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Size of Somatosensory Cortex and of Somatosensory Thalamic Nuclei of the Naturally Blind Mole Rat, *Spalax ehrenbergi*

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With 5 Figures and 1 Table

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Summary: The hypothesis that the somatosensory system in the naturally blind subterranean rodent *Spalax ehrenbergi* (= mole rat) is enlarged was tested by measuring the volume of somatosensory cortex and somatosensory thalamic nuclei (Nuclei ventrales posteromedialis and posterolateralis). Electrophysiology and tracing were used to identify and delineate these areas. On average the somatosensory cortex is 1.7 times larger and the thalamic nuclei are 1.3 times larger in the blind mole rat than in the sighted laboratory rat if different body weights are taken into consideration. This confirms the demands of a life underground where it seems touch would replace vision. The data reveal a remarkable brain plasticity among mammals under natural conditions.

Key words: Mole rat, somatosensory system, morphometry, electrophysiology, subterranean life

Introduction

It has been shown that the superspecies of mole rats (*Spalax ehrenbergi*), which lives underground, has extremely vestigial eyes (for review, see NEVO, 1991; COOPER et al., 1993a) and lacks a visual cortex (NECKER et al., 1992). Furthermore, there is only a minute lateral geniculate body and the VPM-VPL nuclei (Nuclei ventrales posteromedialis and posterolateralis) of the thalamus seem to be enlarged (REHKÄMPER et al., 1994). At the same time, the cortical representation of the somatosensory system covers part of the occipital cortex which serves vision in sighted animals (NECKER et al., 1992). It has been hypothesized that evolutionary adaptation in the mole rat has led to an expansion of the somatosensory system (REHKÄMPER et al., 1994); however this hypothesis must be substantiated by morphometric data. It is the aim of this paper to report data on the size of the somatosensory isocortex as well as on the size of the somatosensory thalamic nuclei.

A suitable reference system must be chosen in order to determine whether there has been an alteration in the size of a brain part. Thus, we compared the mole rat with the laboratory rat (*Rattus norvegicus*) using allometric methods and data from many mammalian species (see Material and Method). The rat, like the mole rat is a rodent, a sighted animal, and biologically it is more a generalist than the extremely specialized mole rat. At the same time the rat has been more thoroughly investigated, both morphologically and physiologically, than other rodent species.

Material and Methods

Electrophysiologically controlled mapping and marking of cortical areas of the somatosensory system

8 mole rats of the superspecies *Spalax ehrenbergi* (diploid number of chromosomes = 60) were used. They were caught in the wild near Anza, Israel, and maintained in the laboratory for several weeks. Under urethane anesthesia (1.5 g/kg i.p.) a tube was inserted into the trachea to prevent obstruction. The head was fixed to a stereotaxic instrument (rat head holder), and a unilateral craniectomy was done to expose all cortex from the midline as far laterally as possible. After removal of the dura, the cortex was covered with Ringer's agar to prevent desiccation. Body temperature was kept at about 37°C by a heating pad.

Single and multiple unit recordings were obtained with glass capillaries (impedance 1-4 MOhm) filled with pontamine

sky blue (2% in 0.5M Na-acetate, pH 7.2). Receptive fields were located and mapped using air puffs directed to the skin or by manipulating hairs with a small hook or wooden or glass rods.

The technique for mapping of the somatosensory cortex was similar to that described in a previous study (NECKER et al., 1992). Raster-like arrays of electrode tracks were made with 0.5-mm separation and 2-mm track length. Special attention was given to the boundaries of the somatosensory area. A series of tracks always began within the somatosensory representation and progressed towards the outside. If there was no response in two tracks, the position of the next to the last track was repenetrated to mark this position iontophoretically with pontamine sky blue (-2 μA, 10 min) at a depth of about 1 mm. This means that all markings were outside but within 0.5 mm of the somatosensory area (Fig. 1, 2). The rostral, medial and caudal boundaries were thoroughly mapped in five animals and partially mapped in three others. The most lateral boundary was usually not assessed because it lay on the lateral surface of the hemisphere which was difficult to reach with the vertical approach chosen in the present investigation.

Identification of thalamic areas of the somatosensory system

We identified the VPL-VPM-complex in the thalamus of the mole rat in the brains used for a previous publication (REHKÄMPER et al., 1994). There, we had injected fluorescent tracers into the electrophysiologically identified somatosensory areas of the cortex which served to identify thalamic nuclei posteromedialis (VPM, trigeminal somatosensory system of the head) and posterolateralis (VPL, spinal somatosensory system of the postcranial body).

Morphometry

– Cortex

Following the mapping and marking of the somatosensory cortex, the animals were sacrificed by an overdose of urethane. The brains were removed and weighed before being deep-frozen in isopentane. 14 μm sections (5 series) were cut on a cryostat, and the blue marks were located in a series of unstained sections. Parallel sections were stained with neutral red.

The locations of the marks (Fig. 1, 2) were transferred onto photomicrographs of 20 μm cresyl violet-stained sections of another eight paraffin embedded brains from animals that had not been used for electrophysiologically controlled mapping. The animals were weighed and afterwards perfused with Bodian's fixative. Immediately after perfusion the brains were carefully dissected and weighed without meninges. This brain weight has been shown to be equal to a fresh brain weight (WREE et al., 1992). Then, these brains were dehydrated, embedded in paraffin and serially sectioned. At least every 5th, 8th, and 9th section were mounted and parallel series were stained for cell bodies using MERKER's (1983) protocol, for rough ER using cresyl violet and for myelinated fibers using a modified GALLYAS (1979) technique. Such brains are suitable for architectonic studies (Fig. 3), and they are also preferred for volumetrical analysis, because they allow a more precise correction for shrinkage than cryostat sections do.

