Die folgende Beobachtung verringert wieder den Abstand zwischen A. sylvaticus aus Europa und A. sylvaticus aus Asien. Der Unterschied zwischen beiden im IPO-Allel ist hier nicht absolut. In einer A. sylvaticus-Population aus den Nordalpen wurde inzwischen einmal auch das für A. flavicollis typische Allel entdeckt (GEMMEKE unpubl.). Damit ist gezeigt, daß die ursprüngliche Form auch bei A. sylvaticus in Europa noch nicht völlig eliminiert ist.

### Zusammenfassung

Eine Untersuchung der Karyogramme der Apodemus-Arten aus Nepal (Abb. 1 und 2) stützt die Annahme, daß Apodemus sylvaticus von dort in die Untergattung Sylvaemus, A. gurkha aber in die Untergattung Alsomys gehört.

Ein proteinelektrophoretischer Vergleich der Waldmäuse A. sylvaticus aus Nepal ergab deutliche Unterschiede zu A. sylvaticus aus Europa, aber Übereinstimmung mit A. sylvaticus aus dem Iran (Tab. 1 und 2). Ob die Waldmäuse aus Nepal wirklich zu A. sylvaticus gehören, muß danach vorerst offen bleiben.

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# Relative brain size in Muridae with special reference to Colomys goslingi

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Receipt of Ms. 10. 8. 1981

## Abstract

Calculated the brain size in 18 species of Muridae either directly from brain weights (12 species) or indirectly from cranial capacity measurements (12 species incl. Colomys goslingi). In six species data from both sets are presented. In Colomys (a predator in limnetic ecosystems) relative brain size (encephalization) and foramen magnum size are larger than in terrestrial Muridae of equal body weight. The differences are similar to those found when comparing water adapted with terrestrial Insectivora. Comparative brain studies are in preparation.

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# Introduction

Colomys goslingi, the african velvet or forest brook rat, is evidently a predator in limnetic ecosystems, as DIETERLEN and STATZNER (1981) have shown recently. Species with similar habits are found in the Insectivora families Tenrecidae (*Limnogale mergulus*; Potamogalinae: *Micropotamogale lamottei*, *M. ruwenzorii* and *Potamogale velox*), Soricidae (e.g. *Neomys fodiens*) and Talpidae (*Desmana moschata*, *Galemys pyrenaicus*). All of these species have large brains when compared with their purely or mainly terrestrial relatives. Within their brains there is a reduction in size of the structures of the olfactory system and an enlargement of the medulla oblongata, both of which are especially pronounced in *Potamogale*. As a consequence of the large medulla oblongata the foramen magnum also was found to be relatively large.

The enlargement of the medulla oblongata in *Potamogale* is due to a marked development of the trigeminal system, especially of the nucleus of the spinal trigeminal tract. The trigeminal nerves, which also are extremely thick, innervate the strongly developed vibrissae of the muzzle. The vibrissae are considered to be vibration receptors adapted for detecting prey under water. In *Colomys* they seem to be "the only sense organ used in detecting the prey" in waters (DIETERLEN and STATZNER 1981). In predators in limnetic ecosystems the trigeminal system is thought to replace the olfactory system and to become the main sensory system used in the search for food in water (STEPHAN and SPATZ 1962; STEPHAN 1967; BAUCHOT and STEPHAN 1967, 1968, 1970).

Since we do not have well preserved brains of *Colomys* we cannot make exact measurements for comparative quantitative studies. However, an indication of the size of the brain can be obtained from cranial capacity measurements, and the size of the medulla oblongata can be inferred from the cross sectional area of the foramen magnum. By comparing these data with those of terrestrial Muridae we are able to evaluate, whether *Colomys* shows differences from other Muridae similar to those shown by the water adapted Insectivora from other Insectivora.

# Material and methods

The cranial capacities (CrC) and foramen magnum areas (FMA) were measured in 10 skulls of *Colomys goslingi* and compared with corresponding measurements in other murid species with similar body weights (*Hybomys univittatus, Lemniscomys striatus, Praomys natalensis*). The average data and the standard error of the mean (SEM) are given in Table 1. In order to make well founded allometric comparisons similar measurements were made on skulls of especially small-bodied (*Micromys minutus, Leggada minutoides*) and large-bodied murids (*Thamnomys venustus, Oenomys hypoxan-thus, Dasymys incomtus, Pelomys fallax, Rattus norvegicus, Malacomys longipes*), and brain weight and body weight data were collected from 12 species (Table 2).

For CrC and FMA measurements skulls, which came from specimens close to the average body weight of the given species, were selected. Average body weigths were calculated from the large collections of the Staatliches Museum für Naturkunde, Stuttgart. The CrC measurements were made by introducing fine dust shot into the cranial cavity through the foramen magnum, weighing the skull before and after introducing the dust shot, and by dividing the weight difference by 5.6121, which was found to be the weight in grams per cubic centimeter dust shot. The FMA measurements were made from enlarged photos of the foramen magnum by planimetry and/or by cutting out and weighing the photographic paper (STEPHAN et al. 1981).

Table 1

# Data on body weights, cranial capacities, and foramen magnum areas in Colomys goslingi and three terrestrial species of African Muridae of similar body weight

	Sex	ц	Body weight (BoW)		SEM	Cranial capacity (CrC)	SF	SEM	Foramen magnum area (FMA)	SEM	м
			8	80	%	Emm	mm³	%	mm <sup>2</sup>	mm <sup>2</sup>	%
Colomys goslingi	шш	υ υ	58.8	2.4	4.1	1240	40.6	3.1	23.1	1.1	4.9
mean	11 mm + ff	o 01	58.2 58.2	9.9 6.8	11.7	1324	6/.1 58.5	0.4	23.0	1.7	5.8
Lemniscomys striatus	um H	n n	58.0 49.0	3.2	5.5 10.6	1012 932	52.4 46.6	5.2	16.2 16.2	1.0	6.2 4.4
mean % deviation from Colomys	ff + mm	10	53.5 (-8.1%)	6.2	11.7	972 (-26.6 %)	62.9	6.5	16.2 (-29.6 %)	0.8	5.1
Hybomys univittatus	um Hf	υ n	54.4 59.2	5.6 4.6	10.2 7.8	1092 1126	71.9 39.9	6.6 3.5	18.6 18.8	0.7	3.7 4.9
mean % deviation from Colomys	mm + ff	10	56.8 (-2.4%)	5.4	9.6	1109 (-16.2 %)	57.7	5.2	18.7 (-18.7%)	0.8	4.1
Praomys natalensis	um Hf	υ n	71.6 54.4	8.8	12.2 8.4	900 848	26.9 71.9	3.0	15.6 16.6	1.1	6.7 9.2
mean % deviation from Colomys	tf + ff	10	63.0 (+8.2%)	11.2	17.8	874 (-34.0%)	58.2	6.7	16.1 (-30.0%)	1.3	8.2

Body weights, brain weights and foramen magnum areas, expected values on the regression lines, indices, and percentage deviation

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of the indices from Colomys

When individuals with unknown body weights are included, the average body weights are set in brackets. \* brain weights converted from cranial capacities;

