Brain atlas of the African mole-rat *Fukomys anselli*

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**Abstract**

African mole-rats are subterranean rodents that spend their whole life in underground burrow systems. They show a range of morphological and physiological adaptations to their ecotope, for instance severely reduced eyes and specialized somatosensory, olfactory, and auditory systems. These adaptations are also reflected in the accessory sensory pathways in the brain that process the input coming from the sensory organs. So far, a brain atlas was available only for the naked mole-rat (*Heterocephalus glaber*). The Ansell’s mole-rat (*Fukomys anselli*) has been the subject of many investigations in various disciplines (ethology, sensory physiology, and anatomy) including magnetic orientation. It is therefore surprising that an atlas of the brain of this species was not available so far. Here, we present a comprehensive atlas of the Ansell’s mole-rat brain based on Nissl and Klüver-Barrera stained sections. We identify and label 375 brain regions and discuss selected differences from the brain of the closely related naked mole-rat as well as from epigeic mammals (rat), with a particular focus on the auditory brainstem. This atlas can serve as a reference for future neuroanatomical investigations of subterranean mammals.

**KEYWORDS**

auditory system, magnetoreception, nervous system, neuroanatomy, Nissl, rodent, RRID: SCR_005910, RRID:SCR_014199, subterranean mammal

**1 | INTRODUCTION**

More than 250 rodent species spend their whole life underground in self-dug tunnel systems. With the exception of Antarctica and Australia, subterranean rodents can be found on all continents. African mole-rats (Bathyergidae) are a family of strictly subterranean rodents endemic to sub-Saharan Africa that comprises six genera of small to medium sized (40–2000 g) species. At least 18–29 species of African mole-rats are currently recognized (Monadjem, Taylor, Denys, & Cotterill, 2015; Wilson, Mittermeier, Ruff, Martínez-Vilalta, & Cavallini, 2016).

African mole-rats share a common phenotype that reflects the selective pressures of their underground habitat. It includes a cylindrical body shape, elastic skin, a short tail and short fur, reduced pinnae, and enlarged extrabuccal incisors (reviewed in Begall, Burda, & Schleich, 2007; cf. Figure 1). Physiologically, these animals show a high tolerance to hypoxic and hypercapnic conditions (Chung, Dzal, Seow, Milsom, & Pamenter, 2016; Larson & Park, 2009; Nevo, 1999; Park et al., 2017). Their sensory organs have also adapted to the dark and featureless underground environment (Burga, Bruns, & Müller, 1990). Eye size is much reduced and the visual acuity very low (Kott, Němec, Fremlová, Mazoch, & Šumbera, 2016; Němec et al., 2008; Peichl, Němec, & Burda, 2004). The visual capabilities are sufficient, however, for brightness discrimination (detection of opened burrows; Kott, Šumbera, & Němec, 2010; Němec, Čveková, Burda, Benada, & Peichl, 2007; Wegner, Begall, & Burda, 2006a), and they might help (at least in the laboratory) entrainment to the photoperiod (de Vries, Oosthuizen, Sichilima, & Bennett, 2008). Hearing is restricted to the low-frequency range which propagates best in underground tunnel systems (Gerhardt, Henning, Begall, & Malkemper, 2017; Lange et al., 2007). The somatosensory system is generally well-developed (Catania & Remple, 2002) and the animals detect seismic cues that are used for communication and orientation (Mason & Narins, 2010). Olfaction is also well developed and plays an important role in foraging and the recognition of conspecifics (Heth et al., 2002; Heth & Todrank, 2007). Furthermore, several species of African mole-rats...
have a magnetic sense, most likely to aid navigation in the dark (Burda, Marhold, Westenberger, Wiltschko, & Wiltschko, 1990; Malewski et al., 2018; Olivieriusová, Němec, Králová, & Sedláček, 2012).

Given the many physiological and sensory adaptations of African mole-rats, it is of interest to know how their brains differ from epigeic, that is, mostly surface-dwelling, rodent counterparts. Kruska and Steffen (2009) studied the gross anatomy and encephalization indices of brains of the genus Fukomys. Superficially, the brains look very much like other rodent brains and the encephalization index is similar to that of surface-dwelling rodents. Total neuron and glia cell numbers in African mole-rats conform to scaling rules established for other rodents (with the exception of the naked mole-rat, see below; Kverková et al., 2018). Immunohistochemical analysis of the cholinergic, putative catecholaminergic, and serotoninergic neuron systems of two mole-rat species (Cryptomys hottentotus pretoriae, Bathycypris sulii) by Bhagwandin, Fuxe, Bennett, and Manger (2008), concluded in line with former studies that their brains, in principle, exhibit the same complement of homologous nuclei as in other rodents. The central olfactory system is well-developed, the olfactory bulbs and olfactory allocortex are larger (relative to brain size) in mole-rats than in rats (Kruska & Steffen, 2009). The somatosensory cortex of the naked mole-rat is significantly enlarged, occupying most of the areas that are visual in epigeic rodents, with an over-representation of the incisural (Catania & Remple, 2002; Henry, Remple, O’Riain, & Catania, 2006). As a consequence, the visual cortex is small in bathyergid mole-rats and also the subcortical visual pathways show particularly strong deviations from those in other rodents. The optic nerve and optic chiasm are extremely thin (Kruska & Steffen, 2009; Němec et al., 2007). The central areas involved in visual processing, such as the lateral geniculate body and the superficial layers of the superior colliculus are significantly reduced in bathyergid mole-rats compared to epigeic rodents (Němec et al., 2008; Němec, Burda, & Peichl, 2004). Strong neuronal activation (c-fos labeling) in the retina, suprachiasmatic nucleus, lateral geniculate body, olivary pretectal nucleus, retrosplenial cortex, and visual cortex in animals exposed to light for 1 hr, however, demonstrated that the visual system is functional (Oelschlager, Nakamura, Herzog, & Burda, 2000). This has been confirmed in behavioral experiments (Kott et al., 2016; Wegner et al., 2006a). C-fos labeling has also provided seminal evidence for a mole-rat magnetic sense by showing that changing magnetic fields activate areas of the superior colliculus and the rodent navigation circuit (Burger et al., 2010; Němec, Altman, Marhold, Burda, & Oelschlager, 2001). The brains of African mole-rats are further interesting with respect to the complexity of sociality in these animals (Kverková et al., 2018). Since the social systems occurring in this rodent family span the full range from strictly solitary (i.e. only one individual inhabits a burrow system outside of the mating season) to eusocial, a unique platform to study the neural correlates of social behavior and brain evolution is provided. Expression patterns of oxytocin receptors, vasopressin and its receptors, corticotropin-releasing factors as well as markers of adult neurogenesis have been related to sociality, social ranks, and mating systems (Amrein et al., 2014; Coen et al., 2015; Kalamatianos et al., 2010; Peragine, Simpson, Mooney, Lovern, & Holmes, 2014; Rosen, De Vries, Goldman, Goldman, & Forger, 2007; Valesky, Burda, Kaufmann, & Oelschlager, 2012).