Matching between sections from experimental brains and paraffin brains was facilitated via the neutral red series (Fig. 1, 2). There are landmarks such as hippocampal structures, commissures, olfactory cortices and nuclei of the amygdala which allow one to find congruent levels in both series.

Before transferring the marks onto the photographs of the paraffin series, the cytoarchitectonic boundaries of the somatosensory cortex were drawn on the same photographs. The most valid identifying criterion for this structure is a strong development of the lamina 4 (internal granular layer), particularly a high packing density of small perikarya (Fig. 3). This corresponds to the characteristics of the somatosensory Par(ietal)-areas, including FL (forelimb) and HL (hindlimb) fields, in the atlas of the cortex of the laboratory rat brain (Fig. 4; ZILLES, 1985; ZILLES and WREE, 1995).

In every case, the cytoarchitectonic boundaries were within 0.5 mm of the blue marks. Because the cytoarchitectonic boundaries lay in the expected position relative to the electrophysiologically determined borders, the cytoarchitectonic boundaries were used in determining the somatosensory cortical volume. The satisfying congruence of electrophysiologically determined and cytoarchitectonically determined borderlines allow one to delineate confidently the lateral borderline only cytoarchitectonically.

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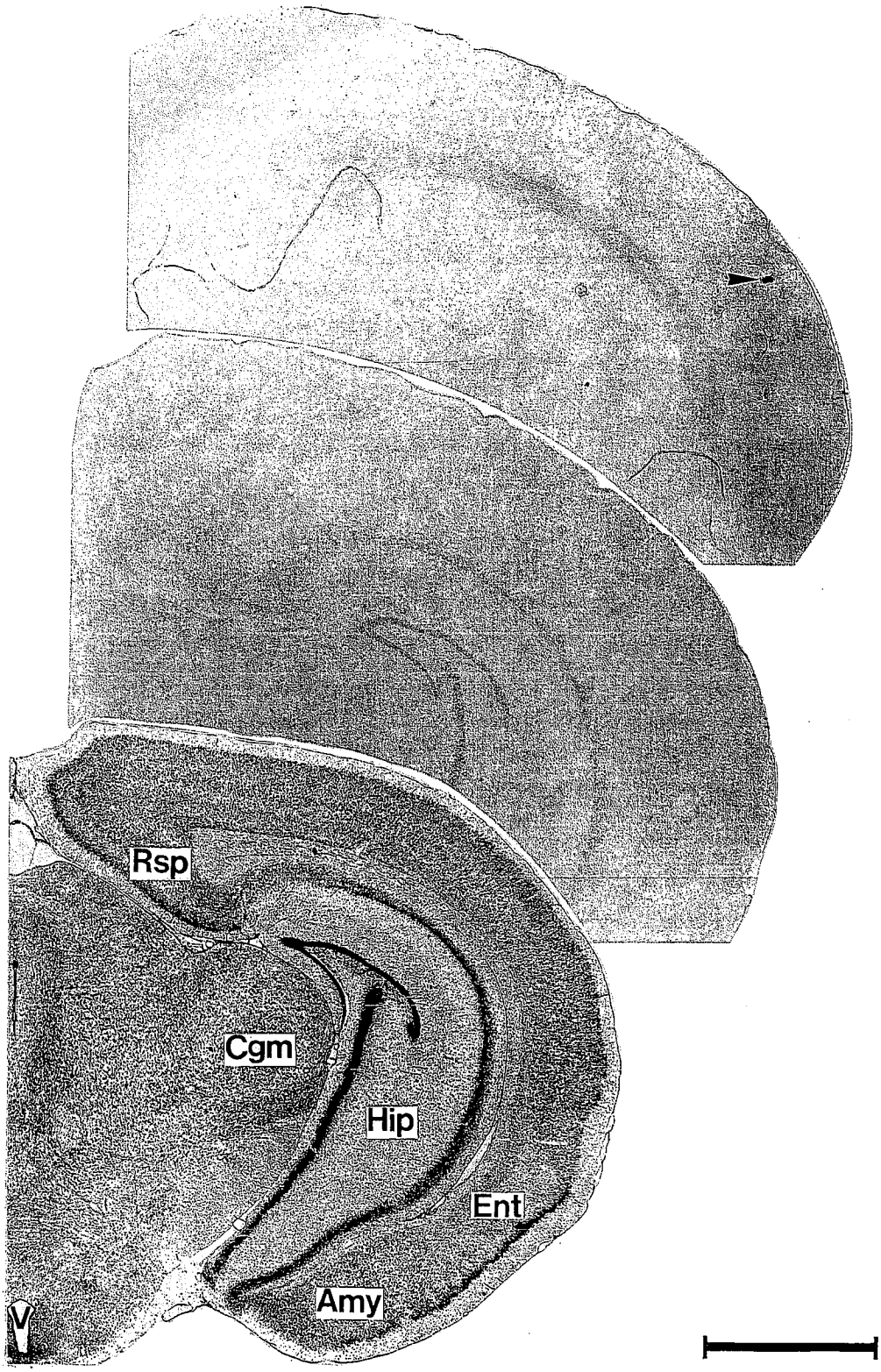
Fig. 1. Cross sections through the middle part of the somatosensory cortex in the mole rat (*Spalax ehrenbergi*) to illustrate the transfer of electrophysiologically defined borderlines to cytoarchitectonic material. Tap: Cryostat section, unstained, with a pontamine sky blue point mark (arrowhead) just lateral to the somatosensory cortex as identified cytoarchitectonically; middle: Section parallel to (tap), stained with neutral red; below: corresponding paraffin section stained for cell bodies. Scale bar = 2 mm

