### H. Stephan and F. Dieterlen

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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### 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 hypoxanthus, 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

For CrC and FMA measurements skulls, which came from specimens close to the average body weight of the given species, were selected. Average body weights 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).

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# 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	c	Body weight	SE	M	Cranial capacity	SE	W	Foramen magnum area (FMA)	SE	м
			(mor)	مە	%	) mm	, mm	%	mm <sup>2</sup>	mm²	%
Colomys goslingi	шш	Ś	58.8	2.4	4.1	1299	40.6	3.1	23.1	1.1	4.9
0	Ħ	5	57.6	9.9	17.1	1349	67.1	5.0	22.9	1.7	7.3
mean	mm + ff	10	58.2	6.8	11.7	1324	58.5	4.4	23.0	1.3	5.8
Lemniscomys striatus	шш	5	58.0	3.2	5.5	1012	52.4	5.2	16.2	1.0	6.2
	Ħ	ŝ	49.0	5.2	10.6	932	46.6	5.0	16.2	0.7	4.4
mean	mm+ff	10	53.5	6.2	11.7	972	62.9	6.5	16.2	0.8	5.1
% deviation from Colomys			(-8.1%)			(-26.6%)			(-29.6%)		
Hybomys univittatus	шш	ŝ	54.4	5.6	10.2	1092	71.9	6.6	18.6	0.7	3.7
•	Ħ	S	59.2	4.6	7.8	1126	39.9	3.5	18.8	0.9	4.9
mean	mm + ff	10	56.8	5.4	9.6	1109	57.7	5.2	18.7	0.8	4.1
% deviation from Colomys			(-2.4 %)			(-16.2%)			(-18.7%)		
Praomys natalensis	mm	5	71.6	8.8	12.2	006	26.9	3.0	15.6	1.1	6.7
•	ff	5	54.4	4.6	8.4	848	71.9	8.5	16.6	1.5	9.2
mean	mm + ff	10	63.0	11.2	17.8	874	58.2	6.7	16.1	1.3	8.2
% deviation from Colomys			(+8.2%)			(-34.0%)			(-30.0%)		

Body weights, brain weights and foramen magnum areas, expected values on the regression lines, indices, and percentage deviation 7 ALAN I

in weights and totalicit magnum areas, expected values on the regres

When individuals with unknown body weights are included, the average body weights are set in brackets. \* brain weights converted from cranial capacities;  $^{+}$  values combined from brain weights and converted cranial capacities

Species	E	Body weight (BoW)	Brain weight (BrW)	Expected brain weight (FBrW)	BrW EBrW	Percentage deviation from	Foramen magnum area	Expected fora- men magnum	FMA EFMA	Percentage deviation from	FMA CrC
	(1)	8 (2)	mg (3)	(4)	(EI)	(6)	$(1 \text{ mm}^2)$ (7)	(EF.MA) mm <sup>2</sup> (8)	(FI) (9)	Colomys (10)	mm <sup>2</sup> /cm <sup>3</sup> (11)
1 Colomys goslingi	101	58.2	1372*	1041	131.9	0	23.0	18.1	127.2	c	17.4
2 Micromys minutus	ຕ່	5.5	267	251	106.4	-19.3			!	þ	L. / I
	10 <sup>2</sup>	6.1	282*	267	105.6	-19.9	8.7	9.0	96.8	-23.9	32.0
	13	5.95	278+	263	105.7	-19.9				Ì	2
3 Apodemus flavicollis	10	30	750	698	107.5	- 18.5					
4 Apodemus sylvaticus	$282^{3}$	19.4	590	536	110.0	- 16.6					
5 Thamnomys venustus		(82.5)	1350	1284	105.1	-20.3					
	81	82.5	$1284^{*}$	1284	100.0	-24.2	20.9	20.1	103.8	- 18 4	16.9
	6	(82.5)	$1291^{+}$	1284	100.5	-23.8				1.01	10.7
6 Oenomys hypoxanthus	ຕີ	(62)	1150	1371	83.9	-36.4					
	81	92	$1166^{*}$	1371	85.0	-35.6	18.9	20.8	90.7	- 28 7	16.8
	11	(92)	$1162^{+}$	1371	84.7	-35.8					10.01
7 Dasymys incomtus	8 <sup>1</sup>	102.5	1574*	1464	107.5	-18.5	22.8	21.5	105.8	- 16.8	15.0
8 Pelomys fallax	1	121	1460	1618	90.2	-31.6					
	8	110	1406*	1527	92.1	-30.2	17.9	22.0	81.3	-36.1	13.2
	6	111	$1412^{+}$	1536	91.9	-30.3					
9 Lemniscomys striatus	5	53	1050	983	106.8	-19.0					
	101	53.5	1007*	686	101.8	-22.8	16.2	17.6	92.0	- 27.7	16.7
	12	53.4	$1014^{+}$	988	102.6	-22.2				i	
10 Hybomys univitatus	101	56.8	1149*	1025	112.1	-15.0	18.7	17.9	104.2	- 18.1	16.9
11 Mus musculus	$312^{4}$	18	430	513	83.9	-36.4		1			
12 Leggada sp.	Ś	7.7	288	307	93.7	-29.0					
13 Leggada minutoides	81	10.4	327*	368	88.8	-32.7	10.4	10.6	98.1	-22.9	37.9
14 Rattus norvegicus	3545	291	2270	2746	82.7	-37.3					
	52	(291)	2248*	2746	81.9	-37.9	28.0	29.8	94.0	- 26.1	179
	359	(291)	2270+	2746	82.7	-37.3					
15 Praomys natalensis	101	63.0	*906	1091	83.0	-37.1	16.1	18.5	86.9	-317	18.4
16 Malacomys longipes	91	98	1825*	1425	128.1	- 2.9	26.9	21.2	126.6	2 U	15.3
17 Lophuromys sikapusi	5	63.5	1200	1097	109.4	-17.1				2	
18 Acomys dimidiatus	286	50.5	884	955	92.5	-29.9					
				:							
(1960) - <sup>4</sup> data of 2 individua	eum tür Na Is are from	Wreer (199	tuttgart	<sup>2</sup> skulls from	Senckenb	erg Museum,	Frankfurt.	$-^{3}$ data of 2	41 individ	uals are from	KLEMMT
266 individuals are from Dor	NALDSON ar	w евек (107 1d Натаг (1	911). 50 fro	welcker and m Fringer	DRANDT ( (1977) 77	1903), 6 trom	HRDLICKA	(1905), and	298 from N	VORD (1963)	<sup>2</sup> data of
from Kretschmann (1966);	animals are	bred under	laboratory	conditions.	((- // 1)		ECAER (177	7), allu 0 111		те(с/41) v	l data are

### H. Stephan and F. Dieterlen

### 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 cranial capacity =  $1.971 + 0.585 \cdot \log body$  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)

### Brain size in Muridae



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:

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

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. <sup>®</sup> = Colomys goslingi. (Numbers as in Table 2)

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

log foramen magnum area =  $0.710 + 0.310 \cdot \log \text{ body weight}$ 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* 

### Brain size in Muridae

45

(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.

### H. Stephan and F. Dieterlen

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.

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### 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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### 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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