	—	95.0	124.3
	25	7.9	3.2	18.4	1.3	96.6	122.9
	31	—	3.60	21.6	—	—	—
	54	8.6	—	—	—	—	—
			3.64	—	—	—	—
	55	—	—	—	—	—	—
			3.43	21.8	—	—	—
	56	—	—	—	—	—	—
			3.71	22.6	—	—	—
	57	7.24	—	—	—	—	—
			3.681	21.610	—	—	—
60	—	—	—	—	—	—	—
			3.730	22.746	—	—	—
			3.26	23.34	—	—	—
			3.30	24.56	—	—	—
			3.639	21.76	—	—	—
60	—	—	—	—	—	—	—
			3.770	22.58	—	—	—
60	—	—	—	~22.7	—	—	—
			—	—	—	—	—
<i>Niviventer bukit</i> (= <i>Rattus n. bukiti</i>) (white-bellied rat)	43	11.0	—	44.0	—	97.0	152.0
<i>Niviventer cremoriventer</i> (= <i>Rattus n. cremoriventer</i>) (dark-tailed tree rat)	43	9.0	—	35.0	—	75.0	110.0
<i>Niviventer rapit</i> (= <i>Rattus n. rapit</i>) (tufted-tailed lesser spiny rat)	43	11.0	—	46.0	—	80.0	125.0
<i>Notomys alexis</i> (spinfex hopping mouse)	44	5.8	—	23.27	—	70.0	100–105
<i>Notomys cervinus</i> (fawn hopping mouse)	44	9.0	—	26.0	—	80.0	115.0

Table 1, cont.

Species (common name)	Source	Head		Midpiece		Principal piece length	Total
		Length	Width	Length	Width		
<i>Notomys fuscus</i> (dusky hopping mouse)	45	7.0	—	22.0	—	77.0	106.0
<i>Notomys mitchelli</i> (Mitchell's hopping mouse)	45	9.0	—	24.0	—	65.0	98.0
<i>Pseudomys apodemoides</i> (silky mouse)	44	8.0	—	22.0	—	90.0	120.0
<i>Pseudomys australis</i> (plains rat)	44	9.0	—	23.0	—	88–93	120–125
<i>Pseudomys delicatulus</i> (delicate mouse)	45	4.0	—	19.0	—	65.0	88.0
<i>Pseudomys fumeus</i> (smokey mouse)	45	8.0	—	20.0	—	100.0	128.0
<i>Pseudomys gracilicaudatus</i> (eastern chestnut mouse)	45	10.0	—	21.0	—	98.0	129.0
<i>Pseudomys hermannsburgensis</i> (sandy inland mouse)	44	8–10	—	23.0	—	85.0	116–118
<i>Pseudomys higginsii</i> (long-tailed mouse)	44	8.0	—	20–22	—	70–85	98–115
<i>Pseudomys nanus</i> (western chestnut mouse)	44	9.0	—	22.0	—	96.0	127.0
<i>Pseudomys novaehollandiae</i> (New Holland mouse)	45	6.0	—	22.0	—	78.0	106.0
<i>Pseudomys shortridgei</i> (heath rat)	45	5.0	—	22.0	—	69.0	96.0
<i>Rattus colletti</i> (dusky rat)	44	12.0	—	51.0	—	95.0	158.0
<i>Rattus exulans</i> (Polynesian rat)	43	12.0	—	67.0	—	97.0	164.0
<i>Rattus fuscipes</i> (bush rat)	44	12.0	—	48.0	—	102.0	162.0
<i>Rattus leucopus</i> (Cape York rat)	44	12.0	—	—	—	—	147.0
<i>Rattus lutreolus</i> (swamp rat)	44	13–15	—	54.0	—	95.0	162–164
<i>Rattus norvegicus</i> (white) (common white rat)	37	11.7	—	67.0	—	110.0	188.7
<i>Rattus norvegicus</i> (brown) (common brown rat)	37	12.1	—	67.0	—	110.0	190.1
<i>Rattus rattus diardii</i>	37	10.8	—	65.0	—	90.0	166.0
	25	11.0	1.8	—	1.0	—	158.0
(ship (black) rat)	43	10.0	—	—	—	—	162.0
<i>Rattus sordidus</i> (canefield rat)	44	12.0	—	49–50	—	95.0	152–157
<i>Rattus tiomanicus</i> (Malaysian wood rat)	43	10.0	—	67.0	—	95.0	162.0
<i>Rhabdomys pumilio</i> (striped mouse)	43	10.0	—	22.0	—	85.0	117.0
<i>Saccostomus campestris</i> (pouched mouse)	43	6.0	—	22.0	—	115.0	143.0
<i>Sundamys muelleri</i> (= <i>Rattus muelleri</i>) (Mueller's rat)	43	12.5	—	47.0	—	100.0	150.0
<i>Tatera leucogaster</i> (bushveldt gerbil)	43	5.0	—	30.0	—	110.0	145.0
<i>Uromys caudimaculatus</i> (white-tailed rat)	44	8–10	—	20.0	—	72–82	100–112
<i>Zyzomys argurus</i> (common rock rat)	44	7.0	—	22.0	—	108.0	137.0