Given the number of neuroanatomical studies in different mole-rat species and their significance for the understanding of mammalian adaptation to the subterranean habitat it is astonishing that only a single anatomical atlas of a mole-rat brain was available until now (Xiao, Levitt, & Buffenstein, 2006). Previous investigators of mole-rat brains had to rely on the brain atlas of the naked mole-rat (Xiao et al., 2006) in combination with atlases of the laboratory mouse (Paxinos, 2013) and the laboratory rat (Paxinos & Watson, 2013; Swanson, 2004). While the naked mole-rat probably is the most popular and most intensively studied mole-rat species (Sherman, Jarvis, & Alexander, 2017), it shows several traits not shared by its closest relatives, such as an extreme litter size, furlessness and poikilothermy (Kock, Ingram, Frabotta, Honeycutt, & Burda, 2006). Indeed, this species is so distinct from other African mole-rats that it has recently been proposed to constitute its own rodent family, Heterocephalidae (Patterson & Upham, 2014). Furthermore, the brain of the naked mole-rat has been shown to differ from other African mole-rat brains and general rodent brain scaling rules in that it is relatively smaller and has fewer neurons than expected for a rodent of its body size (Kverková et al., 2018). It is therefore likely that the naked mole-rat brain is not representative for subterranean mammals. The extent to which the neuroanatomy of the naked mole-rat differs from that of other subterranean rodents has not been investigated mainly because studies on brain anatomy of other mole-rats are scarce.

About half of the African mole-rat species belong to the genus Fukomys. Within this genus, one of the most studied species is the Ansell’s mole-rat Fukomys anselli (previously called Cryptomys anselli, Kock et al., 2006). The Ansell’s mole-rat is a medium-sized (50–120 g) mole-rat endemic to Zambia that digs large and highly complex underground tunnel systems of up to 2.8 km length (Šklíba et al., 2012). It is eusocial and lives in small family groups of about 10–15 animals composed of a single breeding pair and its nonreproductive offspring (Patzenhauerová, Šklíba, Bryja, & Šumbera, 2013). The animals feed on plant tubers and roots and only rarely leave their burrow system (Scharff & Grütjen, 1997). With an average life expectancy of 7–8 years, the animals are extremely long-lived (with a thus far recorded maximum life span of nearly 20 years) for a rodent of their body size and they show a unique bimodal aging pattern with reproductive animals aging considerably slower than nonbreeders (Damann & Burda, 2006). The Ansell’s mole-rat has been studied for many decades as a paradigm for sensory and ecophysiological

**FIGURE 1**  Adult Ansell’s mole-rat (Fukomys anselli). Note the prominent rhinarium, vibrissae, and incisors as well as the severely reduced eyes and external ears (photo by Sarah Maria Wilms) [Color figure can be viewed at wileyonlinelibrary.com]
adaptations to the underground environment, the evolution of social systems, and animal navigation (reviewed in Begall et al., 2007). Notably, it was the first mammal for which a magnetic compass sense was convincingly proven and characterized (Burda, Marhold, et al., 1990; Burger et al., 2010; Marhold, Burda, Kreilos, & Wiltshcko, 1997; Marhold, Wiltshcko, & Burda, 1997; Némec et al., 2001; Thalau, Ritz, Burda, Wegner, & Wiltshcko, 2006; Wegner, Begall, & Burda, 2006b).

Here, we present a comprehensive atlas of the brain of *Fukomys anselli* based on Nissl and Klüver-Barrera stained sections. We identified and labeled 375 brain regions and discuss some similarities to and differences from those of other subterranean and epigeic rodents including the rat. This atlas can serve as a reference guide for future neuroanatomical and physiological studies of mole-rat brains.

## 2 | MATERIALS AND METHODS

This atlas is based on serial brain sections of altogether 17 individuals of Ansell's mole-rat. Table 1 gives an overview of the Ansell's mole-rat histological material used in this study. The animals were deeply anesthetized and then transcardially perfused with heparinized saline followed by fixation with 4% paraformaldehyde (PFA) in phosphate buffer. The perfused animals were decapitated and their brains carefully dissected and postfixed in PFA overnight. Paraffin sections (14 μm) and cryo-sections (60 μm) were prepared according to standard histological procedures (Némec et al., 2001).

The atlas plates display a selection of transverse (coronal) sections of 14 μm thickness at a regular spacing of 280 μm from two subadult individuals, C25 (female) and C26 (male, plate 381). In other words, every 20th section was stained with cresyl violet (Nissl), predominantly individuals, C25 (female) and C26 (male, plate 381). In other words, every 20th section was stained with cresyl violet (Nissl), predominantly including both somata and fiber tracts. In addition, three intact Ansell's mole-rat brains were used for macroscopic documentation and description (Figure 2). Nissl-stained serial brain sections of 24 individuals of adult Wistar and Sprague-Dawley rats were included for comparisons.

We decided to show paraffin sections because their histological quality is superior to that of cryo-sections. Tissue shrinkage, however, is higher in paraffin sections which must be kept in mind when taking absolute measurements from the atlas plates presented. The plates are not fitted into a stereotaxic framework because all the slides mainly served for identification and interpretation of many Ansell's mole-rat brain structures investigated in several publications, for example, on the magnetic orientation of these animals (Burger et al., 2010; Némec et al., 2001).

To prepare the atlas plates, the serial sections of the two Ansell's mole-rat individuals C25 and C26 were scanned at 200x magnification with a microscopic slide scanner (Leica Aperio AT Turbo). The sections were aligned and optimized for tones and brightness in Photoshop (CC2017, Adobe) before they were reduced to 15% of their original size for the final 300 dpi plates. The identification of brain regions in the Ansell's mole-rat was based on detailed comparisons to rat brain sections along with a rat brain atlas (Paxinos & Watson, 2013), a mouse brain atlas (Paxinos, 2013), and a naked mole-rat brain atlas (Xiao et al., 2006). Cortical areas were identified based on cytoarchitecture.

