Functional morphology of the rostral head region of *Cryptomys hottentotus* (Bathyergidae, Rodentia)

Judith Banke
Andrea Mess
Ulrich Zeller

Introduction

The African rodent family Bathyergidae (mole-rats) is characterized by a fossorial lifestyle (TULLBERG, 1899/1900; STARCK, 1995). As digging tools mole-rats use the strong gnawing teeth and the forehand (SHERMAN *et al.*, 1991). Previous, morphological studies concerning fossorial adaptations of the Bathyergidae in an evolutionary and, simultaneously, phylogenetic context, have only dealt with external features of the forehand (ADE and ZIEKUR, 1999).

Though morphological examinations of several mole-rat species were conducted in recent studies of the rhinarium (ADE, 1998) and the nasal skeleton (MESS, 1997, 1999) of rodents, as well as the facial musculature of mammals (GAMBARYAN, 1989), a comprehensive picture of the rostral head region, including the spatial relations between integument, skeleton and musculature, was not available. Thus, the present study concentrates on the morphology of the rostral nasal and oral region, with special reference to the gnawing teeth, the external rhinarium, the cartilaginous rostral nasal skeleton, the upper *inflexa pellita*, and the associated facial musculature. Based on the presented morphological characters, function is inferred to get an idea of the organismical context of the rostral head region with regard to the fossorial lifestyle of *Cryptomys*. We have chosen the common mole-rat *Cryptomys hottentotus* (Lesson 1826), because it is regarded as a representative of the Bathyergidae exhibiting the largest number of plesiomorphic characters (MAIER and SCHRENK, 1987; ADE, 1998).

Material and methods

The study is based on the combination of macroscopic and microscopic examinations (tabl. 1). Macroscopic observations and dissection were carried out under a stereomicroscope. Microscopic examination is based on transverse serial sections (40 µm) which were stained according to standard histological techniques (AZAN after Heidenhain). Microscopic drawings, made with the aid of an occular-grid or camera lucida, were used to produce a 3-dimensional graphic reconstruction of the cartilaginous rostral nasal skeleton, i.e., the cupula nasi anterior. The material is part of the collection at the Museum für Naturkunde, Berlin and the Smithsonian Institution, Washington, D.C.

Methodology and terminology

The scope of the present study covers external features and skeletal structures as well as the associated facial musculature. From a functional perspective the discussion elucidates the biological role of the respective structures with regard to fossorial lifestyle. However, it has to be noted that a consideration of the facial musculature in greater detail is beyond the scope of the present paper. For detailed descriptions of the mimetic muscles, the reader is referred to BANKE (1999).

In terms of nomenclature, the description of the rhinarium follows ADE (1998), that of the nasal skeleton MESS (1997, 1999). Terminology of the mimetic muscles is based on MEINERTZ (1942*a-d*,

Material	Methods	Investigated structures
*C. hottentotus** (alcohol-preserved juvenile specimen, HL 35 mm, CRL 97 mm)	macroscopic examination dissection	external features mimetic musculature
*C. hottentotus*** (head of a juvenile specimen, embedded in celloidin, HL 32 mm)	microscopic examination	rostral nasal skeleton, mimetic musculature

* *Museum für Naturkunde zu Berlin*
** Smithsonian Institution, Washington, D.C.

Table 1
Material and methods (CRL: crown-rump-length; HL: head-length)

1951) and SABAN (1970). Since the homology of the various portions of the *M. naso-labialis profundus* is not analysed within rodents (MEINERTZ, 1942, 1951), the applied terminology functionally refers to the origin of portions.

Results

Strong, rostrally orientated (proodont) incisors form the rostral pole of the head (figure 1A, B). Immediately behind the upper incisors the rostral nasal region exhibits a broad, hairless integument differentiation, i.e., the *Regio rhinarica* (figure 1A). This forms an almost vertically orientated plate that extensively surrounds the small nares. The *Regio rhinarica* continues gradually into the normal hairy skin and is therefore not precisely delimitable. Medially, the *Regio rhinarica* is divided by a vertical *sulcus medianus* (figure 1A) that runs from the supranaric to the supralabial part of the *Regio rhinarica*. The internaric region exhibits two indistinct triangular elements between the *sulcus medianus* and the dorsomedial margin of the nares (fig. 1A). Surface patterns, i.e., rhinoglyphs, are absent. The *regio supralabialis* possesses two integument folds that continue ventrocaudally into the oral region (figure 2B). They pass beside the protruding upper incisors and accompany the palatal rugae caudally. Since the ventral margin of the *Regio supralabialis* turns directly into the gingiva (figure 1A, 2B), the area above the upper gnawing teeth lacks a hairy lip portion and the gingiva takes a prominent, rostral position.