Table 1, cont.

Species (common name)	Source	Head		Midpiece		Principal piece length	Total
		Length	Width	Length	Width		
Family Octodontidae							
<i>Octodon degus</i>	46	7.7	5.9	—	—	—	48.7
(degu)	36	5.12	6.83	5.90	—	—	50.93
<i>Octodontomys gliroides</i>							
(choz choz)	36	5.29	6.50	5.32	—	34.57	45.18
Family Sciuridae							
<i>Sciurus niger</i>							
(eastern fox squirrel)	25	12.1	11.6	—	1.9	—	122.2
<i>Sciurus carolinensis</i>							
(grey squirrel)	2	—	—	—	—	—	27.47*
<i>Tamiasciurus hudsonicus</i>							
(red (spruce) squirrel)	25	14.0	12.2	—	2.1	—	131.0
Family Zapodontidae							
<i>Zapus hudsonius</i>							
(meadow jumping mouse)	25	5.1	2.9	—	0.8	—	76.1
MARSUPIAL MAMMALS							
Family Dasyuridae							
<i>Dasyercus cristicauda</i>							
(mulgara)	50	9.5	1.9	—	—	—	—
<i>Dasykulata rosamondae</i>							
(= <i>Antechinus rosamondae</i>)							
(little red antechinus)	50	9.8	1.6	—	—	—	—
<i>Dasyuroides byrnei</i>							
(kowari)	47	12.7	2.5	40.7	3.1	201.4	254.8
<i>Dasyurus viverrinus</i>							
(eastern quoll)	50	11.0	1.9	—	—	—	—
<i>Sarcophilus harrisii</i>							
(Tasmanian devil)	47	11.1	2.2	34.4	2.6	173.4	218.5
Family Macropodidae							
<i>Macropus eugenii</i>							
(tammar wallaby)	6	6.67	3.38	10.53	1.20	89.2	106.4
<i>Macropus kangaru</i>							
(= <i>M. giganteus</i>)							
(eastern grey kangaroo)	47	7.3	2.2	10.7	1.5	100.9	118.9
<i>Macropus parma</i>							
(parma wallaby)	50	5.3	1.4	—	—	—	—
<i>Macropus robustus</i>	8	—	—	—	—	—	49.4*
(common wallaroo)	50	4.5	1.5	—	—	—	—
<i>Macropus rufus</i>							
(= <i>Megaleia rufa</i>)	47	5.1	3.4	7.9	1.4	116.0	123.9
(red kangaroo)	50	3.3	2.0	—	—	—	—
<i>Macropus agilis</i>	47	7.1	1.8	11.0	1.4	—	—
(agile wallaby)	6	7.5	3.2	8.5	1.28	97.0	113.2
<i>Macropus parryi</i>							
(whiptail wallaby)	6	9.27	4.89	10.05	1.43	100.21	119.53
<i>Potorous tridactylus</i>	53	9.0	2.3	15.7	1.7	—	—
(long-nosed potoroo)	50	9.1	1.9	—	—	—	—
<i>Thylogale stigmatica</i>							
(red-necked pademelon)	47	7.2	2.2	10.9	1.5	92.2	110.3
<i>Wallabia bicolor</i>							
(swamp wallaby)	6	7.8	3.05	8.9	1.45	92.2	109.5
Family Peramelidae							
<i>Isodon macrourus</i>	47	6.0	3.3	10.7	1.8	154.4	171.1
(northern brown (brindled) bandicoot)	50	4.5	2.2	—	—	—	—

Table 1, cont.