For labeling of the anatomical structures, the principle of Paxinos and co-workers (Paxinos, 2013; Paxinos & Watson, 2013) was used. Lowercase letters indicate fiber tracts, white matter, recesses, and ventricles, while uppercase letters indicate nuclei and cortex (gray

### TABLE 1  Available histological material from *Fukomys anselli*

| Individual (ID) | Sex   | Age     | Reproductive state     | Body mass | Brain mass | Sectional plane | Type of sections | Thickness of sections |
|-----------------|-------|---------|------------------------|-----------|------------|----------------|------------------|----------------------|
| C25             | Female | 34 weeks| Subadult, nonreproductive | 57 g      | Unknown    | Coronal        | Paraffin         | 14 μm                |
| C26             | Male   | 26 weeks| Subadult, nonreproductive | 52 g      | Unknown    | Coronal        | Paraffin         | 14 μm                |
| C9 CKA3-5       | Female | 16 weeks| Juvenile, nonreproductive | 26 g      | 0.80 g     | Coronal        | Cryo             | 60 μm                |
| C10 CKA3-2      | Male   | 7 years | Adult, reproductive     | 94 g      | 1.26 g     | Coronal        | Cryo             | 60 μm                |
| C11 CKA3-1      | Female | 11 years| Adult, reproductive     | 106 g     | 1.10 g     | Coronal        | Cryo             | 60 μm                |
| C12 CKA3-4      | Female | 40 weeks| Subadult, nonreproductive | 48 g      | 1.07 g     | Coronal        | Cryo             | 60 μm                |
| C13 CKA3-6      | Female | 16 weeks| Juvenile, nonreproductive | 14 g      | 0.73 g     | Coronal        | Cryo             | 60 μm                |
| C14 CKA3-3      | Female | 2 years | Adult, nonreproductive  | 76 g      | 1.10 g     | Coronal        | Cryo             | 60 μm                |
| FA23 6,931      | Male   | 1 year  | Adult                  | Unknown   | 1.10 g     | None           | None             | None                 |
| FA47 1,455      | Male   | Unknown | Unknown                | Unknown   | 1.15 g     | None           | None             | None                 |
| FA47 2,472      | Female | Unknown | Adult, reproductive     | Unknown   | 1.18 g     | None           | None             | None                 |
| C0 291294       | Female | Unknown | Unknown                | 49 g      | Unknown    | Coronal        | Cryo             | 60 μm                |
| C0 291294       | Female | Unknown | Unknown                | 48 g      | Unknown    | Coronal        | Cryo             | 60 μm                |
| C0 060295       | Male   | Unknown | Unknown                | 55 g      | Unknown    | Coronal        | Cryo             | 60 μm                |
| C0 060295       | Female | Unknown | Unknown                | 51 g      | Unknown    | Coronal        | Cryo             | 60 μm                |
| C220595         | Male   | Unknown | Unknown                | 57 g      | Unknown    | Coronal        | Cryo             | 60 μm                |
| C220595         | Male   | Unknown | Unknown                | 55 g      | Unknown    | Coronal        | Cryo             | 60 μm                |
| C190995         | Male   | Unknown | Unknown                | 71 g      | Unknown    | Coronal        | Cryo             | 60 μm                |
| C100995         | Female | Unknown | Unknown                | 62 g      | Unknown    | Sagittal       | Cryo             | 60 μm                |
| C0 190995       | Male   | Unknown | Unknown                | 68 g      | Unknown    | Coronal        | Cryo             | 60 μm                |
matter). This allows optimal orientation within the brain sections by keeping the information content of the plates high: Short abbreviations, adequate size of letters, and good discrimination of the anatomical structures.

3 | RESULTS AND DISCUSSION

The brain of *Fukomys anselli* (body mass: 50–120 g) resembles a rat brain but is less elongated in shape (Figure 2). With an average adult brain mass of $1.15 \pm 0.06$ g (mean ± SD, $n = 6$) it is about two thirds the size of a rat brain (body mass: 300–500 g; Herculano-Houzel, 2009), but more than double the size of a naked mole-rat brain (body mass: 40–60 g; Kverková et al., 2018) or mouse brain (body mass: 15–40 g; Herculano-Houzel, 2009). The brain mass of the individuals used in the present study compares well to that reported for a similar sample size of Ansell’s mole-rats in a recent study (Kverková et al., 2018). Macroscopic inspection of the Ansell’s mole-rat brains (Figure 2) revealed several features related to the underground lifestyle, such as very thin optic nerves, a delicate optic chiasm but well-developed trigeminal nerves, ganglia, and branches (Figure 2).

The brain atlas contains 28 Cresyl violet stained coronal sections and 28 adjacent Klüver-Barrera stained sections that illustrate the myelinated fiber tracts. In the Cresyl violet sections of the brain stem, the cerebellum is omitted to allow higher magnification of details. Fiber tracts are indicated by lowercase abbreviations, brain nuclei by uppercase labeling. The approximate coronal plane of the section is shown in the schematic midsagittal inset in the upper left of each plate. All plates of this atlas can be viewed online on the Biolucida Server (https://wiley.biolucida.net/images/?page=images&selectionType=collectionandselectionId=166). A high-quality PDF will be provided by the authors upon request.

All major brain areas typical for rodents are found in the Ansell’s mole-rat, in total we identified 375 different structures (Figure 4, Table 2 and online plates). Because no electrophysiological data are available for Ansell’s mole-rats, we only annotated neocortical areas that were clearly identifiable based on cytoarchitecture. Whereas, in general, the shape and size of the brain structures in the Ansell’s mole-rat are similar to other rodents, their topography is often rather different. This is reflected in the number of sections in the rat brain atlas (Paxinos & Watson, 2013) that had to be consulted in order to identify and denominate the brain regions found on single brain sections of the Ansell’s mole-rat. The rat-to-mole-rat ratios (calculated for each Ansell’s mole-rat brain section) varied between 1:1 and 45:1 and were particularly high in the midbrain region. In part, this can be attributed to some deviation of the sectional angle in the rat and mole-rat brains. The marked structural differences in the topography of brain structures in the two species, however, emphasize the necessity for and value of a brain atlas for the Ansell’s mole-rat.

Remarkable characteristics in the brain of the Ansell’s mole-rat were found in the thalamus. The oval paracentral (OPC) as well as the paracentral thalamic nucleus (PC) were much more prominent in the
Ansell’s mole-rat (plate 620) than in the rat. Not much is known about the function of these nuclei but together with other intralaminar thalamic nuclei they are thought to be involved in processes related to awareness and arousal (Binder, Hirokawa, & Windhorst, 2009). The OPC has further been shown to receive nocuous input from the masticator muscle, which is extremely well-developed in African mole-rats and provides them with one of the strongest bite forces (relative to body mass) in the animal kingdom (Cox & Faulkes, 2014; Sugiyi, Takemura, Dubner, & Ren, 2006; Van Daele, Herrel, & Adriaens, 2008). The lateral reticular nucleus in the medulla oblongata (LRt, plates 1,000–1,100) had both a larger rostrocaudal extension and a higher neuron density in the Ansell’s mole-rat than in the rat. This nucleus is involved in locomotor-respiratory coordination (Ezure & Tanaka, 1997) and its larger size in the Ansell’s mole-rat might be related to the specific respiratory conditions underground. Interestingly, the average respiratory rate of 36 breaths per minute in sleeping (not anesthetized) Ansell’s mole-rats is very low for a rodent of their size (Garcia Montero, Burda, & Begall, 2015). We were not able to identify the paratrigeminal nucleus in the Ansell’s mole-rat, a brain area involved in the integration of somatosensory reflexes related to nociceptive, respiratory, and cardiovascular mechanisms (Caous, de Sousa Buck, & Lindsey, 2001). This nucleus was also not demonstrated in the naked mole-rat (Xiao et al., 2006), a species for which reduced pain sensitivity has been reported (Omerbašić et al., 2016; Park et al., 2008).