$ \begin{array}{lcccccccccccccccccccccccccccccccccccc$	$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$		ц	Body weight	Brain weight	Expected brain weight	<u>BrW</u> EBrW	Percentage deviation from	Foramen magnum area		<u>FMA</u>	Percentage deviation from	FMA
	Colomys goding:         10'         58.2         1372*         1041         111.9         0         23.0         18.1         127.2         0           Micromys minutus         3         5.5         267         251         105.5         -199.3         8.7         9.0         96.8         -23.9           Apodemus fluctiollis         10         5.95         238.4         105.5         -199.3         8.7         9.0         96.8         -23.9           Apodemus fluctiollis         10         5.95         238.4         105.1         -20.3         8.7         9.0         96.8         -23.9           Tharmomys venueus         1         (22)         1336         1284         100.0         -141.3         20.9         13.4         -18.5           Oeromys hypocanthus         3         22.1         110         127.1         83.9         -20.3         13.0         18.4         -23.9           Dasymys incornus         1         22.5         1137         84.7         -35.8         10.5         -23.9         -16.8           Dasymys instrutus         1         1         22.5         13.9         -13.7         84.7         -36.4         -16.8           Dasymys intet		(1)	(BoW) g (2)	(BrW) mg (3)	(EBrW) mg (4)	· 100 (EI) (5)	Colomys (6)	(FMA) mm <sup>2</sup> (7)		· 100 (FI) (9)	Colomys (10)	mm <sup>2</sup> /cm <sup>3</sup> (11)
Micromys minutus         3         5.5         2.67         2.51         10.64         -11.3	Micromystrinuius         3         5.5         3.67         2.51         106.1         10.3         6.13         2.52         3.67         2.51         106.1         10.3         6.13         2.52         3.67         2.51         105.1         10.3         6.13         2.52         3.67         10.35         6.13         2.52         2.51         10.35         6.13         2.53         10.35		101	58.2	1372*	1041	131.9	C	23.0	181	1777		
Apodemus fluxicalis         10°         6.1         288*         267         1055         -199         8.7         9.0         96.8         -239           Apodemus fluxicalis         10         30         5.95         278         581         105.7         -199         8.7         9.0         96.8         -239           Apodemus fluxicalis         10         30         5.95         278         581         1050         -16.6         9.0         96.8         -23.9           Apodemus fluxicuits         1         (22.5)         1284         100.0         -24.0         20.1         1038         -18.4           Paramonys venustus         1         (22.5)         1291         1284         100.0         -23.3         20.9         13.8         -18.4           Oeromys hypoxanthus         8         9.2         116.6         1371         83.0         -36.4         13.8         -16.8         -18.4           Daymys incomuts         1         12.5         116.4         1371         84.7         -35.8         20.9         20.1         10.8         -16.8           Dayma incomuts         1         12.5         16.4         1371         84.7         -35.8         21.5	Holdemus/fracticalis         10 <sup>2</sup> 6.1         28.2         26.3         105.7         -19.9         8.7         9.0         96.8         -23.9           Apodemus/fracticalis         10         30         596         100.0         -16.6         -18.3         -18.3           Apodemus/fracticalis         11         82.5         13.84         100.0         -24.2         20.9         20.1         100.3           Performs systematus         81         82.5         1284*         1284         100.0         -24.2         20.9         20.1         103.8         -18.4           Oeromys systematus         81         82.5         1284*         1284         100.5         -24.2         20.9         20.1         103.8         -18.4           Oeromys systematus         81         10.25         1371         83.0         -36.4         18.9         20.8         90.7         -28.7           Dasymy streamutus         81         10.1         107.8         51.7         51.8         0.0         20.1         10.3         -36.1           Dasymis incomutus         81         10.1         107.5         51.3         107.5         21.5         10.6         20.6         20.1         10.6<		3	5.5	267	251	106.4	-19.3		1.01	7. 121	5	1/.4
Apodemus flaricollis         13         5.95         2.84         2.63         105.7 $-19.9$ Apodemus flaricollis         10         3.05         5.96         5.96         105.1 $-20.3$ $-18.5$ Apodemus sylvaticus         282         19.4         590         536         100.0 $-16.6$ $-18.5$ Thamnomys venuestus         1         (82.5)         1380         1384         100.0 $-24.2$ 20.9         103.8 $-18.4$ Oeromys hypoxanthus         8         92.5         1180         1371         83.9 $-36.4$ 183.9 $-20.3$ $20.7$ $-28.7$ Daymys incontus         8         102.5         1574*         1371         83.9 $-36.4$ $103.8$ $-16.8$ Daymys incontus         8         102.5         1574* $146.4$ $107.5$ $-18.4$ $-30.2$ Daymys incontus         8         102.1 $102.5$ $1574*$ $117.8$ $102.5$ $22.4$ $16.8$ $-16.8$ Daymys incontus         8         102.1 $107.5$ $21.4$ $107.5$ <td>Apdemus/faciolis         13         5.95         2.84         2.63         105.7         -19.9        </td> <td></td> <td>10<sup>2</sup></td> <td>6.1</td> <td>282*</td> <td>267</td> <td>105.6</td> <td>- 19.9</td> <td>8.7</td> <td>0.6</td> <td>96.8</td> <td>- 73 9</td> <td>17.0</td>	Apdemus/faciolis         13         5.95         2.84         2.63         105.7         -19.9		10 <sup>2</sup>	6.1	282*	267	105.6	- 19.9	8.7	0.6	96.8	- 73 9	17.0
Apodemus fluction         10         30         750         698         107.5 $-18.5$ Thammomys venuests         1         (22)         129.4         590         556         110.0 $-16.6$ Thammomys venuests         8         82.5         128.4         105.1 $-20.3$ 20.1         103.8 $-18.4$ 9         (82.5)         1320         1371         83.9 $-36.4$ 18.9         20.1         103.8 $-18.4$ 0enomys lypoxanthus         8         92         116.4         1371         83.9 $-36.4$ 18.9         20.1         103.8 $-18.4$ Denomys fallux         8         100         157.4         146.4         107.5 $-18.5$ 22.0         80.7 $-28.7$ Dasymic runus         8         100         166.8         107.5 $-18.5$ 22.0         80.7 $-28.7$ Dasymic runus         8         100         166.8         90.7 $-18.4$ $-50.1$ $-16.8$ Dasymic runus         8         100 $-16.6$ 90.7 $-28.7$ $-16.8$ $-16.8$	Apodemus (pleation)         10         30         556         688         107.5         -18.5           Tharmonys cemestus         1         82.5         1534         155.1         -20.3         20.9         20.1         103.8         -18.4           Tharmonys cemestus         8         82.5         1534         1531         -20.3         20.9         20.1         103.8         -18.4           Octomys sylvacturus         8         82.5         1294+         1284         100.5         -23.3         20.9         20.1         103.8         -18.4           Octomys sylvacturus         8         22.5         1166*         1371         83.0         -35.6         18.9         20.8         -18.4           Dasymys incomus         8         102.5         1574*         1464         107.5         -18.5         22.8         21.6         90.7         -28.7           Pelomys faitur         8         100         140.6         152.5         91.9         -30.2         17.9         20.6         20.1         10.8         20.1         16.8           Pelomys faitures         1         1         121         140.6         152.5         91.9         -20.3         17.9         10.4 </td <td></td> <td>13</td> <td>5.95</td> <td>278+</td> <td>263</td> <td>105.7</td> <td>- 19.9</td> <td></td> <td></td> <td>2.22</td> <td>1.04</td> <td>74.0</td>		13	5.95	278+	263	105.7	- 19.9			2.22	1.04	74.0
Apodemus yleatics         282 <sup>2</sup> 19.4         500         536         110.0 $-16.6$ Thamnomys venustus         1         (82.5)         1396         1284         105.1 $-20.3$ 20.9         20.1         103.8 $-18.4$ Oenomys bypoxanthus         8         (82.5)         1291 <sup>+</sup> 1284         100.5 $-23.8$ 20.9         20.1         103.8 $-18.4$ Oenomys bypoxanthus         8         120.5         1371         83.9 $-36.4$ 18.9         20.9         20.1         103.8 $-18.4$ Dasymy sincomtus         8         102.5         1464         107.5 $-35.8$ 21.5         10.8 $-16.8$ Pelomys falax         8         100 $146.4$ 107.5 $-33.5$ 21.5         20.9         20.1         21.8           Pelomys falax         8         1010 $1406.4$ 152.7         91.9         20.2         81.3 $-36.1$ Lemniscomys striatus         101         107.5         91.9 $-30.2$ 17.9         20.0         20.1         11.8         11.6           Lemniscom	Apodemus sylvaticiss         282 <sup>3</sup> 194         500         536         110.0         -16.6           Thammomys venuestus         1         (82.5)         1350         1284         100.0         -24.2         20.1         103.8         -18.4           Cenomys hypoxambus         3         (92)         1150         1371         85.0         -35.6         18.9         20.1         103.8         -18.4           Cenomys hypoxambus         3         (92)         1150         1371         85.0         -35.6         18.9         20.3         103.8         -18.4           Dasymps incomtus         8         10.2         116.4         107.1         85.0         -35.8         20.1         103.8         -18.4           Pelomys fallax         8         10.0         166.8         90.7         -28.7         90.7         -28.7           Dasymic field         8         10.0         998         10.1         104.8         90.2         -16.8           Hybomy sincitatus         10         1412 <sup>+</sup> 132.7         92.1         17.9         20.2         81.3         -20.1           Hybomy sincitatus         10         1412 <sup>+</sup> 100.8         90.2         17.9 <td></td> <td>10</td> <td>30</td> <td>750</td> <td>698</td> <td>107.5</td> <td>-18.5</td> <td></td> <td></td> <td></td> <td></td> <td></td>		10	30	750	698	107.5	-18.5					