Species (common name)	Source	Head		Midpiece		Principal piece length	Total
		Length	Width	Length	Width		
<i>Isodon obesulus</i> (southern brown (brindled) bandicoot)	43	5	—	—	—	—	167.0
<i>Perameles nasuta</i> (long-nosed bandicoot)	47	5.7	3.0	14.0	2.0	180.1	199.8
Family Petauridae							
<i>Petaurus breviceps</i> (sugar glider)	47 50	5.9 5.5	2.5 1.9	8.3 —	1.4 —	93.0 —	107.1 —
<i>Petaurus norfolcensis</i> (squirrel glider)	50	4.1	2.3	—	—	—	—
<i>Pseudocheirus cupreus</i> (ringtail possum)	47	5.4	2.6	6.2	1.5	78.5	90.1
<i>Pseudocheirus peregrinus</i> (common ringtail possum)	47 50 51	5.9 5.0 —	3.8 3.2 —	6.9 — 7.7	2.1 — 2.9	100.0 — —	112.8 — —
Family Phalangeridae							
<i>Trichosurus vulpecula</i> (common brushtail possum)	6 50 51	5.53 3.7 —	2.58 1.6 —	10.26 — 12.4	1.06 — 1.2	78.35 — —	94.17 — —
Family Phascolarctidae							
<i>Phascolarctos cinereus</i> (koala)	6 60	11.75 6.0	3.32 —	9.60 7.3	0.96 0.9	63.5 66.7	83.01 79.0
Family Tarsipedidae							
<i>Tarsipes rostratus</i> (= <i>T. spenserae</i>) (honey possum, noolbenger)	6 50	13.97 10.6	3.57 3.0	86.0 —	3.25 —	256.3 —	356.27 —
Family Thylacinidae							
<i>Thylacinus cynocephalus</i> (thylacine)	50	10.6	2.3	—	—	—	—
Family Vombatidae							
<i>Lasiorhinus latifrons</i> (southern hairy-nosed wombat)	43	7.5	—	22.0	—	50.0	79.5
<i>Vombatus ursinus</i> (= <i>Phascolomis mitchelli</i>) (common wombat)	47	5.7	1.7	18.0	0.9	69.0	93.6
MONOTREME MAMMALS							
Family Ornithorhynchidae							
<i>Ornithorhynchus anatinus</i> (duckbilled platypus)	49	43.0	—	5.0	—	54.0	112.0
Family Tachyglossidae							
<i>Tachyglossus aculeatus</i> (echidna, spiny anteater)	48 49	50.4 —	— —	6.0 —	— —	64.8 —	121.0 123.0

Those lengths given in square brackets are approximations from Retzius' illustrations (see 'Materials and Methods'). Measurements marked with an asterisk are of suspect accuracy, as they come from three papers (Knepp, 1936a,b, 1938) in which sperm measurements were made from testicular histology specimens, and several of these are obviously inaccurate (e.g. *Felis catus* and *Canis familiaris*). With this exception, all results have been presented uncritically, and the reader is referred to the original source for details of methodology. The midpiece length values for marsupials are measured from the point of insertion on the mid-ventral surface of the head, except for *Phascolarctos* (6, 60).