The central auditory pathway of Ansell’s mole-rats can be expected to show specific features because the hearing range is restricted to low frequencies and absolute sensitivities are rather low (Brückmann & Burda, 1997; Gerhardt et al., 2017). The hearing range comprises frequencies between 0.1 and 13 kHz and the cochlea is highly specialized in the Ansell’s mole-rat (Gerhardt et al., 2017; Müller & Burda, 1989). Whereas there are more turns of the cochlea in this underground-dwelling species and the basilar membrane is slightly longer than in the rat, the overall spiral ganglion cell density is much lower (Müller, Laube, Burda, & Bruns, 1992) and half of the cochlea is part of an acoustic fovea dedicated to the analysis of a narrow frequency band between 0.6 and 1 kHz. Taken together, these data indicate that the Ansell’s mole-rat is anatomically adapted to low-frequency hearing in tunnels where these frequencies are found to propagate most efficiently (Heth, Frankenberg, & Nevo, 1986; Lange et al., 2007). Furthermore, sound localization is expected to be rather poor in strictly subterranean rodents as having been demonstrated for the naked mole-rat (Heterocephalus glaber; Heffner & Heffner, 1993), the blind mole rat (Spalax ehrenbergi; Heffner & Heffner, 1992) and the pocket gopher (Geomys bursarius; Heffner & Heffner, 1990).

How is this specialization in hearing reflected in the central ascending auditory pathway of the Ansell’s mole-rat? In the blind mole rat, the pocket gopher and in the naked mole-rat all nuclei typical for the mammalian auditory pathway are present (Bronchti, Heil, Scheich, & Wollberg, 1989; Glendenning & Masterton, 1998; Heffner & Heffner, 1990, 1993), and the same is true for the Ansell’s mole-rat. We did observe some features in nuclei of the auditory brainstem in the Ansell’s mole-rat that might be related to a subterranean lifestyle and to low frequency hearing. The cochlear nucleus of Ansell’s mole-rat, as the first central area receiving auditory information (plates 820–940), has a specialized dorsal subnucleus (DCN). The cochlea of Ansell’s mole-rat has a prominent DCN (Dollas et al., 2018) and the cochlear nucleus of Ansell’s mole-rat, as the first central area receiving auditory information (plates 820–940), has a specialized dorsal subnucleus (DCN). The cochlea of Ansell’s mole-rat has a prominent DCN (Dollas et al., 2018) and the cochlear nucleus of Ansell’s mole-rat, as the first central area receiving auditory information (plates 820–940), has a specialized dorsal subnucleus (DCN).
**TABLE 2**  List of abbreviations

| Abbreviations | long name of structure | Plate |
|---------------|------------------------|-------|
| 10N           | Dorsal motor nucleus of vagus | 1.020–1.110, Figure 4 |
| 10n           | Vagus nerve             | 1.040 |
| 11N           | Accessory nerve nucleus | 1.120 |
| 12N           | Hypoglossal nucleus     | 1.000–1.110, Figure 4 |
| 12n           | Hypoglossal nerve       | 1.040–1.110 |
| 2n            | Optic nerve             | 440–460, Figure 2 |
| 3n            | Oculomotor nerve        | 720   |
| 3N            | Oculomotor nucleus      | 680–720 |
| 3v            | Third ventricle         | 440–640, Figure 4 |
| 4N            | Trochlear nucleus       | 700–740 |
| 4v            | Fourth ventricle        | 780–1.040, Figure 4 |
| 5n            | Trigeminal nerve        | Figure 2 |
| 5N            | Motor trigeminal nucleus| 800–880 |
| 5Sol          | Trigeminal-solitary transition zone | 980–1.040 |
| 6N            | Abducens nucleus        | 920–940 |
| 7n            | Facial nerve            | 860–880, 920 |
| 7N            | Facial nucleus          | 880–980 |
| 8cn           | Cochlear root of the vestibulocochlear nerve | 840–880 |
| 8vn           | Vestibular root of the vestibulocochlear nerve | 860–920 |
| a             | Aqueduct                | 620–760, Figure 4 |
| ac            | Anterior commissure     | 440–460, Figure 4 |
| aka           | Anterior commissure, anterior part | 280–420 |
| AcbC          | Accumbens nucleus, core | 340–400 |
| AcbS          | Accumbens nucleus, shell | 340–400 |
| aci           | Anterior commissure, intrabulbar part | 200–260 |
| ACo           | Anterior cortical amygdaloid nucleus | 500–540 |
| acp           | Anterior commissure, posterior part | 440 |
| AD            | Anterodorsal thalamic nucleus | 480–520 |
| AH            | Anterior hypothalamic area | 520–580 |
| AHC           | Anterior hypothalamic area, central part | 500 |
| AHP           | Anterior hypothalamic area, posterior part | 500 |
| AM            | Anteromedial thalamic nucleus | 480–520 |
| Amb           | Ambiguous nucleus       | 1.060 |
| AOB           | Accessory olfactory bulb | 180–200 |
| AOD           | Anterior olfactory nucleus, dorsal part | 200–240 |
| AOL           | Anterior olfactory nucleus, lateral part | 200–240 |
| AOM           | Anterior olfactory nucleus, medial part | 200–240 |
| AOV           | Anterior olfactory nucleus, ventral part | 200–240 |
| AP            | Area postrema           | 1.040–1.060, Figure 4 |
| APit          | Anterior lobe of the pituitary | 700–780, Figure 4 |
| APT           | Anterior pretectal nucleus | 600–680 |
| Arc           | Arcuate hypothalamic nucleus | 620–640 |
| AuD           | Auditory cortex         | 480, 520, 620 |
| AV            | Anteroventral thalamic nucleus | 480–520 |
| azp           | Azygous pericallosal artery | 300–381 |
| Bar           | Barrington’s nucleus    | 820–860 |
| bic           | Brachium of the inferior colliculus | 680–720 |
| BIC           | Nucleus of the brachium of the IC | 720 |
| BLA           | Basolateral amygdaloid nucleus, anterior part | 460–580 |
| BMA           | Basomedial amygdaloid nucleus, anterior part | 460–580 |
| BMP           | Basomedial amygdaloid nucleus, posterior part | 580 |
| C             | Central canal           | 1.040–1.120 |