Thamnomys venustus1(82.5)13501284105.1 $-20.3$ $-20.3$ $8$ 82.512911284100.0 $-24.2$ 20.1103.8 $-18.4$ $9$ $82.5$ 12911284100.0 $-24.2$ 20.920.1103.8 $-18.4$ $0$ $8^{1}$ 921166*137185.0 $-35.6$ 18.920.890.7 $-28.7$ $11$ $92$ 1166*137185.0 $-35.6$ 18.920.890.7 $-28.7$ $11$ $92$ 1166*137185.0 $-35.6$ 18.920.890.7 $-28.7$ $11$ $92$ 1166*1577137185.0 $-35.6$ 17.920.8 $-16.8$ $11$ $92$ 1111412*1460161890.2 $-31.6$ 17.920.081.3 $-36.1$ $12$ $11$ $121$ $1460$ 161890.2 $-31.6$ 17.920.081.3 $-36.1$ $11$ $121$ $1460$ 161890.2 $-31.6$ 17.920.081.3 $-36.1$ $121$ $1412^{+}$ $1464$ $107.5$ $-13.6$ $17.9$ $20.2$ $81.3$ $-36.1$ $11$ $121$ $1460$ $1618$ $90.2$ $20.1$ $17.9$ $10.7$ $90.7$ $121$ $1100$ $1460$ $1618$ $90.2$ $17.9$ $10.7$ $10.4$ $10.4$ $111$ $112^{+}$ $1464$ $1025$ $102.6$ $17.9$ $10.7$	Thammonys remustus         1         (82.5)         1350         1284         105.1         -20.3           Parmomys remustus         8'         82.5         1291 <sup>+</sup> 1284         100.5         -23.8         90.1         103.8         -18.4           Oenomys hypoxanthus         3         92.5         1186*         1371         83.9         -36.4         103.5         -28.7           Dasymps incomtus         8'         102.5         1574*         1464         107.5         -18.5         21.5         103.8         -18.4           Dasymps incomtus         8'         101.0         140.6         161.8         90.7         -28.7         -28.7           Dasymps incomtus         8'         101.0         140.4         107.5         -18.5         21.8         20.0         8'1.1           Pelomys failur         1         111         141.2 <sup>+</sup> 155.6         91.9         -30.2         17.9         20.0         21.6         18.7         -36.1           Lemniscomys striatus         10'         53.5         100.7         91.8         17.9         20.0         21.6         18.7         17.9         10.4         21.6           Hybomys unicitatus         10'		282 <sup>3</sup>	19.4	590	536	110.0	-16.6					
$8^{\circ}$ 82.5         1284*         1284         100.0 $-24.2$ 20.9         20.1         103.8 $-18.4$ Oenomys bypoxantbus         3         (82.5)         1291+         1284         100.0 $-24.2$ 20.9         20.1         103.8 $-18.4$ Denomys bypoxantbus         3         (82.5)         1150         1371         83.9 $-35.6$ 18.9         20.1         103.8 $-18.5$ Dasymys incontus         8'         10.25         1574*         1464         107.5 $-13.6$ 82.9 $20.2$ $-16.8$ $90.7$ $-28.7$ Pelomys falax         8'         110         146.4         107.5 $-13.6$ $18.7$ $-16.8$ Pelomys falax         8'         110 $146.4$ $107.5$ $-13.7$ $20.2$ $216.8$ $-16.8$ Desting falax         8'         100 $146.4$ $107.5$ $-13.7$ $20.2$ $20.16.8$ $20.6$ $20.7$ $20.7$ $20.7$ Hybomys univitatus         10'         56.8 $100.4$ $102.5$ $12$	8         8.2.5         1.2.8.4         1.2.0         -2.4.2         2.0.9         2.0.1         10.3.8         -1.8.4 <i>Cenomys hypoxanthus</i> 3         (9.2.5)         1.2.91         1.2.81         100.0         -2.4.2         2.0.9         2.0.1         10.3.8         -1.8.4 <i>Denomys hypoxanthus</i> 3         (9.2.5)         1.2.91         1.8.5         -3.5.6         1.8.9         2.0.8         9.0.7         -2.8.7           Dasymys incomtus         8 <sup>1</sup> 10.2.5         1.5.4         1.371         85.0         -3.5.6         1.8.5         2.0.8         9.0.7         -2.8.7           Dasymys incontus         8 <sup>1</sup> 10.2.5         1.5.4         1.371         85.0         -3.5.6         1.8.5         2.1.6.8         -16.8           Pelomys fallax         1         1         1.2.1         1.66.4         1.7.7         3.5.3         2.0.2         1.7.9         2.0.3         9.0.7         2.8.7           Hypomys univitatus         10         5.5         1.0.5         9.0.2         1.7.9         2.0.2         1.7.9         10.4.2         10.1.2           Mas musculus         10         5.8         1.0.5         1.7.9         1.7.9         <		1	(82.5)	1350	1284	105.1	-20.3					
Oeromys hypoxanthus         9         (82.5)         1291 <sup>+</sup> 1284         100.5 $-23.8$ Denomys hypoxanthus         8         92         1166 <sup>+</sup> 1371         83.9 $-36.4$ 18.9         20.8         90.7 $-28.7$ Dasymys incontus         8         11         (92)         1166 <sup>+</sup> 1371         83.9 $-36.4$ 18.9         20.8         90.7 $-28.7$ Dasymys incontus         8         102.5         1574 <sup>+</sup> 1464         107.5 $-18.5$ 21.5         105.8 $-16.8$ Pelomys falax         8         100         1648         90.7 $-28.7$ $-36.4$ $-36.4$ $-36.1$ $-36.1$ Lemniscomys striatus         2         35.5         1007         90.1 $-19.0$ $16.2$ $11.412^+$ $155.6$ $91.9$ $-20.7$ $16.8$ Hybomys univitiatus         10 <sup>1</sup> 55.4         1014 <sup>+</sup> 988         100.8 $-22.2$ $17.9$ $104.2$ $-18.1$ $17.9$ $16.2$ $16.8$ $16.2$ $16.8$ $16.8$ $16.2$	Oeromys hypoxanthus         9         (22.5)         1291         1284         100.5 $-23.8$ Darymys incontus         8'         92         11550         1371         83.0 $-36.4$ 90.7 $-28.7$ Darymys incontus         8'         102.5         1574         1371         83.0 $-36.4$ $-28.7$ Darymys incontus         8'         102.5         1554         1371         83.0 $-36.4$ $-28.7$ Darymys incontus         8'         102.5         1557         92.1 $-30.2$ $-16.8$ Dennys failax         8'         101         1466*         1577 $92.1$ $-27.7$ Hybomys univitatus         2         53.5         1007*         983         101.8 $-22.2$ $81.3$ $-46.4$ Hybomys univitatus         10'         53.5         1007*         983         101.8 $-22.2$ $16.2$ $17.6$ $92.0$ $-22.7$ Hybomys univitatus         10'         53.5         1007*         983 $102.6$ $102.5$ $16.4$ $16.1$ $12.9$ $12.6$ $12.2$ <		81	82.5	1284*	1284	100.0	-24.2	20.9	20.1	103.8	-184	16.9
Oenomys bypoxanthus         3         (92)         1150         1371         83.9 $-36.4$ Dasymys incomtus         8'         92         1166*         1371         83.0 $-35.6$ 18.9         20.8 $90.7$ $-28.7$ Dasymys incomtus         8'         102.5         1164*         1371         85.0 $-35.6$ 18.9         20.8 $90.7$ $-28.7$ Dasymys incomtus         8'         102.5         154.4*         1460         1618         90.2 $-31.6$ 18.9         20.8 $90.7$ $-28.7$ Pelomys failux         8'         110         1406*         1527         92.1 $-30.2$ 17.9         20.0         81.3 $-16.8$ Lemniscomys striatus         10'         53.5         1006*         1527         92.1 $-30.2$ 17.9         10.4 $-27.7$ Mus musculus         10'         53.5         1007*         989         101.8 $-22.22$ 11.7 $12.6$ $92.0$ $-28.7$ Mus musculus         11'         12'         33.10'         14.10' $53.7$ 10.4	Oenomys bypoxanthus         3         (92)         1150         1371         83.9         -56.4           Daymys incomus         8'         92         1166*         1371         83.0         -56.6         18.9         20.8         90.7         -28.7           Daymys incomus         8'         102.5         1574*         1464         107.5         -18.5         21.5         105.8         -16.8           Dayms incomus         8'         102.5         1574*         1464         107.5         -18.5         22.8         21.5         105.8         -16.8           Dayms incomus         8'         100         1668         90.2         -30.1         17.9         20.0         81.3         -56.8           Lemiscomy striatus         10'         53.4         101+*         98         10.2.6         17.9         22.0         81.3         -57.7           Hyborys striatus         10'         56.8         1149*         102.5         112.1         -15.0         18.7         17.9         104.2         18.1           Mascardus         31.2         57         20.1         23.3         10.4         107.5         22.0         81.1         -22.9           Leggada sp.?		6	(82.5)	1291 +	1284	100.5	-23.8					1.01
$B_1$ $92$ $1166^*$ $1371$ $85.0$ $-35.6$ $18.9$ $20.8$ $90.7$ $-28.7$ $Pelomys jacomtusB102.51162^+137184.7-35.821.5105.8-16.8Pelomys faltaxB102.51574^*1464107.5-131.622.821.5105.8-16.8Belomys faltaxB1101466^*157784.7-35.821.5105.8-16.8B1101466^*157792.1-30.221.522.081.3-36.1B1101406^*155792.1-30.217.922.081.3-36.1B1101412^+155691.9-30.217.9105.811.9-22.2Hybomys univitatus10^{2}56.81149^*1025112.1-15.081.3-22.216.217.9104.2-18.1Mus musculas312^+18.81007^+988102.6112.1-15.018.717.9104.2-18.1Mus musculas312^+18.81007^+32.956.81007^+22.738.2-22.2104.2-18.1Mus musculas312^+8.30^ 51.3102.8102.8102.8102.2102.8102.2102.2102.2102.2102.2$	Bit optimize         92         1166*         1371         85.0         -35.6         18.9         20.8         90.7         -28.7           Dasymys incomtus         11         (92)         1162*         1371         84.7         -35.8         18.9         20.8         90.7         -28.7           Dasymys incomtus         8         102.5         154.4         164.8         90.2         -35.8         21.5         105.8         -16.8           Demosys failax         8         110         1402*         153.5         1007*         99.1         110         140.5         -18.5         20.8         21.6         92.0         -23.7           Hybomys striatus         2         53.5         1007*         988         102.6         -12.2         18.7         17.9         10.4         20.7         -23.7           Max macduas         312*         18         430         51.1         -15.8         10.4         20.6         92.1         -16.8           Max macduas         312*         18         430         51.1         -15.9         10.7         -23.2         10.4         10.4         20.6         92.0         -20.7         93.1           Max macduas <t< td=""><td>6 Oenomys hypoxanthus</td><td>3</td><td>(92)</td><td>1150</td><td>1371</td><td>83.9</td><td>-36.4</td><td></td><td></td><td></td><td></td><td></td></t<>	6 Oenomys hypoxanthus	3	(92)	1150	1371	83.9	-36.4					
Dasymys incomtus11(92)1162 <sup>+</sup> 1371 $84.7$ $-35.8$ Dasymys incomtus8'102.51574*1464107.5 $-18.5$ 22.821.5105.8 $-16.8$ Pelomys faltax8'112114101466151790.2 $-31.6$ 91.9 $-30.2$ 17.922.0 $81.3$ $-36.1$ Demiscomys striatus253.51007*983106.8 $-19.0$ $17.9$ 22.0 $81.3$ $-36.1$ Hybomys univitatus10'55.41014 <sup>+</sup> 988100.6 $-22.2$ $17.9$ 22.0 $81.3$ $-36.1$ Hybomys univitatus10'56.81149 <sup>+</sup> 102.6 $-22.2$ $18.7$ $17.9$ $104.2$ $-18.1$ Hybomys univitatus10'56.8 $1149^+$ $102.6$ $-22.2$ $18.7$ $17.9$ $104.2$ $-18.1$ Hybomys univitatus10'56.8 $1149^+$ $102.6$ $-22.2$ $18.7$ $17.9$ $104.2$ $-18.1$ Kattus morvegius $312^+$ 18 $430$ $51.2$ $23.7$ $23.7$ $23.7$ $23.7$ $23.7$ $23.7$ $24.0$ $22.9$ Sadda minutoides $354^+$ $291$ $2270^+$ $2746$ $82.7$ $-37.7$ $10.4$ $10.6$ $94.0$ $-22.9$ Hybomys univolutes $5^+$ $291$ $2270^+$ $2746$ $82.7$ $-37.7$ $10.4$ $10.6$ $98.1$ $-22.9$ Radia minutoides $354^+$ $291$ $2270^+$ $2746$	Daymys incomtus         11         (92)         1162 <sup>+</sup> 1371         84.7         -35.8           Pelomys fallax         8         102.5         1574 <sup>+</sup> 1371         84.7         -35.8         21.5         105.8         -16.8           Pelomys fallax         8         102.5         1574 <sup>+</sup> 1371         84.7         -30.3         10.5         91.1         112.4         135.6         91.9         -30.3         17.9         22.0         81.3         -36.1           Hybomys striatus         2         53.5         1007         983         106.8         -19.0         17.9         22.0         81.3         -36.1           Hybomys univitatus         10'         56.8         1014 <sup>+</sup> 988         102.6         -22.2         16.2         17.9         104.2         -18.1           Mas muculus         312 <sup>+</sup> 18         430         51.3         53.4         23.7         10.4         10.4         22.0         81.3         -22.9           Mas muculus         8         10.4         32.7         12.9         10.4         10.4         22.0         81.3         22.0         81.3         22.0           Mas muculus         312 <sup>+</sup>		81	92	1166*	1371	85.0	-35.6	18.9	20.8	90.7	- 28.7	16.8