continued overleaf

References: (1) Morgenthal, 1967; (2) Knepp, 1936b; (3) Venkataswami & Vedanayagam, 1962; (4) Knepp, 1936a; (5) J. M. Cummins, personal measurements from Retzius' monographs; (6) J. M. Cummins, personal observations; (7) Couturier, 1956; (8) Knepp, 1938; (9) Abdel-Raouf & El Naggar, 1965; (10) Andersen, 1973; (11) Altman & Dittmer, 1962; (12) Dott & Utsi, 1971; (13) Velhankar *et al.*, 1973; (14) Niwa & Mizuho, 1954; (15) Perez-Garcia, 1957, cited by Asdell, 1964; (16) Beck, 1936; (17) Velhankar *et al.*, 1967; (18) Platz *et al.*, 1983; (19) Chittleborough, 1955; (20) Ballowitz, 1907; (21) Fleming *et al.*, 1981; (22) Yamane, cited by Asdell, 1964; (23) Forman, 1968; (24) Ballowitz, 1909; (25) Hirth, 1960; (26) Green & Dryden, 1976; (27) Bishop & Walton, 1960; (28) Nishikawa *et al.*, cited by Asdell, 1964; (29) Asdell, 1964; (30) J. D. Skinner, personal communication; (31) Beatty & Sharma, 1960; (32) Martin *et al.*, 1975; (33) Jainudeen *et al.*, 1971; (34) Johnson & Buss, 1967; (35) Pfeiffer, 1956; (36) R. C. Jones, personal communication; (37) Friend, 1936; (38) Bishop & Walton, 1960: breakdown of component lengths by Cummins from illustration in Austin, 1965; (39) Austin, 1957; (40) Linzey & Layne, 1974; (41) Helm & Bowers, 1973; total length of *Ototylomys* spermatozoon estimated from diagram; (42) Feito & Gallardo, 1976 (head length does not include the post-acrosomal process); (43) W. G. Breed, personal communication; (44) Breed & Sarafis, 1979; (45) Breed, 1980; (46) Berrios *et al.*, 1978; (47) Hughes, 1965; (48) Griffiths, 1968; (49) F. N. Carrick, personal communication; (50) Harding *et al.*, 1982: measurements of nucleus alone, from electron microscopy and light microscopy; (51) Harding *et al.*, 1979: measurements by electron microscopy; (52) Beatty & Napier, 1960; (53) Hughes, 1964; (54) Braden, 1959, range for several strains, measurements in μm calculated using given magnification; (55) Sharma, 1960; (56) Pant & Beatty, 1973; (57) Illison, 1969, measurements in μm calculated using given magnification; (58) Burgoyne, 1975; (59) Woolley & Beatty, 1967; (60) Hughes, 1977; (61) van Duijn & van Voorst, 1971; (62) J. M. Cummins, personal measurements from illustration in Bedford & Millar (1978) using given magnification; (63) Genoways, 1973; (64) Davis, 1982; (65) Landowski & Gill, 1964; (66) Serres *et al.*, 1983 (midpiece length includes neck, and principal piece length includes "terminal filament"); (67) P. F. Woodall, personal observations; (68) Feito & Gallardo, 1982 (head lengths do not include the post-acrosomal process, where present in *C. maulinus* and *C. magellanicus*); (69) Chandley *et al.*, 1974; (70) van Duijn, 1960b; (71) van Duijn, 1960a; (72) van Duijn, 1958 (principal piece includes estimate of 6–10 μm for the "tail end"; (73) S. K. Robson & G. W. Rouse, personal communication; (74) Flechon & Hafez, 1976.

While the available information is probably sufficient for us to ask some interesting questions about the evolution of sperm form and function, Table 2 also highlights our ignorance. In particular, it would appear worthwhile to concentrate research on some of the more 'primitive' groups, such as the Insectivora and, amongst the Rodentia, the Sciuridae. The Chiroptera, in particular would be valuable to examine, as flight seems to have imposed certain restrictions on reproductive strategy, and they are anomalous in terms of the inverse sperm length–body mass relationship which seems to hold true for most mammals (Cummins, 1983; and see below).

We have not attempted here to correlate sperm dimensions with any other aspect of gamete morphology such as head shape. For qualitative analyses of mammalian sperm morphology in a wide range of groups the reader is referred to reviews by Bishop & Austin (1957), Austin & Bishop (1958), Fawcett (1958, 1970, 1976), Bishop & Walton (1960), Fawcett, Anderson & Phillips (1971), Bedford (1974), Jones (1974), Gould, Martin & Hafez (1975), Matano, Matsubayashi, Omichi & Ohtomo (1976), Gould (1980) and Elder & Hsu (1981). In addition, Retzius (1906, 1909a, b, c, 1910) published some beautiful illustrations of spermatozoa of some rare species among, for example, the Carnivora and the Insectivora, which are of undoubted qualitative value in surveying sperm morphology. For a comparative review of sperm morphology in invertebrates as well as vertebrates, see Baccetti & Afzelius (1976).