(Continues)
| Abbreviations | long name of structure | Plate |
|---------------|------------------------|-------|
| CA1           | Field CA1 of the hippocampus | 480–660 |
| CA2           | Field CA2 of the hippocampus | 460–660 |
| CA3           | Field CA3 of the hippocampus | 460–660 |
| Cb            | Cerebellum | Figures 2 and 4 |
| CbN           | Cerebellar nuclei | 920 |
| cc            | Corpus callosum | 360–520, Figure 4 |
| Ce            | Central amygdaloid nucleus | 520–540 |
| CeCv          | Central cervical nucleus of the spinal cord | 1,060 |
| CG            | Central gray | 840–880 |
| cg            | Cingulum | 300–600 |
| Ch            | Cerebral hemisphere | Figure 2 |
| chp           | Choroid plexus | 360–580, 900–1,020 |
| CIC           | Central nucleus of the inferior colliculus | 740–760 |
| cic           | Commissure of the inferior colliculus | 700–740 |
| CI            | Caudal interstitial nucleus of the medial longitudinal fasciculus | 300–480 |
| CL            | Centrolateral thalamic nucleus | 500–580 |
| CLI           | Caudal linear nucleus of the raphe | 740 |
| CM            | Central medial thalamic nucleus | 480–580, Figure 4 |
| CnF           | Cuneiform nucleus | 740–780 |
| cp            | Cerebral peduncle | 580–740 |
| CPu           | Caudate putamen (striatum) | 300–560 |
| csc           | Commissure of the superior colliculus | 600–640 |
| cu            | Cuneate fasciculus | 1,020–1,120 |
| Cu            | Cuneate nucleus | 1,020–1,120 |
| DA            | Dorsal hypothalamic area | 580 |
| das           | Dorsal acoustic stria | 940, Figure 3 |
| DB            | Diagonal band | Figure 4 |
| DCDp          | Dorsal cochlear nucleus, deep core | 900–940, Figure 3 |
| DCFu          | Dorsal cochlear nucleus, fusiform layer | 920–940, Figure 3 |
| DCIC          | Dorsal cortex of the inferior colliculus | 740–780 |
| DCMo          | Dorsal cochlear nucleus, molecular layer | 900–940, Figure 3 |
| Den           | Dorsal endopiriform nucleus | 360–560 |
| dhc           | Dorsal hippocampal commissure | 460–540 |
| Dk            | Nucleus of Darkschewitsch | 640–680 |
| DLG           | Dorsal lateral geniculate nucleus | 600–640 |
| DLL           | Dorsal nucleus of the lateral lemniscus | 760–780 |
| dlo           | Dorsal lateral olfactory tract | 200 |
| DM            | Dorsomedial hypothalamic nucleus | 640–660, Figure 4 |
| DMC           | Dorsomedial hypothalamic nucleus, compact part | 620 |
| DMD           | Dorsomedial hypothalamic nucleus, dorsal part | 600–620 |
| DMTg          | Dorsomedial tegmental area | 800–840 |
| DMV           | Dorsomedial hypothalamic nucleus, ventral part | 620 |
| DpG           | Deep gray layer of the SC | 680 |
| DpWh          | Deep white layer of the SC | 680 |
| DR            | Dorsal raphe nucleus | 740–820, Figure 4 |
| DS            | Dorsal subiculum | 540–580 |
| dsc           | Dorsal spinocerebellar tract | 980–1,080 |
| DTg           | Dorsal tegmental nucleus | 780–840 |
| dtgx          | Dorsal tegmental decussation | 700 |
| DTT1          | Dorsal tenia tecta layer 1 | 280–320 |

(Continues)
| Abbreviations | long name of structure                                                      | Plate      |
|---------------|---------------------------------------------------------------------------|------------|
| DTT2          | Dorsal tenia tecta layer 2                                               | 280–320    |
| E             | Ependyma and subependymal layer                                           | 100–180    |
| ec            | External capsule                                                          | 300–620    |
| ECIC          | External cortex of the inferior colliculus                                | 740–780    |
| Ect           | Ectorhinal cortex                                                         | 520–580    |
| ECu           | External cuneate nucleus                                                  | 1,000–1,060|
| EGP           | External part of globus pallidus                                          | 460        |
| eml           | External medullary lamina                                                 | 500–580    |
| ep            | Olfactory epithelium                                                     | 20         |
| EP            | Entopeduncular nucleus                                                    | 520–560    |
| EPI           | External plexiform layer of the olfactory bulb                            | 20–200     |
| EW            | Edinger-Westphal nucleus                                                  | 680–700    |
| F             | Fornix                                                                    | 420–700, Figure 4 |
| FC            | Fasciola cinereum                                                        | 480        |
| fi            | Fimbria of the hippocampus                                                | 440–580    |
| fmj           | Forceps major of the corpus callosum                                      | 540–720    |
| fr            | Fasciculus retroflexus                                                    | 480–680    |
| g7            | Genu of the facial nerve                                                  | 880–920    |
| Ge5           | Gelatinous layer of the caudal spinal trigeminal nucleus                  | 1,080–1,120|
| Gi            | Gigantocellular reticular nucleus                                         | 900–1,040, Figure 4 |
| GiA           | Gigantocellular reticular nucleus, alpha part                             | 900        |
| GV            | Gigantocellular reticular nucleus, ventral part                           | 980        |
| Gi            | Glomerular layer of the olfactory bulb                                    | 20–200     |
| GP            | Globus pallidus                                                           | 480–520    |
| gr            | Gracile fasciculus                                                        | 1,080–1,120|
| Gr            | Gracile nucleus                                                           | 1,040–1,100|
| GrC           | Granule cell layer of cochlear nuclei                                    | 820–940, Figure 3 |
| GrDG          | Granular layer of the dentate gyrus                                       | 460–620    |
| hbc           | Habenular commissure                                                      | 560        |
| HDB           | Nucleus of the horizontal limb of the diagonal band                       | 360–480    |
| I             | Intercalated nuclei of the amygdala                                       | 480–580    |
| IB            | Interstitial nucleus of the vestibulocochlear nerve                       | 840–920    |
| IAD           | Interanterodorsal thamic nucleus                                          | 480        |
| IAM           | Interanteromedial thamic nucleus                                          | 500        |
| IB            | Interstitial nucleus of the medulla                                       | 1,100–1,120|
| IC            | Inferior colliculus                                                       | 720–780, Figures 2, 4 |
| ic            | Internal capsule                                                          | 420–560    |
| ICj           | Islands of Calleja                                                       | 300–340    |
| ICjm          | Islands of Calleja, major island                                          | 360–381    |
| icp           | Inferior cerebellar peduncle (restiform body)                            | 880–1,020  |
| IEEn          | Intermediate endopiriform nucleus                                        | 360–460    |
| IG            | Indusium griseum                                                          | 340–480    |
| IGL           | Intergeniculate leaf                                                      | 600–640    |
| ILL           | Intermediate nucleus of the lateral lemniscus                            | 760–800    |
| iml           | Internal medullary lamina                                                 | 480–500    |
| InC           | Interstitial nucleus of Cajal                                             | 700        |
| InGi          | Inner sublayer of the intermediate gray layer superior colliculus        | 680        |