Dasymys incomtus8102.51574**1464107.5 $-18.5$ $22.8$ $21.5$ 105.8 $-16.8$ Pelomys fallax111211460161890.2 $-31.6$ 21.5105.8 $-16.8$ $8^{0}$ 1101406**152792.1 $-30.2$ 17.922.081.3 $-36.1$ Lemniscomys striatus253.51007**983106.8 $-19.0$ $14.12^{+}$ 153.691.9 $-20.2$ $17.9$ $22.0$ $81.3$ $-57.7$ Hybomys unvirtatus10'53.51007**983100.6 $-22.2$ $16.2$ $17.6$ $92.0$ $-27.7$ Hybomys unvirtatus10'53.51007**983102.6 $-22.2$ $16.2$ $17.6$ $92.0$ $-27.7$ Mus musculus312' $8.8$ $102.6$ $-22.2$ $16.2$ $17.9$ $104.2$ $-18.1$ Leggada minutoides8' $100'$ $53.8$ $102.6$ $1225$ $112.1$ $-150.0$ $18.7$ $17.9$ $104.2$ $-18.1$ Leggada minutoides8' $10.4$ $32.7^{+6}$ $82.7$ $-37.7$ $10.4$ $10.4$ $22.79$ $22.00$ $98.1$ $-22.9$ $28.0$ $29.0$ $-22.9$ Sattus norvegicus $35.4^{+5}$ $2716$ $81.9^{-}$ $-37.7$ $10.4$ $10.6$ $98.1$ $-22.9$ $28.0^{-}$ $22.9^{-}$ $22.9^{-}$ $22.9^{-}$ $22.9^{-}$ $22.9^{-}$ $22.9^{-}$ $22.9^{-}$ $22.9^{-}$ $22.9^{-$	Dasymys incontus         8'         102.5         1574*         1464         107.5         -18.5         22.8         21.5         105.8         -16.8           Pelomys fallax         1         1         121         1460         1618         90.2         -31.6         12.9         -30.1         13.9         -36.1           Pelomys fallax         1         1         121         1460         1537         92.1         -30.2         17.9         22.0         81.3         -36.1           Hybomys striatus         2         53.5         1007*         988         102.6         -22.2         16.2         17.6         92.0         -27.7           Hybomys univitatus         10'         56.8         11.9         102.6         -22.2         18.7         17.9         104.2         -18.1           Kast motidus         312*         18         430         51.3         83.9         -32.6         10.4         106.5         98.1         -22.2         18.7         17.9         104.2         -18.1           Kast motidus         312*         18         430         51.3         83.9         -32.7         10.4         10.4         0.4         0.4         0.4         0.4		11	(92)	1162+	1371	84.7	- 35.8					0.01
Pelomys faltax11211460161890.2 $-31.6$ $Pelomys faltax81101406*152792.1-30.217.922.081.3-36.191111412+153691.9-30.317.922.081.3-36.110^{1}53.51007*983100.68-19.016.217.692.0-27.711^{2}53.41014+988102.6-22.216.217.692.0-27.7Hybomys univitatus10^{1}56.81149*1025112.1-15.018.717.9104.2-18.1Mus mosculus312^{4}181014^{+}988102.6-22.218.717.9104.2-18.1Leggada minutoides810,156.81149*1025112.1-15.018.717.9104.2-18.1Leggada minutoides810,151.383.9-36.4102.482.7-37.310.410.2.9Leggada minutoides354^{5}2912270274681.9-37.310.410.698.1-22.9Segada minutoides354^{5}2912270274681.9-37.328.029.894.0-22.9Segada minutoides910,22248*274681.9-37.328.029.894.0-20.9Segada minutoides910,2221.727762$	Felomys falax         1         121         1460         1618         90.2         -31.6           Felomys falax         1         121         1406*         1527         92.1         -30.2         17.9         22.0         81.3         -36.1           Lemniscomys striatus         2         53         1050         983         106.8         -19.0         81.3         -36.1           Hybomys univitatus         10 <sup>1</sup> 53.5         1007*         983         101.8         -22.2         81.3         -36.1           Hybomys univitatus         10 <sup>1</sup> 53.5         1007*         983         102.6         -22.2         81.3         -36.1           Mus musculus         312 <sup>4</sup> 18         430         513         83.9         -36.4         10.4         22.0         81.1         -22.9           Mus musculus         312 <sup>4</sup> 18         430         513         83.9         -36.4         10.4         22.0         92.0         -22.7           Rattus norvegicus         312 <sup>4</sup> 18         430         513         83.9         -36.4         10.4         20.4         22.9         92.0         22.9           Rattus norvegicus         51		81	102.5	1574*	1464	107.5	-18.5	22.8	21.5	105.8	- 16.8	15.0
B <sup>1</sup> 110       1406*       1527       92.1       -30.2       17.9       22.0       81.3       -36.1         Cenniscomys striatus       2       53       1050       983       106.8       -19.0       81.3       -36.1         Hybomys univittatus       10 <sup>1</sup> 53.5       1007*       989       101.8       -22.2       16.2       17.6       92.0       -27.7         Hybomys univittatus       10 <sup>1</sup> 56.8       1149 <sup>+</sup> 988       101.6       -22.2       16.2       17.6       92.0       -27.7         Mus musculus       312 <sup>+</sup> 18       430       513       83.9       -36.4       -18.7       17.9       104.2       -18.1         Mus musculus       312 <sup>+</sup> 18       430       513       83.9       -36.4       -19.0       18.7       17.9       104.2       -18.1         Mus musculus       312 <sup>+</sup> 18       430       513       83.9       -36.4       10.4       227.0       22.1       17.9       104.2       -18.1         Mus musculus       312 <sup>+</sup> 18       430       513       83.9       -36.4       10.4       10.4       27.0       27.9       27.9       27.9	Bit         110         1406*         1527         92.1         -30.2         17.9         22.0         81.3         -36.1           Lemniscomys striatus         2         31         1405         153.5         1007         893         106.8         -19.0         81.3         -36.1           Hybomys univitatus         10'         53.5         1007         983         10.6         -22.2         11.7         92.0         -27.7           Hybomys univitatus         10'         55.8         1149*         1025         112.1         -15.0         18.7         17.9         104.2         -18.1           Mus musculus         312 <sup>4</sup> 56.8         1149*         1025         112.1         -15.0         18.7         17.9         104.2         -18.1           Leggada p:         5         7.7         288         307         33.9         -35.4         101.2         51.3         10.4         10.6         98.1         -22.9           Leggada minutoides         8         10.4         327*         368         88.8         -32.7         10.4         10.4         22.6         91.0         -22.9           Rattus norvegicus         354 <sup>5</sup> 2910         227.4		1	121	1460	1618	90.2	-31.6					2
Lemniscomys striatus         9         111         1412 <sup>+</sup> 1536         91.9         -30.3           Hybomys striatus         10 <sup>1</sup> 53.5         1000 <sup>++</sup> 983         106.8         -19.0           Hybomys striatus         10 <sup>1</sup> 53.5         1000 <sup>++</sup> 983         101.8         -22.8         16.2         17.6         92.0         -27.7           Hybomys univittatus         10 <sup>1</sup> 56.8         1149 <sup>++</sup> 988         102.6         -222.8         16.2         17.6         92.0         -27.7           Mus musculus         10 <sup>1</sup> 56.8         1149 <sup>++</sup> 1025         112.1         -15.0         18.7         17.9         104.2         -18.1           Mus musculus         312 <sup>4</sup> 8         10.4         327         383.9         -36.4         10.4         20.2         -27.7           Leggada minutoides         8         10.4         327         368         83.7         -32.7         10.4         10.6         98.1         -22.9           Ratus norvegicus         5         (291)         2248 <sup>+</sup> 2746         82.7         -37.7         37.3         28.0         29.1         22.0         26.1         -26	Lemniscomys striatus         9         111         1412 <sup>+</sup> 1536         919         -30.3           Hybomys striatus         10 <sup>1</sup> 53.5         1007*         983         100.6         -19.0         22.0         -27.7           Hybomys striatus         10 <sup>1</sup> 53.5         1007*         983         100.6         -22.2         16.2         17.6         92.0         -27.7           Mus misculus         10 <sup>1</sup> 56.8         1149*         1025         112.1         -15.0         18.7         17.9         104.2         -18.1           Leggada minutoides         8 <sup>1</sup> 10,4         32.7         112.1         -15.0         18.7         17.9         104.2         -18.1           Leggada minutoides         8 <sup>1</sup> 10,4         32.7         36.8         33.9         -36.4         104.2         -18.1           Leggada minutoides         354 <sup>5</sup> 291         2270         2746         82.7         -37.7         10.4         10.6         92.0         -22.9           Rattus norvegicus         354 <sup>5</sup> 291         2270 <sup>+</sup> 2746         82.7         -37.7         10.4         10.6         92.0         -22.9           P		8	110	1406*	1527	92.1	-30.2	17.9	22.0	81.3	-36.1	13.2
Lemniscomys striatus         2         53         1050         983         106.8         -19.0           Hybomys univitatus         10'         53.5         1007*         989         101.8         -22.8         16.2         17.6         92.0         -27.7           Hybomys univitatus         12         53.4         1014 <sup>+</sup> 988         102.6         -22.2         18.7         17.9         104.2         -18.1           Mus muscilus         312 <sup>+</sup> 18         430         513         83.9         -36.4         104.2         -18.1           Leggada spi?         5         7.7         288         307         93.7         -22.0         18.7         17.9         104.2         -18.1           Leggada spi?         5         7.7         288         307         93.7         -22.7         10.4         10.4.2         -18.1           Rattus norvegicus         354*         291         2270         2746         81.9         -37.3         28.0         29.1         -22.9           Rattus norvegicus         357         291         2246         81.9         -37.3         28.0         29.1         -21.9           Rattus norvegicus         5         291	Lemniscomys striatus         2         53         1050         983         106.8         -19.0           Hybomys univititatus         10'         53.5         1007*         989         101.8         -22.8         16.2         17.6         92.0         -27.7           Hybomys univititatus         10'         56.8         1149*         102.6         -22.2         18.7         17.9         104.2         -18.1           Mus musculus         312*         18         430         513         83         102.6         -22.2         18.7         17.9         104.2         -18.1           Mus musculus         312*         18         430         513         83         -32.7         18.7         17.9         104.2         -18.1           Mus musculus         312*         18         430         51         1025         18.7         17.9         104.2         -18.1           Regada sp.?         5         7.7         288         307         93.7         -22.0         88.1         -22.9         0.4         0.4         -22.9           Rattus norvegicus         54*         2746         82.7         -37.3         28.0         29.2         29.0         26.1         14.0<		6	111	1412+	1536	91.9	-30.3					