Table 3 summarizes the range of sperm dimensions and body masses within mammalian Orders. It is clear that the greatest diversity in sperm length is seen in the Chiroptera, Insectivora, Rodentia and Marsupialia. In Table 4, some of the information previously summarized (Cummins, 1983) has been expanded and reanalysed. Correlations and regressions are based on analysis of $\log_{10}$ total sperm lengths and $\log_{10}$ body masses within mammalian orders, using the median figure for each genus when more than one species is represented. Only data of reasonably good accuracy were used here. In this analysis, in which both variables are subject to error, it is inappropriate to use linear regression. Instead, a Model II regression must be used, calculating the slope of the major or principal axis. When the correlation is reasonably high, the slope of the linear regression b and

Table 2. Extent of data coverage for mammals

Order	Families		Genera		Species	
Artiodactyla	7/9*	77.8%	25/82*	30.2%	29/197*	15.2%
Carnivora	6/7	85.7%	12/101	11.9%	12/243	4.9%
Cetacea	3/8	37.5%	5/38	13.2%	5/90	5.6%
Chiroptera	4/18	22.2%	21/180	11.7%	38/804	4.7%
Dermoptera	0/1	—	0/1	—	0/2	—
Edentata	2/3	66.7%	2/14	14.3%	2/30	6.2%
Hyracoidea	1/1	100%	1/3	33.3%	1/9	11.1%
Insectivora	4/8	50.0%	5/63	7.9%	5/~300	1.7%
Lagomorpha	1/2	50%	4/10	40.0%	8/64	12.5%
Perissodactyla	1/3	33.3%	3/6	50.0%	3/17	17.6%
Pholidota	0/1	—	0/1	—	0/7	—
Pinnipedia	1/3	33.3%	2/20	10.0%	2/31	6.5%
Primates	7/11	63.6%	17/60	28.3%	25/193	13.0%
Proboscidea	1/1	100%	2/2	100%	2/2	100%
Rodentia	16/35	45.7%	55/351	15.7%	122/~2300	5.3%
Sirenia	0/2	—	0/2	—	0/4	—
Tubulidentata	0/1	—	0/1	—	0/1	—
All Eutheria	54/114	47.4%	154/935	16.5%	254/4294	5.9%
All Marsupialia	9/16	56.3%	19/80	23.8%	28/250	10.8%
All Monotremata	2/2	100%	2/3	66.7%	2/6	33.3%
All Mammalia	65/132	49.2%	175/1018	17.2%	284/4550	6.2%

*Number of groups for which some quantitative data exist/total number of groups. Numbers of families, genera and species in each order are from Walker (1975), except for the Marsupialia, where the classification is based on Kirsch (1977).

the slope of the principal axis α will be close in value. It is clear that, in general, total sperm length is inversely correlated with body mass, with the exception of the Chiroptera. As pointed out previously (Cummins, 1983), a negative relationship of this sort is highly unusual. It is not, strictly speaking, negative allometry, in which an organ increases less rapidly than body size when the two are plotted against each other (Clutton-Brock & Harvey, 1983). The only other commonly cited examples of aspects of body function bearing negative relationships to body mass are metabolic rate and the surface area:volume ratio (Gould, 1966; Clutton-Brock & Harvey, 1983; Schmidt-Neilsen, 1984). Body mass is also inversely related to population density (Damuth, 1981; Peters & Raelson, 1984), to species density (Peters, 1983) and to the rate of generation turnover in time—presumably in itself related to the capacity of species to adapt to changing or rapidly fluctuating environments (Lindstedt & Calder, 1981; Fowler & MacMahon, 1982; Calder, 1983). Thus, some small predators may increase their ability to exploit short-term fluctuations in prey numbers by reducing their generation time (reviewed by Clutton-Brock & Harvey, 1983).

A negative relationship between sperm size and body mass is by no means universal among mammals, with the Chiroptera being the outstanding exception (Table 4). It is also worth pointing out that, while no 'large' (> 10 kg) mammals have very large spermatozoa, quite clearly the reverse is not necessarily true. A good example of this can be seen in the murid rodent *Micromys minutus*, which has a mean body weight of only 6 g and also very small spermatozoa of 63.7 μ m (Austin, 1957).