Figures on pages 50 and 51

Fig. 2. Cross sections through the posterior part of the somatosensory cortex in the mole rat to illustrate the transfer of electrophysiologically defined borderlines to cytoarchitectonic material. Tap: Cryostat section, unstained, with a pontamine sky blue point mark (arrowhead) just medial to the somatosensory cortex as identified cytoarchitectonically; middle: Section parallel to (tap), stained with neutral red; below: corresponding paraffin section stained for cell bodies. Scale bar = 2 mm

Fig. 3. Series of cross sections (paraffin series) through the rostral to caudal extent of the somatosensory cortex in the mole rat. The somatosensory cortex, as identified electrophysiologically, is characterized architectonically by a high density of small perikarya in lamina 4 (internal granular layer). Note that the occipital area seen in the most posterior position is covered by somatosensory cortex. Scale bar = 2 mm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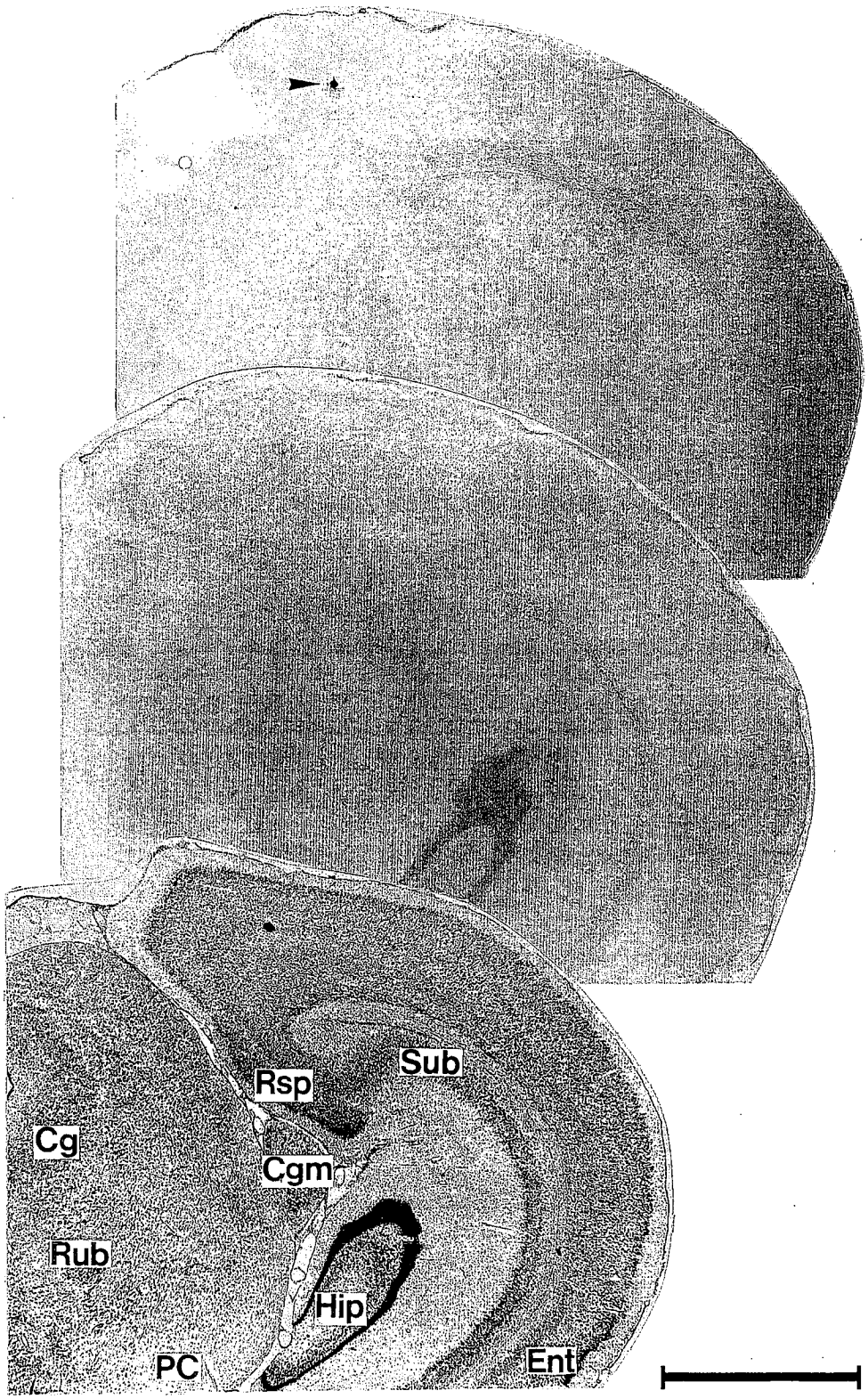
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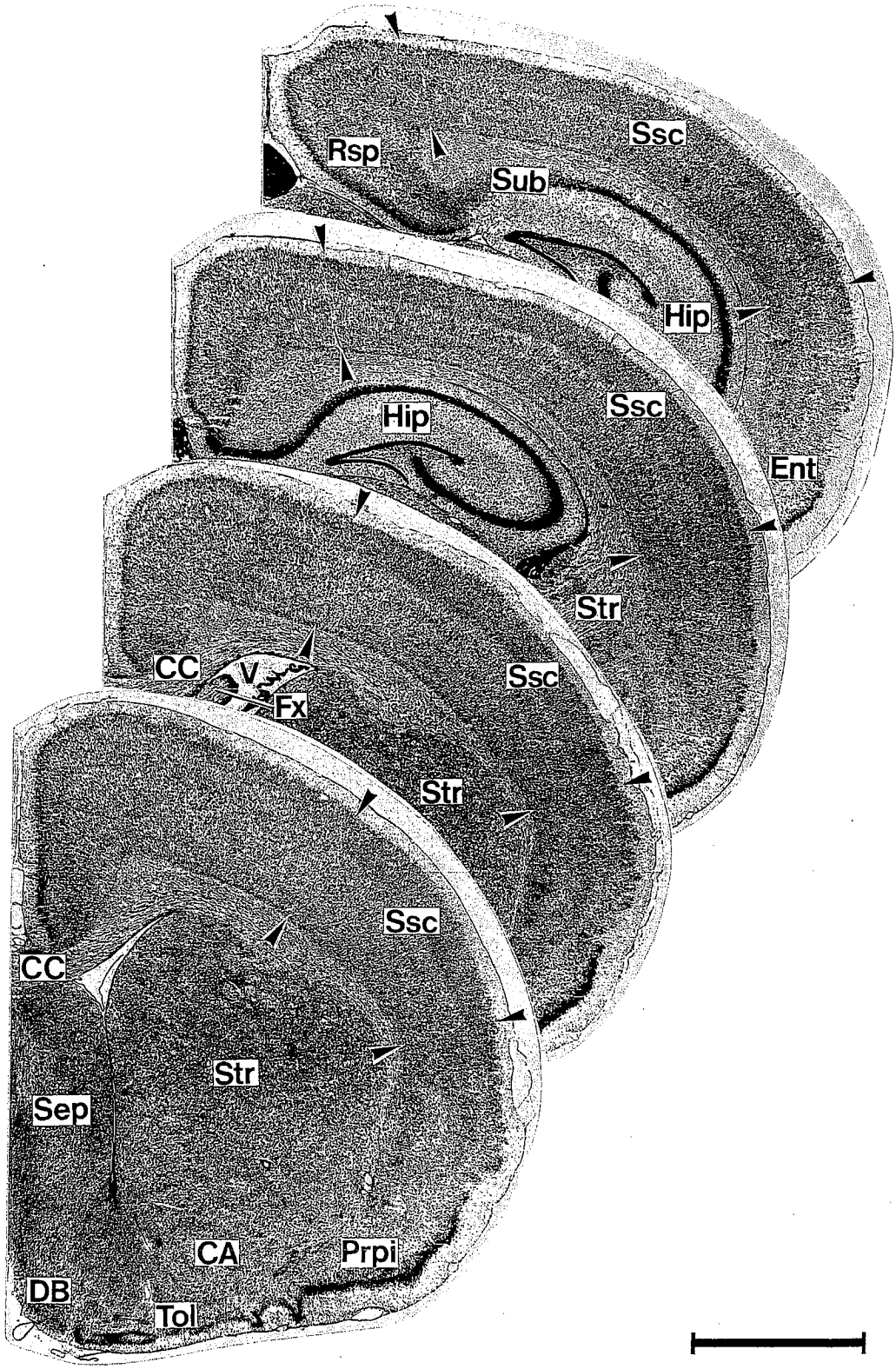
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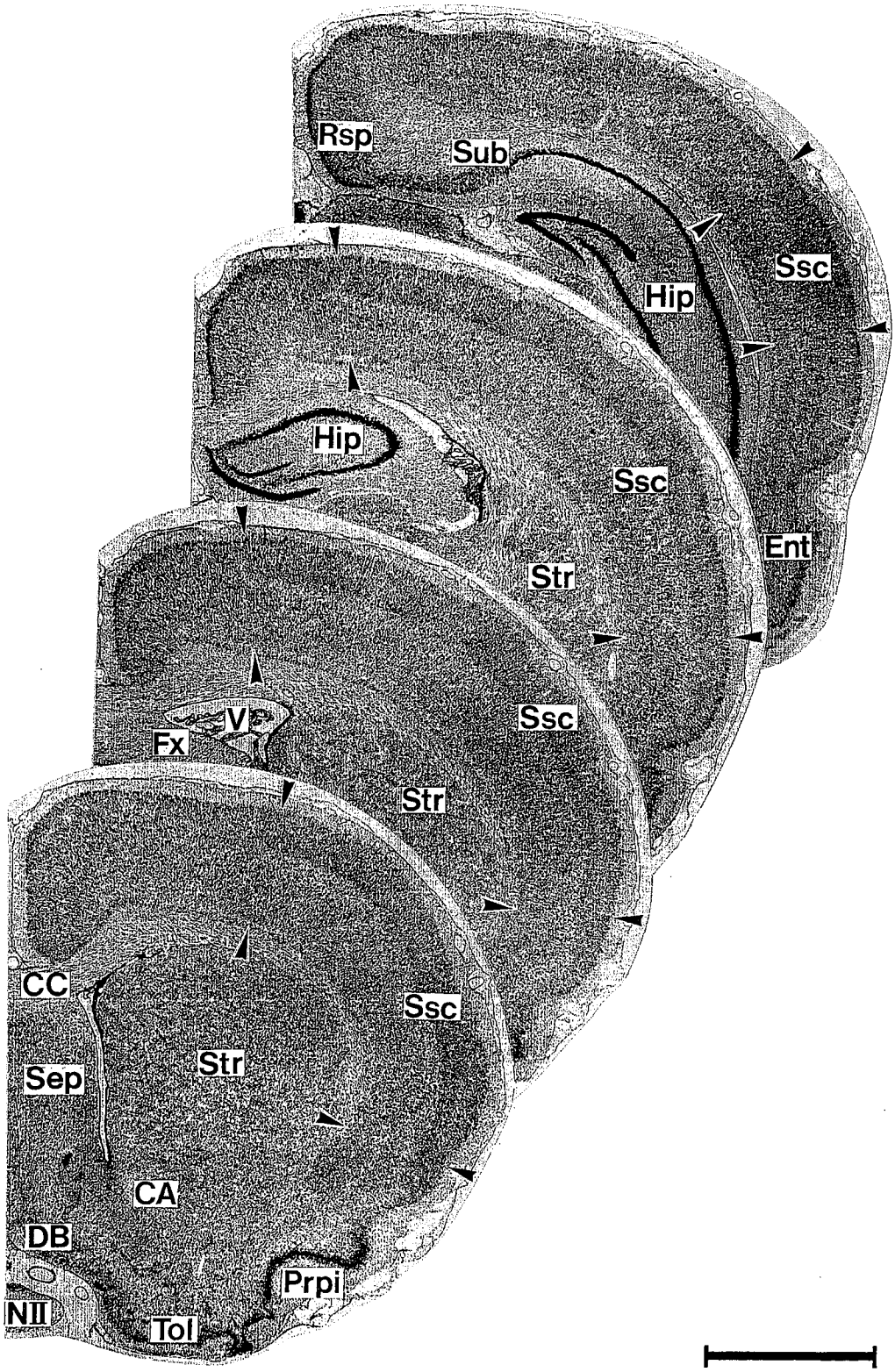
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– *Thalamus*