(Continues)
| Abbreviations | long name of structure | Plate |
|---------------|------------------------|-------|
| InGo          | Outer sublayer of the intermediate gray layer superior colliculus | 680   |
| INS           | Insular cortex         | 480   |
| InWh          | Intermediate white layer of the SC | 680   |
| IO            | Inferior olivary nucleus | 980–1,080, Figure 4 |
| IOA           | Inferior olive, subnucleus A of medial nucleus | 1,020–1,060 |
| IOB           | Inferior olive, subnucleus B of medial nucleus | 1,000–1,060 |
| IOBe          | Inferior olive, beta subnucleus | 1,060 |
| IOC           | Inferior olive, subnucleus C of medial nucleus | 1,020–1,060, Figure 4 |
| IOD           | Inferior olive, dorsal nucleus | 1,000–1,020 |
| IOK           | Inferior olive, cap of Kooy of the medial nucleus | 1,060 |
| IOPr          | Inferior olive, principal nucleus | 1,000 |
| IP            | Interpeduncular nucleus | 700–760, Figure 4 |
| ipf           | Interpeduncular fossa | 700, Figure 4 |
| IPI           | Internal plexiform layer of the olfactory bulb | 40–200 |
| IRt           | Intermediate reticular nucleus | 880–1,120 |
| isRt          | Isthmic reticular formation | 740–760 |
| KF            | Kölliker-fuse nucleus | 800 |
| LaDL          | Lateral amygdaloid nucleus, dorsolateral part | 520–580 |
| LC            | Locus coeruleus | 860 |
| Ld            | Lamboid septal zone | 400 |
| LD            | Laterodorsal thalamic nucleus | 520–560 |
| LDB           | Lateral nucleus of the diagonal band | 440–480 |
| LDTg          | Laterodorsal tegmental nucleus | 780–820 |
| LDTgV         | Laterodorsal tegmental nucleus, ventral part | 780–820 |
| lfp           | Longitudinal fasciculus of the pons | 760–820, Figure 4 |
| LH            | Lateral hypothalamic area | 560 |
| LHB           | Lateral habenular nucleus | 500–560 |
| II            | Lateral lemniscus | 760–800 |
| LM            | Lateral mammillary nucleus | 680 |
| lo            | Lateral olfactory tract | 200–400 |
| LOT           | Nucleus of the lateral olfactory tract | 480–500 |
| LP            | Lateral posterior thalamic nucleus | 560–580 |
| LPB           | Lateral parabrachial nucleus | 800–860 |
| LPMC          | Lateral posterior thalamic nucleus, mediocaudal part | 660 |
| LPO           | Lateral preoptic area | 480 |
| Ir4v          | Lateral recess of the 4th ventricle | 900–1,020 |
| LRt           | Lateral reticular nucleus | 1,000–1,100 |
| LSD           | Lateral septal nucleus, dorsal part | 360–420 |
| LSI           | Lateral septal nucleus, intermediate part | 360–420 |
| LSO           | Lateral superior olive | 820–860 |
| LSS           | Lateral stripe of the striatum | 360–420 |
| LSV           | Lateral septal nucleus, ventral part | 360–420 |
| Lth           | Lithoid nucleus | 600–640 |
| Lv            | Lateral ventricle | 300–620 |
| LVe           | Lateral vestibular nucleus | 880–920 |
| M             | Motor cortex | 520 |
| M1            | Primary motor cortex | 480 |
| M2            | Secondary motor cortex | 480 |
| m5            | Motor root of the trigeminal nerve | 740–800 |
| MBO           | Mammillary body | Figure 4 |

(Continues)
TABLE 2  (Continued)

| Abbreviations | long name of structure                                      | Plate       |
|---------------|------------------------------------------------------------|-------------|
| mcp           | Middle cerebellar peduncle                                 | 740–860     |
| M CPC         | Magnocellular nucleus of the posterior commissure          | 640         |
| MD            | Mediodorsal thalamic nucleus                               | 480–580     |
| MdD           | Medullary reticular nucleus, dorsal part                   | 1.060–1.120 |
| mDR           | Dorsal raphe nucleus                                       | 720         |
| MdV           | Medullary reticular nucleus, ventral part                 | 1.060–1.120 |
| ME            | Median eminence                                            | 580         |
| Me5           | Mesencephalic trigeminal nucleus                            | 720–860     |
| me5           | Mesencephalic trigeminal tract                             | 800–860     |
| MePD          | Medial amygdaloid nucleus, posterodorsal part              | 520–560     |
| MePV          | Medial amygdaloid nucleus, posterovenral part              | 520–560     |
| mfb           | Medial forebrain bundle                                    | 540–560     |
| MG            | Medial geniculate nucleus                                  | 660–700     |
| M HB          | Medial habenular nucleus                                   | 480–580     |
| Mi            | Mitral cell layer of the olfactory bulb                    | 40–200      |
| ml            | Medial lemniscus                                           | 540–1,080, Figure 4 |
| mlf           | Medial longitudinal fasciculus                             | 680–1.120, Figure 4 |
| Mlx           | Medial lemniscus decussation                               | 1,040–1,080 |
| MM            | Medial mammillary nucleus, medial part                     | 700         |
| MnA           | Median accessory nucleus of the medulla                    | 1,100–1,120 |
| MnR           | Median raphe nucleus                                       | 780–820     |
| MoDG          | Molecular layer of the dentate gyrus                       | 460–620     |
| MPA           | Medial preoptic area                                       | 480         |
| MPB           | Medial parabrachial nucleus                                | 840–860     |
| MPL           | Medial paralemniscal nucleus                               | 800–820     |
| MPO           | Medial preoptic nucleus                                    | 460         |
| MPT           | Medial pretectal nucleus                                   | 620         |
| M Re          | Mammillary recess of the 3rd ventricle                     | 660–700     |
| m Rt          | Mesencephalic reticular formation                           | 680–720     |
| MS            | Medial septal nucleus                                      | 360–400     |
| MSO           | Medial superior olive                                      | 840–880     |
| mt            | Mammillothalamic tract                                     | 460–680     |
| M Tu          | Medial tuberal nucleus                                     | 620         |
| M Ve          | Medial vestibular nucleus                                  | 880–1,020   |
| Mx            | Matrix region of the medulla                               | 960–1,060   |
| ns            | Nigrostriatal bundle                                       | 580         |
| N v           | Navicular nucleus of the basal forebrain                   | 300–340     |
| OB            | Olfactory bulb                                             | Figures 2, 4|
| Obex          | Obex                                                       | 1.080       |
| oc            | Olivocerebellar tract                                      | 960–1,020   |
| oc b          | Olivocochlear bundle                                       | 920, Figure 4|
| och           | Optic chiasm                                               | 500–560, Figures 2, 4|
| ON            | Olfactory nerve layer                                      | 60–160      |
| OPC           | Oval paracentral thalamic nucleus                           | 620         |
| OPT           | Olivary prepectal nucleus                                  | 600–620     |
| opt           | Optic tract                                               | 520–600     |
| Or            | Oriens layer of the hippocampus                            | 480–580     |
| OT            | Nucleus of the optic tract                                 | 600–620     |
| ov            | Olfactory ventricle (olfactory part of lateral ventricle)  | 200–300     |
| Pa            | Paraventricular hypothalamic nucleus                       | 480–540, Figure 4 |