In analysing the sperm length–body mass relationship, it would appear that the question to ask is, why do some small mammals, but no large mammals, have very large spermatozoa? In a previous analysis (Cummins, 1983) it was suggested that mammals have the choice between producing

Table 3. Summary of sperm lengths and body masses in mammals

Order	Total no. of genera	Genera with data	Species with data	Sperm length (μm)		Log ₁₀ body mass (g)	
				Mean*	Range	Mean	Range.
Artiodactyla	82	21	29	50.8	33.5–80.0	5.24	4.36–6.57
Carnivora	101	9	9	55.2	43.3–80.0	4.18	3.20–5.40
Cetacea	38	5	5	60.7	45.5–73.8	6.20	4.80–7.63
Chiroptera	180	17	28	68.1	42.5–108.9	1.30	0.78–2.51
Edentata	14	1	1	68.0	—	3.78	—
Insectivora	63	5	5	87.3	64.0–121.5	2.36	1.65–3.00
Lagomorpha	10	1	1	56.5	—	3.59	—
Perissodactyla	6	1	3	62.3	50.0–64.1	5.78	4.30–6.00
Pinnipedia	20	2	2	63.4	53.0–73.7	5.84	5.31–6.36
Primates	60	16	22	65.7	50.0–93.6	3.84	1.80–5.32
Proboscidea	2	2	2	58.4	50.3–61.6	6.75	6.70–6.80
Rodentia	351	54	113	95.9	34.6–250.0	2.17	0.78–3.90
All Eutheria	935	134	220	73.4	33.5–250.0	3.22	0.78–7.63
All Marsupialia	80	14	21	133.6	79.5–356.3	3.36	1.02–4.57
All Monotremata	3	2	2	117.0	112.0–122.0	3.48	3.23–3.72
All Mammalia	1018	150	243	78.1	33.5–356.3	3.23	0.78–7.63

*Means are of median values within genera when more than one species per genus is represented. Data from Knepp (1936a, b; 1938) were not included, as their accuracy is suspect. The numbers differ from those in Table 2 because only species for which total sperm length is known have been included.

Table 4. Correlations of sperm length and body mass in mammals

	N	<i>r</i>		<i>b</i>	α	95% limits
Artiodactyla	21	–0.162	$P > 0.1$	–0.023	–0.023	+0.037, –0.083
Carnivora	9	–0.154	$P > 0.1$	–0.021	–0.021	+0.067, –0.109
Cetacea	5	–0.894	$P < 0.05$	–0.056	–0.056	–0.046, –0.142
Chiroptera	19	+0.640	$P < 0.02$	+0.125	+0.128	+0.207, +0.051
Primates	16	–0.059	$P > 0.1$	–0.005	–0.005	+0.037, –0.047
Rodentia	54	–0.301	$P < 0.05$	–0.101	–0.113	–0.019, –0.209
All mammals	149	–0.445	$P < 0.001$	–0.054	–0.555	–0.037, –0.073
Eutherian mammals	133	–0.490	$P < 0.001$	–0.053	–0.053	–0.037, –0.069
Eutheria without Chiroptera	118	–0.593	$P < 0.001$	–0.069	–0.070	–0.053, –0.087
Marsupial mammals	14	–0.710	$P < 0.01$	–0.138	–0.140	–0.067, –0.214

N = Number of genera for which accurate data on total sperm lengths exist; *r* = correlation coefficient; *b* = linear regression; α = principal axis.

few large spermatozoa or many small spermatozoa. In a sense, this argument is based in energetics, supposing that animals tend to invest a relatively constant amount in gamete output. Similar assumptions lie behind most theoretical models concerning the evolution of anisogamy—large sessile female gametes, and small mobile male gametes (Parker, Baker & Smith, 1972; Charlesworth, 1978; Parker, 1978; Bell, 1978, 1982; Sivinski, 1980; Parker, 1982; Hoekstra, Janz & Schilstra, 1984; and see also Calow, 1979). Pressures to produce many small spermatozoa are many and diverse,

not least being inter-male competition in competitive mating situations, and tendencies for spermatozoa to be lost through dispersion in a large female reproductive tract (Parker, 1970, 1982). This may be complicated by other factors such as 'gamete redundancy' (Cohen 1969, 1983; Wallace, 1974) and by variations in breeding system affecting sperm output (Harcourt, Harvey, Larson & Short, 1981). Cummins (1983) suggested that very large spermatozoa may be selected for when dispersion distances are small, and when circumstances in the female tract favour large, vigorous spermatozoa competing between each other to be first to reach the eggs; while this suggestion obviously needs much more work to validate or to refute, it is supported by at least one theoretical model (G. Bell, personal communication).