In a similar way, the information from the 5 mole rat brains in which the thalamic nuclei were marked via retrograde labelling was transferred to photographs of the paraffin series of seven mole rats. A detailed description of the architectonics of the VPM-VPL complex in the mole rat is given in our previous paper (REHKÄMPER et al., 1994).

Area Measurement and Volume Calculation

In the 8 paraffin brains mentioned above the borderlines of the somatosensory cortex as well as the VPM-VPL-complex were delineated on at least 7 sections spanning the entire area under consideration. This allows a calculation of the volume with an error less than 3% (ZILLES et al., 1982). The areas were measured on a graphics tablet with Sigmascan software (Jandel) and the volume was calculated using the formula

(1) Volume = area x section thickness x distance between sections

Such volumes must be corrected for shrinkage, which occurs during histological processing, particularly because of the use of dehydrating alcohol. The degree of shrinkage varies considerably. Even with use of a fixative based on formalin-alcohol such as Bodian, which causes less shrinkage, there is a variation from 29 to 42% (STEPHAN et al., 1991). This variation is not reduced by standardization of histological processing. Thus, we calculated a correction factor which is the quotient of the fresh brain volume divided by the brain volume obtained from the histological series. The latter has been determined by delineating at least 40 equidistant cross sections through the total brain, calculating the area as described above. The weight was converted to volume using the specific weight of brain tissue (=1.036 g/cmm, STEPHAN, 1967). Volumes corrected for shrinkage are thought to represent fresh volumes.

The comparative data for the laboratory rat were gained from seven specimens which were perfused through the left ventricle after their body weights were measured. The brains were dissected immediately, weighed without meninges and embedded in paraffin. They were serially cut (20 µm), and every 6th or 10th section was mounted and stained with cresyl violet (Fig. 3). Parallel series were stained for myelinated fibers with the Heidenhain-Woelcke technique. Again using photoprints, the borderlines of the Par and HL/FL areas of somatosensory cortex were delineated (ZILLES, 1985; ZILLES and WREE, 1995). For the delineation of the VPM-VPL nuclei the stereotaxic atlas of the rat (PAXINOS and WATSON, 1986) was used.

Allometry

Brain size and the size of parts of the brain must be corrected for body size if a comparative evaluation is attempted. To establish a regression line according to the formula

(2) $\log y = \log b + \alpha \cdot \log x$
(x= body weight, y= brain weight, b= y-intercept, α= slope)

data pairs on a wide range of species with different body sizes are needed. Unfortunately, there are little comparative data on the size of the somatosensory cortex; that means, there are no data on the size of the somatosensory cortex in a large variety of mammals covering a wide body weight range with which to establish α in equation (2). As the next best alternative we decided to use a slope α derived from a canonical analysis on the family or subfamily level, which describes the relation of isocortical size to body size in a large number of different mammalian species from the insectivores, primates, and bats. The rationale is that the somatosensory cortex is part of the isocortex, thus the regression of isocortical volume on body size might not be too different from that for somatosensory cortex on body size. This slope, $\alpha = 0.73$, is taken from STEPHAN et al. (1991). MANN et al. (1988) studied the brain/body relationship among myomorph rodents and argued that a slope of 0.7, which expresses the overall relation for mammals, might define the range of evolutionary pathways open to species, with each species following its own pathway from smaller to larger body size. In the same sense we used the above cited slope to describe isocortical size in relation to body size.