Hybomys univittatus       10 <sup>1</sup> 53.5       1007*       989       101.8       -22.8       16.2       17.6       92.0       -27.7         Hybomys univittatus       12       53.4       1014 <sup>+</sup> 988       102.6       -22.2       18.7       17.9       104.2       -18.1         Mus musculus       312 <sup>+</sup> 18       430       513       83.9       -36.4       104.2       -18.1         Mus musculus       312 <sup>+</sup> 18       430       513       83.9       -36.4       10.4       -22.2       -18.1         Leggada sp.?       5       7.7       288       307       93.7       -29.0       18.7       17.9       104.2       -18.1         Rattus norvegicus       354 <sup>5</sup> 291       2270       2746       82.7       -37.3       28.0       29.8       94.0       -26.1         Praomys natalensis       10 <sup>1</sup> 63.0       906*       1091       83.0       -37.3       28.0       29.1       2270 <sup>+</sup> 2746       82.7       -37.3       28.0       29.4       0       -26.1         Praomys natalensis       10 <sup>1</sup> 63.0       96.8       1091       83.0       -37.3       26.9       21.2	Hybomys univitatus         10 <sup>1</sup> 53.5         1007*         989         101.8         -22.2         15.6         92.0         -27.7           Hybomys univitatus         12         53.4         1014 <sup>+</sup> 988         102.6         -22.2         15.3         104.2         -18.1           Mus musculus         312 <sup>+</sup> 18         430         513         83.9         -36.4         104.2         -18.1         -18.0         18.7         17.9         104.2         -18.1           Leggada sp?         5         7.7         288         307         93.7         -29.0         98.1         -22.9           Rattus norvegicus         354 <sup>5</sup> 291         2270         2746         81.9         -37.3         10.4         10.6         98.1         -22.9           Rattus norvegicus         354         291         2270         2746         81.9         -37.3         28.0         94.0         -26.1           Matcomys indratensis         10 <sup>1</sup> 63.0         90.6*         1091         83.0         -37.3         28.0         29.1         22.0         2746         81.9         -17.1         35.5         29.1         26.9         21.2         126.6         -0.5		2	53	1050	983	106.8	-19.0					
Hybomys univitatus1253.4 $1014^+$ 988 $102.6$ $-22.2$ Hybomys univitatus10156.8 $1149^*$ $1025$ $112.1$ $-15.0$ $18.7$ $17.9$ $104.2$ $-18.1$ Mus musculus $312^+$ 18 $430$ 513 $83.9$ $-36.4$ $1014.2$ $-18.1$ Leggada sp.?57.7288 $307$ $93.7$ $-29.0$ $102.6$ $98.1$ $-22.9$ Leggada sp.?57.7288 $307$ $93.7$ $-29.0$ $10.4$ $10.4$ $227^+$ $28.8$ $-32.7$ $10.4$ $10.6$ $98.1$ $-22.9$ Rattus norvegicus $354^5$ $291$ $2270^+$ $2746$ $88.8$ $-32.7$ $10.4$ $10.6$ $98.1$ $-22.9$ Praomys natalensis $10^+$ $63.0$ $906^*$ $1091$ $83.0$ $-37.1$ $16.1$ $18.5$ $86.9$ $-31.7$ Malacomys indensis $9^+$ $90^ 966^*$ $1091$ $83.0$ $-37.1$ $16.1$ $18.5$ $86.9$ $-31.7$ Acomys sikapusi $5$ $63.5$ $1220^+$ $1726^+$ $-29.9$ $20.9^ 20.9^ 20.5^ -2.9^-$ Comburonys sikapusi $5$ $63.5$ $1200^ 1097^+$ $027.5$ $-29.9^ 21.2^ 21.2^ -0.5^-$ Comburonys sikapusi $5$ $63.5$ $1200^ 1097^+$ $-29.9^ 21.2^ -26.9^ -26.9^-$ Comburonys sikapusi $5$ $63.5$ $92.5$ $-29.$	Hybomys univitatus1253.41014 <sup>+</sup> 988102.6 $-22.2$ Mus muculus $10^1$ 56.8 $1149^{**}$ $1025$ $112.1$ $-15.0$ $18.7$ $17.9$ $104.2$ $-18.1$ Mus muculus $312^4$ $18$ $430$ $513$ $83.9$ $-36.4$ $10.7$ $18.7$ $17.9$ $104.2$ $-18.1$ Leggada sp? $8^1$ $0.7$ $228$ $307$ $93.7$ $-29.0$ $98.1$ $-22.9$ Leggada sp? $8^1$ $10.4$ $32.7$ $368$ $8.2.7$ $-37.3$ $10.4$ $10.6$ $98.1$ $-22.9$ Rattus norvegicus $354^5$ $291$ $2270^{\circ}$ $2746$ $82.7$ $-37.3$ $10.4$ $10.6$ $98.1$ $-22.9$ Praomys natalensis $10^1$ $63.0$ $906^*$ $1091$ $83.0$ $-37.1$ $16.1$ $18.5$ $86.9$ $-31.7$ Malacomys longipes $9^1$ $98$ $182.7$ $-37.3$ $28.0$ $29.1$ $2270^{\circ}$ $2274$ $23.1$ $-22.9$ Malacomys sikapusi $5$ $63.5$ $1825^*$ $1425$ $128.1$ $-2.9$ $26.9$ $21.2$ $126.6$ $-0.5$ Lophuromys sikapusi $5$ $63.5$ $884$ $955$ $92.5$ $-22.9$ $26.9$ $21.7$ $26.6$ $-0.5$ Comys dimidiatus $28^*$ $50.5$ $884$ $955$ $92.5$ $-22.9$ $26.9$ $21.2$ $126.6$ $-0.5$ Colls from Statcher Sume from Weener (1980), $3$ from Wencer (1992), $69.9$		101	53.5	1007*	686	101.8	-22.8	16.2	17.6	92.0	-27.7	16.7
Hybomys unveittatus10156.81149*1025112.1-15.018.717.9104.2-18.1Mus musculus312 <sup>4</sup> 1843051383.9-36.410.2-18.1-18.1Mus musculus312 <sup>4</sup> 1843051383.9-36.410.2-18.1-12.9Leggada sp.?57.728830793.7-29.010.410.698.1-22.9Leggada minutoides8110.4327*36888.8-32.710.410.698.1-22.9Ratus norvegicus354 <sup>5</sup> 2912270274681.9-37.328.029.894.0-26.1Praomys natalensis10 <sup>1</sup> 63.0906*109183.0-37.116.118.586.9-31.7Malacomys likapusi563.512001097109.4-17.12.926.921.2126.6-0.5Acomys dimidiatus28650.588495592.5-29.920.921.2126.6-0.5	Hybomys unvertatus10156.81149*1025112.1 $-15.0$ 18.717.9104.2 $-18.1$ Mus musculus312*1843051383.9 $-36.4$ 17.9104.2 $-18.1$ Leggada $p_{1.5}^{?}$ 57.728830793.7 $-29.0$ 98.1 $-22.9$ Leggada minutoides810.4327*36888.8 $-32.7$ 10.410.698.1 $-22.9$ Leggada minutoides810.4327*36888.8 $-32.7$ 10.410.698.1 $-22.9$ Rattus norvegicus3592912270*274682.7 $-37.3$ 28.029.894.0 $-26.1$ Praomys natalensis10163.0906*109183.0 $-37.1$ 16.118.586.9 $-31.7$ Malacomys longipes91921825*1425128.1 $-2.9$ 26.921.2126.6 $-0.5$ Malacomys sikapusi563.51825*1425128.1 $-2.9$ 26.921.2126.6 $-0.5$ Malacomys sikapusi563.51825*1425128.1 $-2.9$ 26.921.2126.6 $-0.5$ Lophuromys sikapusi563.51825*1425128.1 $-2.9$ 26.921.2126.6 $-0.5$ Acomys dimidiatus2850.588495592.5 $-29.9$ 20.921.221.221.226.921.221.6 $-0.5$		12	53.4	1014+	988	102.6	-22.2					
Mus musculus         312 <sup>4</sup> 18         430         513         83.9         -36.4           Leggada sp.?         5         7.7         288         307         93.7         -29.0           Leggada sp.?         5         7.7         288         307         93.7         -29.0           Leggada minutoides         8 <sup>1</sup> 10.4         327*         368         88.8         -32.7         10.4         10.6         98.1         -22.9           Rattus norvegicus         354 <sup>5</sup> 291         2270         2746         81.9         -37.3         10.4         10.6         98.1         -22.9           Praomys natalensis         10 <sup>1</sup> 63.0         906*         1091         83.0         -37.1         16.1         18.5         84.0         -26.1           Malacomys longipes         9 <sup>1</sup> 98         1825*         1425         128.1         -2.9         26.9         21.2         126.6         -0.5           Malacomys likapusi         5         63.5         1200         1094         -17.1         -2.9         26.9         21.2         0.5           Acomys dimidiatus         28 <sup>6</sup> 50.5         884         95.5         92.5	Mus musculus         312 <sup>4</sup> 18         430         513         83.9         -36.4           Leggada sp.?         5         7.7         288         307         93.7         -29.0           Leggada minutoides         8 <sup>1</sup> 10.4         327*         368         88.8         -32.7         10.4         10.6         98.1         -22.9           Rattus norvegicus         354 <sup>5</sup> 291         2270         2746         82.7         -37.3         10.4         10.6         98.1         -22.9           Rattus norvegicus         354 <sup>5</sup> 291         2270 <sup>2</sup> 2746         82.7         -37.3         10.4         10.6         98.1         -22.9           Praomys natalensis         10 <sup>1</sup> 63.0         906*         1091         83.7         -37.3         16.1         18.5         84.9         -31.7           Malacomys longipes         9 <sup>1</sup> 98         1825 <sup>*</sup> 1425         128.1         -2.9         26.9         21.2         126.6         -0.5           Malacomys longipes         9 <sup>1</sup> 98         182.5 <sup>*</sup> 142.5         128.1         -2.9         26.9         21.2         21.6.6         -0.5         26.9		101	56.8	1149*	1025	112.1	-15.0	18.7	17.9	104.2	-18.1	16.9
Leggada sp.?         5         7.7         288         307         93.7         -29.0           Leggada minutoides         8 <sup>1</sup> 10.4         327*         368         88.8         -32.7         10.4         10.6         98.1         -22.9           Rattus norvegicus         354 <sup>5</sup> 291         2270         2746         82.7         -37.3         10.4         10.6         98.1         -22.9           Rattus norvegicus         354 <sup>5</sup> 291         2270         2746         81.9         -37.3         10.4         10.6         98.1         -22.9           Praomys natalensis         10 <sup>1</sup> 63.0         906*         1091         83.0         -37.3         28.0         29.8         94.0         -26.1           Malacomys longipes         9 <sup>1</sup> 98         1825*         1425         128.1         -2.9         26.9         21.2         126.6         -0.5           Acomys dimidiatus         28 <sup>6</sup> 50.5         884         955         92.5         -29.9         20.9         21.2         126.6         -0.5	Leggada sp.?       5       7.7       288       307       93.7       -29.0         Leggada minutoides       81       10.4       327*       368       88.8       -32.7       10.4       10.6       98.1       -22.9         Rattus norvegicus       354 <sup>5</sup> 291       2270       2746       82.7       -37.3       10.4       10.6       98.1       -22.9         Rattus norvegicus       354       291       2270       2746       81.9       -37.3       10.4       10.6       98.1       -22.9         Praomys natalensis       10 <sup>1</sup> 63.0       906*       1091       83.0       -37.1       16.1       18.5       86.9       -31.7         Malacomys longipes       9 <sup>1</sup> 98       1825*       1425       128.1       -2.9       26.9       21.2       126.6       -0.5         Malacomys sikapusi       5       63.5       1200       1097       1094       -17.1       2.0       26.9       21.2       126.6       -0.5         Acomys sikapusi       5       63.5       1200       1097       1094       -17.1       2.0       2.0       2.0       2.0       2.0       2.0       2.0       2.0       2.0		3124	18	430	513	83.9	-36.4					