(Continues)
| Abbreviations | long name of structure | Plate |
|---------------|------------------------|-------|
| PAG           | Periaqueductal gray    | 620–760, Figure 4 |
| PBP           | Parabrachial pigmented nucleus of the VTA | 700–720 |
| PC            | Paracentral thalamic nucleus | 520–620 |
| pc            | Posterior commissure   | 600–640 |
| PCRt          | Parvicellular reticular nucleus | 880–1,040 |
| Pe            | Periventricular hypothalamic nucleus | 520–540 |
| PeF           | Perifornical nucleus   | 600–620 |
| PH            | Posterior hypothalamic nucleus | 640–680 |
| Pi            | Pineal gland           | 580–620, Figure 4 |
| pim           | Pia mater              | 180   |
| Pir           | Piriform cortex        | 280–620 |
| pire          | Pineal recess          | 600   |
| PLH           | Peduncular part of lateral hypothalamus | 500–660 |
| pm            | Principal mammillary tract | 700   |
| Pn            | Pontine nuclei         | 760–820, Figure 4 |
| PnC           | Pontine reticular nucleus, caudal part | 820–880 |
| PnO           | Pontine reticular nucleus, oral part | 740–800 |
| PnV           | Pontine reticular nucleus, ventral part | 820–860, Figure 4 |
| Po            | Posterior thalamic nuclear group | 540–660 |
| PoDG          | Polymorph layer of the dentate gyrus | 500–620 |
| PP            | Peripeduncular nucleus | 660   |
| PPit          | Posterior lobe of pituitary | 640–780 |
| Pr            | Prepositus nucleus     | 900–1,000, Figure 4 |
| PR            | Prerubral field        | 660–680 |
| Pr5           | Principal sensory trigeminal nucleus | 800–880 |
| PrC           | Precommissural nucleus | 600   |
| PrG           | Pregeniculate nucleus of the prethalamus | 600–640 |
| PT            | Paratenial thalamic nucleus | 480   |
| PTe           | Paraterete nucleus     | 600   |
| PTg           | Pedunculopontine tegmental nucleus | 760   |
| PV            | Paraventricular thalamic nucleus | 500–600 |
| PVA           | Paraventricular thalamic nucleus, anterior part | 460–480, Figure 4 |
| PVG           | Periventricular gray   | 600   |
| PVP           | Paraventricular thalamic nucleus, posterior part | Figure 4 |
| Py            | Pyramidal cell layer of the hippocampus | 480–620 |
| py            | Pyramidal tract        | 840–1,100, Figures 2, 4 |
| pyx           | Pyramidal decussation  | 1,100–1,120, Figure 4 |
| R             | Red nucleus            | 700–720 |
| Re            | Reuniens thalamic nucleus | 480–580 |
| REth          | Retroethmoid nucleus   | 660   |
| rf            | Rhinal fissure         | 200–680 |
| Rh            | Rhomboid thalamic nucleus | 520–580, Figure 4 |
| RIP           | Raphe interpositus nucleus | 880   |
| RIs           | Retroisthmic nucleus   | 760   |
| RLI           | Rostral linear nucleus of the raphe | 700   |
| RMg           | Raphe magnus nucleus   | 820–960 |
| RML           | Supramammillary nucleus, lateral part | 700   |
| RMM           | Supramammillary nucleus, medial part | 680   |
| RMS           | Rostral migratory stream | 260–320 |
| Ro            | Nucleus of roller      | 980–1,020 |
| ROOb          | Raphe obscurus nucleus | 960–1,040 |

(Continues)
| Abbreviations | long name of structure | Plate |
|---------------|------------------------|-------|
| RPa           | Raphe pallidus nucleus  | 980–1,060 |
| RPC           | Red nucleus, parvicellular part | 680 |
| RPF           | Retroparafascicular nucleus | 620 |
| RRF           | Retronuclear field       | 740 |
| rs            | Rubrospinal tract        | 800–1,120 |
| RS            | Retrosplenial cortex     | 580 |
| Rt            | Reticular thalamic nucleus | 480–600 |
| RtTg          | Reticulotegmental nucleus of the pons | 780–840, Figure 4 |
| S             | Somatosensory cortex    | 480, 520, 580 |
| s5            | Sensory root of the trigeminal nerve | 740–880 |
| Sag           | Sagulum nucleus         | 760–780 |
| SC            | Superior colliculus     | 640–720, Figure 4 |
| SCh           | Suprachiasmatic nucleus | 520–540 |
| SCO           | Subcommissural organ    | 600 |
| scp           | Superior cerebellar peduncle (brachium conjunctivum) | 680–900, Figure 4 |
| Shi           | Septohippocampal nucleus | 360–420 |
| SHy           | Septohypothalamic nucleus | 420 |
| sm            | Stria medullaris of the thalamus | 480–540 |
| SMV           | Superior medullary velum | 820–880 |
| SN            | Substantia nigra        | 660–740 |
| SO            | Supraoptic nucleus      | 520–540 |
| Sol           | Nucleus of the solitary tract | 940–1,120 |
| sol           | Solitary tract          | 980–1,100 |
| sox           | Supraoptic decussation  | 580 |
| sp5           | Spinal trigeminal tract | 900–1,120 |
| Sp5C          | Spinal trigeminal nucleus, caudal part | 1,060–1,120 |
| Sp5I          | Spinal trigeminal nucleus, interpolar part | 960–1,060 |
| Sp5O          | Spinal trigeminal nucleus, oral part | 900–960 |
| SPTg          | Subpeduncular segmental nucleus | 780 |
| SpVe          | Spinal vestibular nucleus | 940–1,020 |
| ST            | Bed nucleus of the stria terminalis | 420–480 |
| st            | Stria terminalis        | 460–560 |
| STh           | Subthalamic nucleus      | 600–660 |
| STM           | Bed nucleus of the stria terminalis, medial division | 440 |
| str           | Superior thalamic radiation | 600 |
| Sub           | Submedial thalamic nucleus | 520–580 |
| SubB          | Subbrachial nucleus     | 680–700 |
| SubC          | Subcoeruleus nucleus    | 820–860 |
| SubCA         | Subcoeruleus nucleus, alpha part | 820–860 |
| SuL           | Supralemniscal nucleus  | 760 |
| SuVe          | Superior vestibular nucleus | 900 |
| tfp           | Transverse fibers of the pons | 760–820 |
| TGa           | Terminal ganglion       | 20–40 |
| ts            | Tectospinal tract       | 760–800, 980–1,120 |
| TS            | Triangular septal nucleus | 420 |
| tth           | Trigeminothalamic tract | 700–820 |
| Tu            | Olfactory tubercle      | 320–420 |
| TuLH          | Tuberal region of lateral hypothalamus | 520–620 |
| tz            | Trapezoid body          | 800–920 |
| Tz            | Nucleus of the trapezoid body | 840–880 |