In a log-log system, the data of the mole rat and the laboratory rat were plotted, and the reference regression line of slope $\alpha=0.73$ was positioned to run through the average of the data in the laboratory rat (b= 0.386).

For the thalamic nuclei, a similar problem exists, and we used a slope $\alpha = 0.64$, which describes the size of the whole diencephalon in comparison of the body weight in a large variety of mammals (STEPHAN et al., 1991). If the axis runs through the average of the rat data, then the y-intercept is b= -0.489.

An index expressing the distance of individual data from a reference line that runs through the average of the laboratory rat data was calculated to describe the difference in size between the two species. First, the expected volumes on the reference line were calculated for every body weight according to the formula (for somatosensory cortex):

(3) log (volume somatosensory cortex) = 0.386 + 0.73 • log (body weight)

or the formula (for VPM/VPL complex):

(4) log (volume VPM/VPL complex) = -0.489 + 0.64 • log (body weight)

The index of a given specimen is the quotient of the actually measured volume to the expected volume, as calculated with formula (3) or (4).

All experiments were carried out according to the specifications of the German law for the prevention of the cruelty to animals.

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Fig. 4. Series of cross sections (paraffin series) through the rostral to caudal extent of the somatosensory cortex in the laboratory rat. The somatosensory cortex, as identified by a high density of small perikarya in lamina 4 (internal granular layer) in accordance with Zilles's map of the rat cortex (HL, FL, Par 1, Par 2 areas, ZILLES, 1985; ZILLES and WREE, 1995) is demarcated by arrowheads. Note that in the most posterior position the somatosensory cortex is only seen laterally. Scale bar = 2 mm

Results

Individual data of the size of the somatosensory cortex as well as thalamic nuclei are given in table 1. On average the somatosensory cortex in the mole rat measures 125.3 mm^3. By comparison, the somatosensory cortex of the mole rat is on average 1.7 times larger than that of the laboratory rat considering differences in body weight allometrically (Fig. 5). There is no overlap between the mole rat and laboratory rat data; thus no statistics are needed.

The VPM-VPL complex of the mole rat measures on average 8.6 mm^3 and is 1.3 times larger than in the laboratory rat, if body weight is taken into consideration. Applying a t-test to the individual indices of the mole rat and the laboratory rat, it can be shown that this difference is statistically significant on the 99 % level.

Discussion

Blindness and compensation by other sensory systems

The subterranean milieu is an extreme ecological niche that can only be used if extreme adaptations have taken place (NEVO, 1979, 1991). There is no question that darkness in the natural habitat of the mole rat limits the use of a visual system as an image analyzing system. Many subterranean mammals have minute eyes. The mole rat is outstanding in this respect, because its eyes are covered by skin. Only the African golden moles of the family Chrysochloridae or the subterranean marsupial *Notoryctes* exhibit similar extreme adaptations. In the case of the latter two species neurobiological data are very scarce (see STEPHAN et al., 1991), and, in fact, no data on the composition of the isocortex are available. For the mole rat we can say, in contrast, that there is no visual cortex and that the lateral geniculate is nearly absent (COOPER et al., 1993a, b; REHKÄMPER et al., 1994). These data are understandable if one considers function.

In the light of such an extreme reduction of one sensory system, one might reasonably ask whether other sensory systems are affected. The auditory system, which BRONCHTI and coworkers (BRONCHTI et al., 1989; HEIL et al., 1991; DORON and WOLLBERG, 1994) claim has taken over the neurons of the visual system demonstrates allometrically no volume increase for the cochlear nuclei and the inferior colliculi taken together (REHKÄMPER et al., 1995). Additionally there are some problems with this auditory hypothesis, which were discussed in detail in our previous paper (REHKÄMPER et al., 1994). The new finding of retrogradely labelled perikarya after injection into the inferior colliculus in a cortical area that we have shown to be somatosensory cortex (VCI, VCII of DORON and WOLLBERG, 1994) does not prove auditory function. There are several reports for different species of overlapping populations of cortical cells projecting to the inferior and superior colliculi (PAULA-BARBOSA and SOUSA-PINTO, 1973; CASSEDAY et al., 1979; KAWAMURA and KONNO, 1979; FRIES, 1984; MEREDITH and CLEMO, 1989; HOFSTETTER and EHRET, 1992). MASCETTI and STROZZI (1988) have shown electrophysiologically that even visual stimuli reach the inferior colliculus of the cat. In the rat, HERBERT et al. (1991) have demonstrated that efferent fibers originating from the somatosensory cortex reach the inferior colliculus. Additionally, the sensory integration of the inferior colliculus in somatosensory processing is well documented; the dorsal column nuclei send efferent fibers to this tectal region (RING and GANCHROW, 1983; BJORKELAND and BOIVIE, 1984; HARING, 1984; MASSOPUST et al., 1985; WIBERG and BLOMQVIST, 1984; WIBERG et al., 1987). Because of this bimodality and the electrophysiological characteristics COLEMAN and CLERICI (1987) have proposed that at least the external cortex of the inferior colliculus has a general sensory character. Thus, other than auditory systems should be discussed, e.g., the somatosensory system.