Leggada minutoides         81         10.4         327*         368         88.8         -32.7         10.4         10.6         98.1         -22.9           Rattus norvegicus         3545         291         2270         2746         82.7         -37.3         10.4         10.6         98.1         -22.9           Rattus norvegicus         52         (291)         2248*         2746         81.9         -37.3         28.0         29.8         94.0         -26.1           Praomys natalensis         10 <sup>1</sup> 63.0         906*         1091         83.0         -37.1         16.1         18.5         84.9         -31.7           Malacomys longipes         9 <sup>1</sup> 98         1825*         1425         128.1         -2.9         26.9         21.2         126.6         -0.5           Lophuromys sikapusi         5         63.5         1200         1097         1094         -17.1         16.1         18.5         -0.5           Acomys dimidiatus         28 <sup>6</sup> 50.5         884         955         92.5         -29.9         20.9         51.2         0.5	Leggada minutoides $8^1$ 10.4327*36888.8 $-32.7$ 10.410.698.1 $-22.9$ Rattus norcegicus $354^5$ 291 $2270$ $2746$ $82.7$ $-37.3$ $10.4$ $10.6$ $98.1$ $-22.9$ Rattus norcegicus $354^5$ 291 $2270$ $2746$ $81.9$ $-37.3$ $28.0$ $29.8$ $94.0$ $-26.1$ Praomys natalensis $10^1$ $63.0$ $906*$ $1091$ $83.0$ $-37.1$ $16.1$ $18.5$ $86.9$ $-31.7$ Praomys natalensis $10^1$ $63.0$ $906*$ $1091$ $83.0$ $-37.1$ $16.1$ $18.5$ $86.9$ $-31.7$ Malacomys longipes $9^1$ $98$ $1825*$ $1425$ $1228.1$ $-2.9$ $26.9$ $21.2$ $126.6$ $-0.5$ Lophuromys sikapusi $5$ $63.5$ $1200$ $1097$ $1094$ $-17.1$ $18.5$ $86.9$ $-31.7$ Acomys dimidiatus $28^6$ $50.5$ $884$ $955$ $92.5$ $-29.9$ $26.9$ $21.2$ $126.6$ $-0.5$ Acomys dimidiatus $28^6$ $50.5$ $884$ $955$ $92.5$ $-29.9$ $26.9$ $21.2$ $126.6$ $-0.5$ Malk constrained inture $60.0$ $-4$ data of 2 individuals are from Weller (1896), 3 from Weller constrained (1903), 6 from Hradi (1905), and 298 from Nord (1965), $-6$ all $10750, -6$ allM KRETSCHMANN (1966): animals are from Underlined $10721, 220$ from Goldbecker (1972), and 298 from Nord (1975), $-6$ all	-	5	7.7	288	307	93.7	-29.0					
Kattus norvegicus         354°         291         2270         2746         82.7         -37.3           Fattus norvegicus         5²         (291)         2248*         2746         81.9         -37.9         28.0         29.8         94.0         -26.1           Praomys natalensis         10 <sup>1</sup> 63.0         906*         1091         83.0         -37.3         28.0         29.8         94.0         -26.1           Malacomys natalensis         10 <sup>1</sup> 63.0         906*         1091         83.0         -37.1         16.1         18.5         86.9         -31.7           Malacomys longipes         9 <sup>1</sup> 98         1825*         1425         128.1         -         22.9         26.9         21.2         126.6         -         0.5           Lophuromys sikapusi         5         63.5         1200         1097         109.4         -17.1         16.1         18.5         -         0.5           Acomys dimidiatus         28 <sup>6</sup> 50.5         884         95.5         92.5         -29.9	Kattus norvegicus $354^{\circ}$ $291$ $2270$ $2746$ $82.7$ $-37.3$ $5^{\circ}$ $(291)$ $2248^{\circ}$ $2746$ $81.9$ $-37.9$ $28.0$ $29.8$ $94.0$ $-26.1$ $359$ $(291)$ $2248^{\circ}$ $2746$ $81.9$ $-37.9$ $28.0$ $29.8$ $94.0$ $-26.1$ $7raomys natalensis10^{1}63.0906^{\circ}109183.0-37.116.118.586.9-31.7Malacomys longipes9^{1}981825^{\circ}1425128.1-2.926.921.2126.6-0.5Acomys sikapusi563.512001097109.4-17.116.118.586.9-31.7Acomys dimidiatus28^{\circ}50.588495592.5-29.926.921.2126.6-0.5Acomys dimidiatus28^{\circ}50.588495592.5-29.926.921.2126.6-0.560.-4 data of 2 individuals are from Weber (1896), 3 from Welcerken and Brandr (1903), 6 from Hradlerken, (1905), and 298 from Nord (1963).-6 all60.-4 data of 2 individuals are from Donalder laboratory conditions1972, 22 from Gold Bold Berken (1972), and 6 from Kruska (1975), -6 all60.-6 divide laboratory conditions1972, 22 from Gold Bold Berken (1972), and 6 from Kruska (1975), -6 all$		81	10.4	327*	368	88.8	-32.7	10.4	10.6	98.1	-22.9	32.9
52       (291)       2248*       2746       81.9       -37.9       28.0       29.8       94.0       -26.1         Praomys natalensis       359       (291)       2270 <sup>+</sup> 2746       82.7       -37.3       28.0       29.8       94.0       -26.1         Praomys natalensis       10 <sup>1</sup> 63.0       906*       1091       83.0       -37.1       16.1       18.5       86.9       -31.7         Malacomys longipes       9 <sup>1</sup> 98       1825*       1425       128.1       -       22.9       26.9       21.2       126.6       -       0.5         Lophuromys sikapusi       5       63.5       1200       1094       -17.1       16.1       18.5       -       0.5         Acomys dimidiatus       28 <sup>6</sup> 50.5       884       955       92.5       -       29.9	$5^2$ (291) $2248^*$ $2746$ $81.9$ $-37.9$ $28.0$ $29.8$ $94.0$ $-26.1$ $359$ (291) $2270^+$ $2746$ $82.7$ $-37.3$ $28.0$ $29.8$ $94.0$ $-26.1$ $7aomys natalensis$ $10^1$ $63.0$ $906^*$ $1091$ $83.0$ $-37.1$ $16.1$ $18.5$ $86.9$ $-31.7$ $Malacomys longipes$ $9^1$ $98$ $1825^*$ $1425$ $128.1$ $-2.9$ $26.9$ $21.2$ $126.6$ $-0.5$ $Acomys sikapusi$ $5$ $63.5$ $1200$ $1097$ $109.4$ $-17.1$ $16.1$ $18.5$ $86.9$ $-31.7$ $Acomys dimidiatus$ $28^6$ $50.5$ $884$ $955$ $92.5$ $-29.9$ $26.9$ $21.2$ $126.6$ $-0.5$ $Acomys dimidiatus$ $28^6$ $50.5$ $884$ $955$ $92.5$ $-29.9$ $26.9$ $21.2$ $126.6$ $-0.5$ $60.$ $-4$ data of 2 individuals are from Weberk (1896), 3 from Welcken berg Museum, Frankfurt. $-3$ data of 241 individuals are from $60.$ $-4$ data of 2 individuals are from Donaldon and Haral (1911), 50 from Ebincerk (1903), 6 from Hkdderk (1905), and 298 from Nord (1963). $-6$ all $m$ KRESCHMANN (1966): animals are bred under laboratory conditions $202, 225, 226, 93$ $602, 92, 93, 600$ $-602, -602, -602, -202, 93$		3545	291	2270	2746	82.7	-37.3					
Praomys natalensis         359         (291)         2270 <sup>+</sup> 2746         82.7         -37.3           Praomys natalensis         10 <sup>1</sup> 63.0         906*         1091         83.0         -37.1         16.1         18.5         86.9         -31.7           Malacomys longipes         9 <sup>1</sup> 98         1825*         1425         128.1         -         2.9         26.9         21.2         126.6         -         0.5           Lophuromys sikapusi         5         63.5         1200         1097         109.4         -         17.1         126.6         -         0.5           Acomys dimidiatus         28 <sup>6</sup> 50.5         884         955         92.5         -         29.9	Praomys natalensis         359         (291)         2270 <sup>+</sup> 2746         82.7         -37.3           Praomys natalensis         10 <sup>1</sup> 63.0         906*         1091         83.0         -37.1         16.1         18.5         86.9         -31.7           Malacomys longipes         9 <sup>1</sup> 98         1825*         1425         128.1         - 2.9         26.9         21.2         126.6         - 0.5           Lopburomys sikapusi         5         63.5         1200         1097         1094         -17.1         18.5         86.9         -31.7           Acomys dimidiatus         28 <sup>6</sup> 50.5         884         955         92.5         -29.9         26.9         21.2         126.6         - 0.5           Acomys dimidiatus         28 <sup>6</sup> 50.5         884         955         92.5         -29.9         26.9         21.2         126.6         - 0.5           Acomys dimidiatus         28 <sup>6</sup> 50.5         884         955         92.5         -29.9         26.9         21.2         126.6         - 0.5           60 <sup>4</sup> data of 2 individuals are from Weenen für Naturkunde, Stuttgart <sup>2</sup> skulls from Stath Naseum, Frankfurt <sup>3</sup> data of 241 individuals are from (60) <sup>4</sup> data of 2 individuals are		52	(291)	2248*	2746	81.9	-37.9	28.0	29.8	94.0	-26.1	12.9
Praomys natalensis         10 <sup>1</sup> 63.0         906*         1091         83.0         -37.1         16.1         18.5         86.9         -31.7           Malacomys longipes         9 <sup>1</sup> 98         1825*         1425         128.1         -         2.9         26.9         21.2         126.6         -         0.5           Lophuromys sikapusi         5         63.5         1200         1094         -17.1         126.6         -         0.5           Acomys dimidiatus         28 <sup>6</sup> 50.5         884         955         92.5         -         29.9	Praomys natalensis         10 <sup>1</sup> 63.0         906*         1091         83.0         -37.1         16.1         18.5         86.9         -31.7           Malacomys natalensis         9 <sup>1</sup> 98         1825*         1425         128.1         -2.9         26.9         21.2         126.6         -0.5           Lopburomys sikapusi         5         63.5         1200         1097         1094         -17.1         26.9         21.2         126.6         -0.5           Acomys dimidiatus         5         63.5         1200         1097         1094         -17.1         2.9         26.9         21.2         126.6         -0.5           Acomys dimidiatus         28 <sup>6</sup> 50.5         884         955         92.5         -29.9         26.9         21.2         126.6         -0.5           Acomys dimidiatus         28 <sup>6</sup> 50.5         884         955         92.5         -29.9         36.9         54.1         individuals are from           60) <sup>4</sup> data of 2 individuals are from Weber (1896), 3 from Welcerker and BraNDT (1903), 6 from HraDLICKA (1905), and 298 from NORD (1965) 6 all         1066.1         -60.5         -6.1         -6.2         -6.2         -6.2         -6.2         -6.2         -6.2 <td></td> <td>359</td> <td>(291)</td> <td>2270+</td> <td>2746</td> <td>82.7</td> <td>-37.3</td> <td></td> <td></td> <td></td> <td></td> <td></td>		359	(291)	2270+	2746	82.7	-37.3					
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Lophuromys sikapusi 5 63.5 1200 1097 109.4 –17.1 Acomys dimidiatus 28 <sup>6</sup> 50.5 884 955 92.5 –29.9	Lophuromys sikapusi563.512001097109.4-17.1Acomys dimidiatus28650.588495592.5-29.9sulls from Staatliches Museum für Naturkunde, Stuttgart 2 skulls from Senckenberg Museum, Frankfurt 3 data of 241 individuals are from60) 4 data of 2 individuals are from WEBER (1896), 3 from WELCKER and BRANDT (1903), 6 from HRDLICKA (1905), and 298 from NORD (1963) 6 allm KRETSCHMANN (1966): animals are bred under laboratory conditions		91	98	1825*	1425	128.1	- 2.9	26.9	21.2	126.6	- 0.5	15.3
28 <sup>6</sup> 50.5 884 955 92.5	18 Acomys dimidiatus 28 <sup>6</sup> 50.5 884 955 92.5 -29.9 <sup>1</sup> skulls from Staatliches Museum für Naturkunde, Stuttgart <sup>2</sup> skulls from Senckenberg Museum, Frankfurt <sup>3</sup> data of 241 individuals are from KLEMMT (1960) <sup>4</sup> data of 2 individuals are from WELCKER and BRANDT (1903), 6 from HRDLICKA (1905), and 298 from NORD (1963) <sup>5</sup> data of 266 individuals are from DONALDSON and HATAI (1911), 50 from EBINGER (1972), 22 from GOLDBECKER (1972), and 6 from KRUSKA (1975) <sup>6</sup> all data are from KRETSCHMANN (1966): animals are head under laborations.		5	63.5	1200	1097	109.4	-17.1					
	<sup>1</sup> skulls from Staatliches Museum für Naturkunde, Stuttgart <sup>2</sup> skulls from Senckenberg Museum, Frankfurt <sup>3</sup> data of 241 individuals are from KLEMMT (1960) <sup>4</sup> data of 2 individuals are from WEBER (1896), 3 from WELCKER and BRANDT (1903), 6 from HRDLICKA (1905), and 298 from NORD (1963) <sup>5</sup> data of 266 individuals are from DONALDSON and HATAI (1911), 50 from EBINGER (1972), 22 from GOLDBECKER (1972), and 6 from KRUSKA (1975) <sup>6</sup> all data are from KRETSCHMANN (1966): animals are head under laboratory conditions.	18 Acomys dimidiatus	286	50.5	884	955	92.5	-29.9					
		266 individuals are from DON from KRETSCHMANN (1966): ar	IALDSON an	hred under	911), 50 fro	om EBINGER	(1972), 22	from Gold	BECKER (19.	72), and 6 fro	m KRUSKA	A (1975). – <sup>6</sup> al	l data are