If the production of large numbers of small spermatozoa is one way of overcoming tendencies for gametes to be lost by dispersion, then perhaps the anomalous position of the Chiroptera in Table 4 may be explained on the grounds of temporal rather than spatial dispersion. Bats, and particularly small bats of temperate zones, show pronounced capacity for prolonged sperm storage both in the male and the female (Racey, 1975). It would seem to make energetic sense too for chiropterans to invest in many small gametes with limited individual metabolic reserves. Interestingly, the stored spermatozoa appear to enter into a close relationship with the female tract, possibly being nurtured by it (Kruttsch, Crichton & Nagle, 1982). Chiropteran spermatozoa also possess relatively small midpieces, and midpiece lengths do not correlate closely with overall flagellar length, unlike those of other mammals (see below), again suggesting that bat spermatozoa are unusual in terms of the selection pressures moulding their morphology. Finally, many bats show pronounced female-dominant sexual dimorphism (Ralls, 1976; Myers, 1978), suggesting that spatial dispersion in a large female tract may also be a relatively more important factor than in other mammals of comparable size.

Table 5 summarizes the relative linear proportions of head, midpiece and principal piece for all mammals, and for 5 groups for which there are sufficient numbers represented to warrant analysis. It is apparent that, even though the total length of mammalian spermatozoa varies considerably, the mean head length is relatively constant and it is the other components which exhibit most variation. This is, perhaps, not surprising, as the total amount of nuclear material carried by spermatozoa is fairly constant (van Duijn, 1975). In general, the spermatozoa of rodents and artiodactyls have relatively long midpieces and short principal pieces; those of marsupials are the reverse, with short midpieces, while those for primates and bats are intermediate. While it seems intuitively 'right' that the relative length of the midpiece is a measure of the potential energy output of the spermatozoon, it is difficult to interpret the functional significance of these data without further study.

Further analysis showed that there was a significant positive correlation between the length of the midpiece and the length of the head and principal piece (log values) for all groups except Primates and Chiroptera (Table 6). The changes in midpiece length with increasing total sperm

Table 5. Proportions of component sperm dimensions

	No. of species	Mean length (µm)		% of total length		
		Head	Total	Head	Midpiece	Principal piece
All Mammalia	171	7.68	96.9	8.4	19.3	72.6
Artiodactyla	14	6.88	52.2	13.1	19.0	67.9
Chiroptera	23	5.14	66.1	7.9	16.3	75.9
Primates	10	5.22	68.1	7.8	13.7	78.0
Rodentia	92	7.85	108.9	7.4	23.2	70.3
Marsupialia	19	7.64	140.0	6.0	11.4	82.8

Table 6. Allometry in component sperm dimensions

	Log (midpiece length) vs Log (head + principal piece)		
	α , slope of principal axis (95% confidence limits)	Correlation coefficient (r)	Significance level
All mammalia	0.462 (0.379–0.550)	0.630	$P < 0.001$
Artiodactyla	0.361 (0.085–0.694)	0.544	$P < 0.05$
Chiroptera	0.183 (–0.223–0.658)	0.182	$P > 0.05$
Primates	0.167 (–0.116–0.478)	0.341	$P > 0.05$
Rodentia	0.491 (0.416–0.571)	0.793	$P < 0.001$
Marsupialia	0.441 (0.205–0.726)	0.618	$P < 0.01$

length were not isometric ($\alpha \neq 1$), but rather showed negative allometry ($\alpha < 1.036$ – 0.49), with the midpiece length increasing less rapidly than other components as total sperm length increases. Presumably this is because the changes in dimensions are volumetric rather than simply linear, and the midpiece, being thicker than the principal piece, can be expected to show a low value for α (Gould, 1966).

On a final cautionary note, it is worth re-emphasizing that the data here are presented largely uncritically. The problems of measuring spermatozoa have been reviewed by van Duijn (1975), who points out the many possible errors that can arise either from optical artefact or shrinkage due to drying or fixation. It is difficult to accept, for example, the publication of dimensions with a putative accuracy of $0.001 \mu\text{m}$ when the limit of resolution of the light microscope is in the order of $0.2 \mu\text{m}$.

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Note added in proof: Additional information on 24 species is now available.