(Continues)
subterranean pocket gopher (Godfrey et al., 2016). In these species, the DCN amounts to more than 60% (pocket gopher) or almost 90% (mountain beaver) of the total cochlear nucleus volume (cat: 35%; Osen, 1969). Godfrey et al. (2016) interpreted these features of the DCN as possible adaptations facilitating the integration of somatosensory and auditory stimuli in the underground habitat which is in line with the interpretation of the dorsal cochlear nucleus in mammals, generally (see also Malmierca, 2015). The granule cells of the DCN receive direct input from many sources including the trigeminal somatosensory system and this information is likely processed in the molecular layer (Young & Davis, 2002). These layers in the Ansell’s mole-rat might fulfill a similar function which is likely related to the somatosensory system but unrelated to pinna movements and sound localization. Godfrey et al. (2016) were puzzled by the fact that the naked-mole rat DCN did not show the "hypertrophic" features seen in other tunnel-dwelling rodents like the mountain beaver or the pocket gopher but resembled more the DCN of epigeic species. It did not show thickened molecular and granular layers and the relative size of the naked mole-rat DCN was similar to the DCN of the cat. They discussed the special situation in the naked mole-rat as a possible consequence of the social life-style of this species. Our data, however, do not support this idea because the Ansell's mole-rat also lives in social groups and its DCN shows the above-mentioned "hypertrophic" situation. We speculate that the pronounced granular and molecular regions of the DCN in the Ansell's mole-rat indeed may reflect an adaptation to the underground habitat and that the naked mole-rat is an exception that shows signs of "degeneration" in its central auditory pathway as already proposed for the auditory periphery (Mason, Cornwall, & Smith, 2016). Neuroanatomical studies of more subterranean species will hopefully test this hypothesis.

Another nucleus of the auditory brainstem that shows features of low-frequency adaptations in the Ansell's mole-rat is the superior olive. The medial superior olive (MSO, plates 840–880), which is involved in the localization of low-frequency sounds in other mammals (Grothe, Pecka, & McAlpine, 2010), appears more differentiated in the Ansell's mole-rat than the lateral superior olive (LSO, plates 820–860) which is responsible for high frequency sound localization (Grothe et al., 2010). The LSO has also been reported as poorly differentiated in the blind mole rat (Bronchti et al., 1989) and as indistinct in the naked mole-rat (Heffner & Heffner, 1993; but see Gessele, Garcia-Pino, Omerbašiçi, Park, & Koch, 2016). Interestingly, all nuclei of the naked mole-rat's binaural auditory brainstem lack HCN1 channels that are necessary for fast integration times of interaural intensity differences which might explain the poor sound localization (Gessele et al., 2016). Collectively, the auditory pathway of the Ansell's mole-rat shows features found in other subterranean rodents that might represent adaptations to burrow acoustics. It must be noted here, however, that we present qualitative observations that should be quantitatively tested in further studies.

To summarize, we present an atlas that gives a good overview on brain organization in the Ansell's mole-rat together with many details needed for successful experimental neuroanatomical and physiological

| Abbreviations | long name of structure | Plate |
|---------------|------------------------|-------|
| V             | Visual cortex          | 620   |
| VA            | Ventral anterior thalamic nucleus | 480–520 |
| VCA           | Ventral cochlear nucleus, anterior part | 840–900 |
| VCP           | Ventral cochlear nucleus, posterior part | 900–940 |
| VDB           | Nucleus of the vertical limb of the diagonal band | 360–400 |
| VL            | Ventrolateral thalamic nucleus | 500–560 |
| vlh           | Ventrolateral hypothalamic tract | 500   |
| VLL           | Ventral nucleus of the lateral lemniscus | 780–800 |
| VM            | Ventromedial thalamic nucleus | 520–580 |
| VMH           | Ventromedial hypothalamic nucleus | 500–620, Figure 4 |
| VMPO          | Ventromedial preoptic nucleus | 480–500 |
| VP            | Ventral pallidum       | 320   |
| VPL           | Ventral posterolateral thalamic nucleus | 520–640 |
| VPM           | Ventral posteromedial thalamic nucleus | 540–640 |
| VPPC          | Ventral posterior nucleus of the thalamus, parvicellular part | 620   |
| VRe           | Ventral reuniens thalamic nucleus | 500–560 |
| vsc           | Ventral spinocerebellar tract | 800–840, 980–1,120 |
| VTA           | Ventral tegmental area  | 680   |
| VTg           | Ventral tegmental nucleus | 760   |
| VTT           | Ventral tenia tecta    | 240–280 |
| X             | Nucleus X              | 920–980 |
| xscp          | Decussation of the superior cerebellar peduncle | 720–760 |
| Z             | Nucleus Z              | 1,020 |
| Zi            | Zona incerta           | 520–640 |
work in this species. The atlas can also serve as a basis and background material for in-depth analyses concerning evolutionary processes leading to such exotic animals as the Ansell's mole-rat. We hope that the atlas may thus stimulate new questions and answers for promising investigations in the future.

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CONFLICT OF INTEREST

The authors declare no competing financial interests.

AUTHOR CONTRIBUTION

All authors had full access to all the data in the study and take responsibility for the integrity of the data and the accuracy of the data analysis. Study design: HHAO, EPM. Data acquisition: AD. Analysis and interpretation of data: AD, HHAO, SB, HB, EPM. Writing of the manuscript: AD, HHAO, SB, HB, EPM.

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