# Results

# Cranial capacity and/or brain weight

When the three terrestrial species of approximately the same body weight as Colomys are compared with Colomys there is a deficit in the cranial capacity of -16.2 % in Hybomys, -26.6 % in Lemniscomys and -34.0 % in Praomys (Table 1). Since, however, the average body weights in Hybomys and Lemniscomys are somewhat lower (-2.4 % and -8.1 %) and in Praomys somewhat higher (+8.2 %) a regression line analysis is appropriate, and based on it, an allometric comparison. To get a stable reference line it is necessary to include more (and especially smaller and larger) species of Muridae into the comparison. Such a broader basis would not only stabilize the slope of the regression line, but would also give information about the relative position of the four species under consideration and especially of Colomys within the Muridae. Firstly, we plotted log brain weights against log body weights of 12 species of Muridae from which we have data (laboratory mice and rats excluded). The calculated regression line has the formula:

 $\log \text{ brain weight} = 1.998 + 0.567 \cdot \log \text{ body weight}$ 

The coefficient of correlation is 0.987.

Secondly, we plotted log *cranial capacities* (CrC) of the 12 species (so far measured) against log body weights. The calculated regression line has the formula:

 $\log \text{ cranial capacity} = 1.971 + 0.585 \cdot \log \text{ body weight}$ 

The coefficient of correlation is 0.968.

Finally we combined both data sets by multiplying the CrC-values with 1.036 (specific

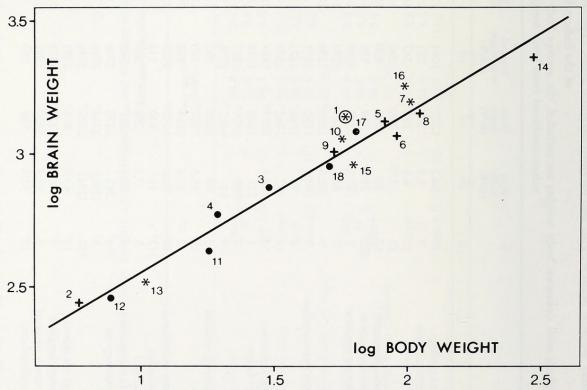


Fig. 1. Plot of log body weight and log brain weight for 18 species of Muridae. The regression line has the formula log brain weight = 1.953 + 0.603 · log body weight. The coefficient of correlation is 0.975.
 \* = species with brain weights converted from cranial capacities; (B) = Colomys goslingi; + = species with brain weights combined from measured brain weights and converted cranial capacities. (Numbers as in Table 2)

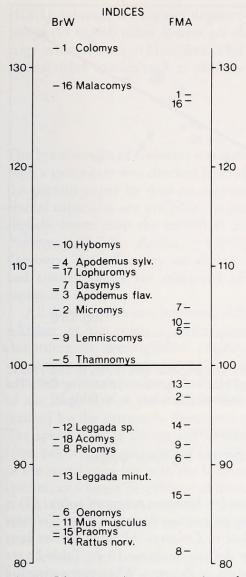


Fig. 2. Diagrammatic representation of the encephalization indices (EI) of 18 murid species (left hand scale) and foramen magnum indices (FI) of 12 murid species (right hand scale). The indices are percentage deviations from the regression lines, all points of which represent 100 %. (Numbers as in Table 2) gravity of the brain) to convert them into brain weights. Brain weights obtained in this way correspond well with the actual brain weights, as was found by STEPHAN et al. (1981) for 83 species of Chiroptera and by us in this study for 6 species of Muridae from which we have both brain weights and cranial capacities (+ in column 3 of Table 2 and in Fig. 1). However, this correlation between brain weight and cranial capacity may be confined to the relatively small-sized animals (e.g. bats and murids) and may not be valid for large species with large brains (e.g. ungulates). The regression line resulting from all 18 species has the formula:

log brain weight =  $1.953 + 0.603 \cdot \log body$ weight

The coefficient of correlation is 0.975.

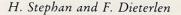
All three regression lines are relatively similar both in slope and y-intercept. For the following analyses we have used the common regression line of the combined material (Fig. 1). For the following comparisons this line is given a value of 100. The relative distances of the various species from this line (= encephalization indices, EI; see column 5 in Table 2 and Fig. 2) and their percentage deviation from *Colomys* (column 6 in Table 2) are given for all 18 species which were used to construct the common regression line of the Muridae.

Only Malacomys is close to Colomys. All other species have distinctly lower EI values than Colomys and the percentage deficits (column 6 in Table 2) are distributed between -15.0 % in Hybomys and -37.3 % in Rattus. When comparing the deficits of Hybomys, Lemniscomys and Praomys with those of the direct comparison of the cranial capacities (see above) they are in Hybomys -15.0 % (versus -16.2 %), in Lemniscomys -22.2 % (versus -26.6 %), and in Praomys -37.3 % (versus -34.0 %). The differences are due to the differences in the body weights between

the species and would not exist if all species had exactly the same body weights. The differences are largest in *Praomys* and *Lemniscomys*, where the average body weights are 8.2 % higher and 8.1 % lower than that of *Colomys* (see Table 1).

### Foramen magnum area

When the terrestrial species of about the same body weight as Colomys are compared with Colomys there is a deficit in the foramen magnum area (FMA) of -18.7 % in Hybomys, -29.6 % in Lemniscomys and -30.0 % in Praomys (Table 1). For the regression line analysis the four species were supplemented by eight species with clearly differing body weights (see column 7 in Table 2).