Evaluating data on the size of the somatosensory system

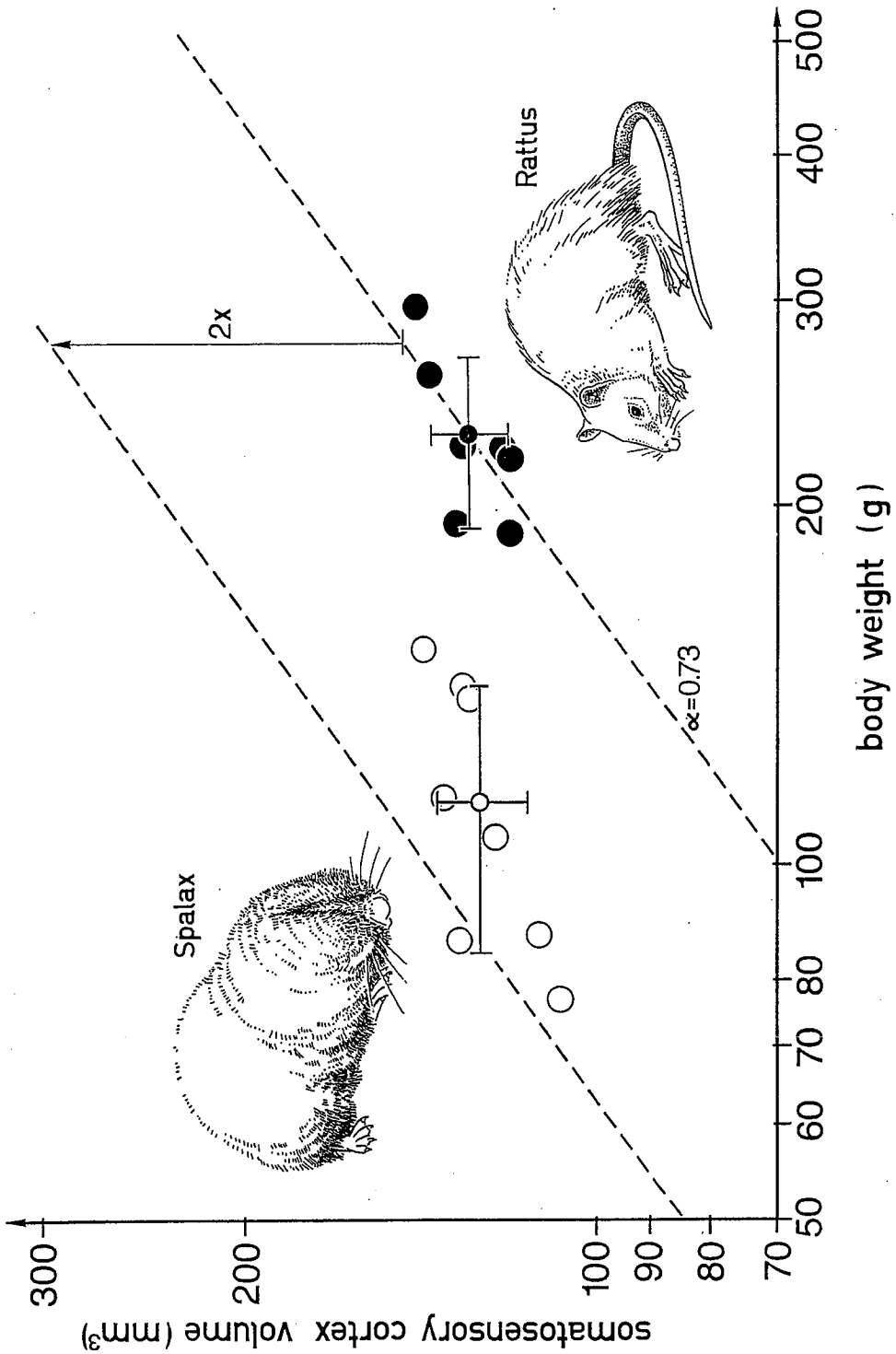
The absolute size of the somatosensory cortex in the mole rat is very similar to that in the laboratory rat. However, there is a general agreement that the differences in body weight must be considered, otherwise conclusions could be drawn which are incompatible with many biological data (for review see STEPHAN et al., 1986). The mole rat is less than half as large as the laboratory rat according to the material used in this study. Allometry can deal with this problem (for critical review see e.g., GOULD, 1975). The calculations used in this paper allow an evaluation of the size of parts of the brain independently of differences in body weight of the species under comparison. The brain of the mole rat is actually twice as large as would be expected for a laboratory rat of its body size (REHKÄMPER et al., 1995). This is not affected by the body weights of both species of this sample being slightly smaller than those reported by REHKÄMPER et al. (1995). According to our calculations the somatosensory system has under-

Table 1. Data on brain and body sizes as well as volumes and size indices of somatosensory cortex and the thalamic ventralis posteromedialis and posterolateralis nucleus complex (in mm^3) in the mole rat and the laboratory rat.