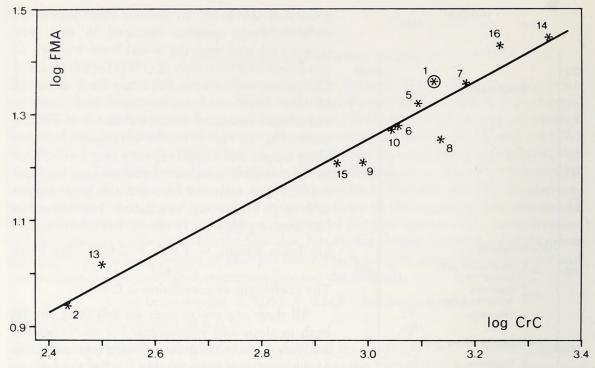


Fig. 3. Plot of log cranial capacity (CrC in mm<sup>3</sup>) and log foramen magnum area (FMA in mm<sup>2</sup>) for 12 species of Muridae. The regression line has the formula log FMA = -0.372 + 0.542 · log CrC. The coefficient of correlation is 0.976. ⊕ = Colomys goslingi. (Numbers as in Table 2)

The formula of the regression line of these 12 species is:

log foramen magnum area =  $0.710 + 0.310 \cdot \log body$  weight The coefficient of correlation is 0.921.

The relative distance of each species from this line (= foramen magnum index, FI) is given in column 9 of Table 2 and in Figure 2, and the percentage deviation from Colomys in column 10 of Table 2. Again only Malacomys is close to Colomys. All other species have lower FI values than Colomys and the percentage deficits (column 10 in Table 2) are distributed between -16.8 % in Dasymys and -36.1 % in Pelomys. When comparing the deficits of Hybomys, Lemniscomys and Praomys with those obtained from the direct FMA comparison (see above), they are in Hybomys -18.1 % (versus -18.7%), in Lemniscomys -27.7 % (versus -29.6 %) and in Praomys -31.7 % (versus -30.0 %). Again the differences are due to differences in the body weights.

In general, the distances of *Malacomys* and *Colomys* from the other species appear to be similar in the foramen magnum indices and in the encephalization indices (compare both parts of Figure 2). In order to investigate whether or not *Colomys* has an disproportionally large FMA in relation to its brain size, we plotted FMA against CrC in a double logarithmic scale and made a regression analysis (Fig. 3). The coefficient of correlation is 0.952. The slope is 0.542 or, when plotting FMA against  $CrC^{2/3}$  (thus equalizing the dimensions of both axes) it is 0.813. According to this slope, which is distinctly smaller than 1, the FMA in species with small brains is relatively larger than in those with large brains. The same results are obtained when FMA is compared with CrC size in each of the investigated species (column 11 in Table 2). The two species with the lowest body and brain size (*Micromys minutus* and *Leggada minutoides*) have the highest values (32.0 and 32.9 mm<sup>2</sup>/cm<sup>3</sup>) whereas the species with the largest body and brain size (*Rattus norvegicus*) has the lowest value (12.9 mm<sup>2</sup>/cm<sup>3</sup>).

When the regression line in Figure 3 is given a value of 100 the highest positive deviations are found in *Malacomys* (110.1), *Colomys* (110.0), and *Leggada minutoides* 

(108.1), whereas the highest negative deviations are found in *Pelomys* (84.4) and *Lemniscomys* (91.6). All other species are close to 100. Thus, in *Colomys*, the FMA is relatively large when related to brain size. This relatively large FMA is, however, not exceptional as several other species such as *Malacomys* and *Leggada* also have relatively large FMA's.

# Discussion

The brain weight of Colomys was indirectly inferred from cranial capacities. The validity of such a procedure was checked in 83 species of bats (STEPHAN et al. 1981) and is verified in the present paper by data on 6 species of Muridae, from which both brain weights and cranial capacities are available. In four of the six species the converted brain weights are slightly lower than the measured ones (*Thamnomys*, -4.9 %; *Lemniscomys*, -4.1 %; *Pelomys*, -3.7 %; *Rattus*, -1.0 %), whereas in the other two (*Micromys*, +5.6 %; *Oenomys*, +1.4 %) they are slightly higher. As in the 83 bat species, the 6 murid species had similar values for measured brain weights and for those converted from cranial capacities.

All these species are, however, either aerial or purely terrestrial and the question arises, whether or not such a direct correspondence also exists for water adapted forms. According to investigations on *Potamogale velox* the conversion factor from cranial capacity to brain weight is 1.113 instead of 1.036 (specific gravity of the brain) as found in bats and terrestrial rodents. In *Potamogale* this difference is expected to be the consequence of the large size of the medulla oblongata and of the proximal parts of the spinal cord (caused by the extremely developed spinal trigeminal nucleus; STEPHAN and SPATZ 1962). The spinal cord is always cut so that the part attached to the brain forms a square (seen from below). The extracranial caudal parts of the medulla oblongata and the proximal parts of the spinal cord left with the brain are in *Potamogale*, and may be in other water adapted species, of a larger percentage of the total brain than in terrestrial and aerial species. Thus, cranial capacity measurements of water adapted species may underestimate brain size since relatively larger parts of the total brain (as recorded by brain weight) may be outside of the skull.

According to our investigations on Insectivora the adaptation to predatory life in limnetic ecosystems is always accompanied by an enlargement of the medulla oblongata. Therefore, it can be expected, that *Colomys* also has a large medulla oblongata. The results of our FMA measurements are compatible with such an expectation, but not conclusive. A final decision only can be obtained from comparative investigations on the brain composition.

If we accept a relatively large medulla oblongata in *Colomys*, it can be expected, that in *Colomys* (1) the brain weight is larger than that resulting from a conversion factor of 1.036, and (2) the EI is somewhat higher than given in Table 2. When the conversion factor of *Potamogale*  $(1.113; = 1.036 \cdot 1.074)$  is used, the brain weight of *Colomys* would be 1474 mg (1372  $\cdot$  1.074) instead of 1372 mg as given in Table 2, and the EI 141.7 instead of 131.9. However, *Potamogale* seems to be more strongly adapted to water than is *Colomys* and, therefore, we expect the average brain weight of *Colomys* to be anywhere between 1372 and 1474 mg, and the EI between 131.9 and 141.7.

The similarly high position of *Malacomys* both in cranial capacity and foramen magnum size needs further attention. It is of interest that *Malacomys* also is found near waters and in swamps (WALKER 1964) and its diet is at least in part animal food. "Termites, crickets, slugs, snails, caterpillars, crabs and a toad are recorded animal foods" (KINGDON 1974). However, according to DIETERLEN *Malacomys* may be found also far away from water, and its hunting strategies in water are clearly different from those of *Colomys*. Not the vibrissae but the hands seem to be used by *Malacomys* in detecting prey in shallow water.

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With reference to these differences a comparative investigation of the composition of the brains (nearly equal in relative size, see Fig. 2) would be of great interest.

In conclusion, there are good indications that Colomys, which is a predator in limnetic ecosystems, has a larger brain and may have a larger medulla oblongata than do terrestrial species of Muridae. A final confirmation as well as an answer to the question, whether or not there is also a reduction of the olfactory structures, as is generally found in water adapted mammals, can only be obtained from investigations of brain components. Brain collection and quantitative investigations are in preparation.

### Acknowledgements

We would like to thank Dr. D. KOCK from the Senckenberg Museum, Frankfurt, for freely making available skulls of Micromys and Rattus. The valuable help of HELGA GROBECKER (photography) and HELMA LEHMANN (typing) is gratefully acknowledged. Thanks are due to JOHN NELSON, Melbourne, for checking the English text.

## Zusammenfassung

### Relative Hirngröße bei Muriden mit besonderer Berücksichtigung von Colomys goslingi

Die Hirngröße von 18 Arten von Muriden wurde teils direkt aus Hirngewichten (12 Arten) oder indirekt aus Messungen der Hirnschädelkapazität (12 Arten inkl. Colomys goslingi) erschlossen. 6 Arten waren mit Daten in beiden Gruppen vertreten. Bei Colomys (einer im Süßwasser jagenden Art) sind relative Hirngröße (Encephalisation) und Foramen magnum größer als bei terrestrischen Muriden gleichen Körpergewichts. Die Unterschiede ähneln jenen, wie man sie beim Vergleich an das Wasserleben angepaßter Insectivora mit terrestrischen Insectivora findet. Vergleichende Hirnuntersuchungen sind in Vorbereitung.

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# The influence of the sexual cycle on the olfactory sensitivity of wild female house mice (Mus musculus domesticus)

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Receipt of Ms. 10. 8. 1981

# Abstract

Studied was the influence of the sexual cycle of the olfactory sensitivity of wild female house mice (*Mus musculus domesticus*), using a two-choice training apparatus. Large fluctuations in olfactory sensitivity related to the sexual cycle were shown with the odourant geraniol ( $C_{10}H_{17}OH$ ). During proestrus the mice recognized a concentration of  $5 \times 10^8$  molecules geraniol/cm<sup>3</sup> air, while in metestrus they did not even respond to a concentration of  $5 \times 10^{11}$  molecules/cm<sup>3</sup>.

# Introduction

The sense of smell plays a major role in social behaviour of house mice. For example, the sexual cycle of female mice may be accelerated when exposed to a male odour (WHITTEN 1958). Olfactory contact with strange males can even lead to a depression of gravidity (BRUCE 1959, 1962; DOMINIC 1966).

While olfactory sensitivity in males is constant over a long period of time, the females' varies in relation to the sexual cycle (SCHMIDT 1979). The results from these electrophysiological experiments and behavioral studies with rats (PIETRAS and MOULTON; PHILLIPS 1974 and VALLOWE 1975) differ greatly. Thus, studies with trained wild mice need to be conducted to determine wheater these differences are a result of methods employed.

# Material and methods

Nine female mice, approximately four months old, whose parents were caught in the wild, were used in this experiment. A two-choice training apparatus consisting of transparent plexiglass half-tubes was used. The gaseous odour was pumped via a nozzle into one of the tunnels, while filtered air entered the other tube. The location of the olfactory stimulus was randomly distributed. Three experimental animals were trained to reject the odour while the other six were trained to choose the olfactory marked side. The animals were punished with an electric shock each time they responded incorrectly. Each correct response was rewarded with food (for details of this method, see SCHMIDT 1979). Vaginal smears were done every day after the mice completed 30 trials in order to determine the stage of the sexual cycle of each mouse (ALLEN 1922; ZONDECK and ASCHHEIM 1926).

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Stephan, Heinz and Dieterlen, Fritz. 1981. "Relative brain size in Muridae with special reference to Colomys gosHngi." *Zeitschrift für Säugetierkunde : im Auftrage der Deutschen Gesellschaft für Säugetierkunde e.V* 47, 38–47.

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