No.	Body Weight (in g)	Brain Weight (in mg)	Somato-sensory Cortex	Indices $\alpha = 0.73$ $b = 0.386$	VPM/ VPL complex	Indices $\alpha = 0.64$ $b = -0.489$
Spalax						
293	77.2	1948	107.051	184	7.478	143
294	141.4	2164	129.567	143	9.227	120
296	138.3	2141	127.726	144	8.445	111
377	86.7	2191	130.378	206		
380	87.6	1990	111.757	175	7.626	134
423	152.0	2028	139.995	147	9.844	122
424	114.0	1987	134.476	174	9.066	135
426	105.6	1920	121.516	166	8.203	128
mean (n = 8)	112.9	2046	125.308	167	8.556	128
SD	28.4	105	11.217	22	0.869	11
Rattus						
1793	224.1	1660	119.420	94	11.218	108
1794	219.5	1770	117.366	94	12.792	125
1801	225.4	1660	129.188	102	9.594	92
1802	259.3	1830	138.378	98	10.400	91
1807	190.1	1680	117.921	105	8.446	91
1814	193.9	1700	131.251	115	10.124	107
1832	298.0	2040	142.034	91	10.670	86
mean (n = 7)	230.0	1763	127.937	100	10.463	100
SD	37.7	137	10.041	8	1.353	14

gone a remarkable increase in the mole rat. The somatosensory area in the isocortex of the mole rat is 1.7 times larger than in the sighted laboratory rat. This is very close to the factor of encephalization of the mole rat (which is 2) compared to the laboratory rat (REHKÄMPER et al., 1995). Thus, the enlargement of the somatosensory system is one of the keys to understanding the relatively large brain of the mole rat. One might argue that the enlargement of the somatosensory area only reflects general brain enlargement without being of biological relevance for itself. Such an "isometry hypothesis" would neglect that not all data available support this argument. For example the absence of a visual cortex in the mole rat (REHKÄMPER et al., 1994) proves that not all areas of the brain necessarily follow isometrically the general enlargement (see also the data on the motor system as mentioned below).

The smaller index of the thalamic nuclei than in the somatosensory cortex might be explained by the fact that we measured only the VPM/VPL complex, not the posterior nucleus, which has also been shown to project to the somatosensory cortex (REHKÄMPER et al., 1994). It looks very large in architec-


somatosensory cortex volume (mm³)
300
200
100
90
80
70
50
60
70
80
100
200
300
400
500
body weight (g)
2x
α=0.73
Rattus
Splax

tonic series, however, because a sharp delineation is difficult we did not include it. On the other hand, it is possible that there is a greater increase in cortical processing than in thalamic processing or projection of sensory information into the cortex.

Somatosensory and motor system

Biologically, the size of the somatosensory system might be seen on the background of the large motor system. Allometrically, the motor cortex of the mole rat is 3.1 times as large as that of the laboratory rat (REHKÄMPER et al., 1995) and the motor nuclei of the trigeminal nerve approximately 3.5 times larger (REHKÄMPER et al., 1995). This points to superior motor activity, probably associated with digging and foraging behavior of this animal that is a teeth digger and eats roots and other subterranean plant parts. The enlargement of neck and chewing muscles can be seen in the same context. Specific motor activity is also used in intraspecific communication, where a series of quick head strokes against the tunnel roof produce low-frequency vibrations ("seismic communication", NEVO et al., 1991). All these motor activities are probably under proprioceptive control. Among mammals, the cortical representation areas of the proprioceptive system are closely associated with those of mechanoreception (MOUNTCASTLE, 1984; CHAPIN and LIN, 1990). Thus, our delineation of the somatosensory cortex probably also includes a proprioceptive representation.

Natural plasticity

KRUBITZER (1995) has reviewed cortical plasticity in different mammals and described a remarkable variability in the expansion of the somatosensory cortex, particularly when the somatosensory system is of outstanding biological importance. Our data are in line with these findings. However, two aspects should be underlined for the mole rat. First, the peculiar adaptation of the mole rat has nearly altered the "bauplan" of the isocortex. Amongst studied species, this one is characterized by a somatosensory cortex which occupies the occipital area of the isocortex and a VPM-VPL complex that reaches the surface of the thalamus. Under experimental conditions, similar changes have been seen (for review see KAAS, 1993; RAUSCHECKER, 1995), but, in the mole rat, they have developed under natural conditions without traumatic lesions.

Second, in this paper data for the somatosensory cortex of the mole rat have been given for the first time, and, using an allometric approach, the degree of alteration in the somatosensory cortex has been elucidated. We can say, for example, that the unusual large brain of the mole rat appears to be caused to a remarkable degree by an expansion of the somatosensory system together with the motor system. More such morphometric data for other species are needed in order to enlarge the basis of allometric comparison of somatosensory and motor systems.

Abbreviations

Amy	Corpus amygdaloideum
CA	Commissura anterior
CC	Corpus callosum
Cg	Griseum centrale
Cgm	Corpus geniculatum mediale
DB	Diagonal band of Broca
Ent	Regio entorhinalis
Fx	Fornix
Hip	Hippocampus retrocommissuralis
N II	Nervus opticus
PC	Pedunculus cerebri
Prpi	Regio praepiriformis
Rsp	Regio retrosplenialis
Rub	Nucleus ruber
Sep	Septum
Ssc	somatosensory cortex
Str	Striatum
Sub	Subiculum
Tol	Tuberculum olfactorium
V	Ventricel
VPL	Nucleus ventralis posterolateralis
VPM	Nucleus ventralis posteromedialis

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Fig. 5. The volume of the somatosensory cortex in the mole rat and the laboratory rat related to body weight in a log-log system. Large open (mole rat) and filled (laboratory rat) circles are individual data. Small circles indicate the average values, with bars indicating the standard deviations. The slope of $\alpha = 0.73$ is drawn as described in the text. Note that there is no overlap between the data points of the two species.

Molecular Evolution established by Florence and Theodore Baumritter of New York.

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