The central aspect of the *Regio rhinarica* is supported by the cartilaginous rostral nasal skeleton, i.e., the *cupula nasi* anterior (figure 1C). The rostral aspect of the *cupula nasi* anterior is characterized by the lack of an anterior wall and the well-developed processus cupularis at the rostroventral margin of the cupula (figure 1C). Two portions of the *M. naso-labialis profundus* originate on the ventral margin as well as on the medial side of this processus (see below). The area between the processus cupularis and the dorsal margin of the cupula nasi anterior corresponds with the internaric region of the *Regio rhinarica.* Because the cupula has a small lateral extension (figure 1C), it only encloses the area immediately around the nares. Thus, the integument beside and above the nares (figure 1A), i.e., the supralabial and supranaric part of the *Regio rhinarica* is movable. Moreover, the cupula has a restricted rostral extension (figure 1C). Thus, the cupula is ventrally almost completely stabilized by the premaxilla and, instead of the nose tip, the proodont incisors form the rostral pole of the snout (figures 1C, 2C).

In *Cryptomys* the facial musculature of the nasal region consists of: 1) the *M. naso-labialis superficialis* associated with the skin of the *dorsum nasi*; 2) the rostrally directed *M. naso-labialis* and *M. maxillo-labialis*, which are characterized by a bony origin and an insertion on the rostrum surrounding skin behind the *Regio rhinarica*; and 3)

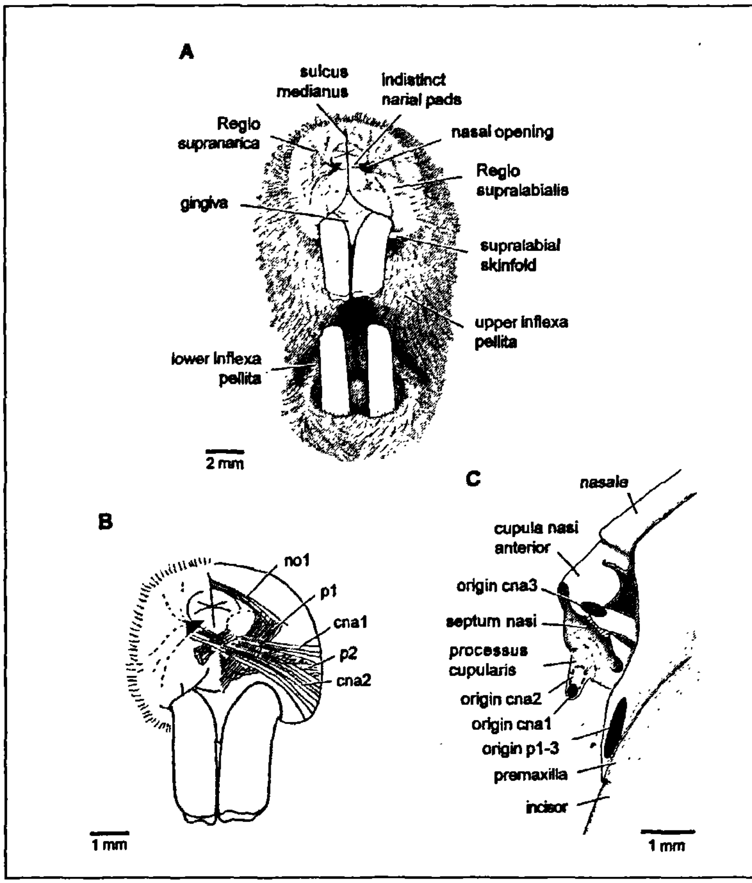
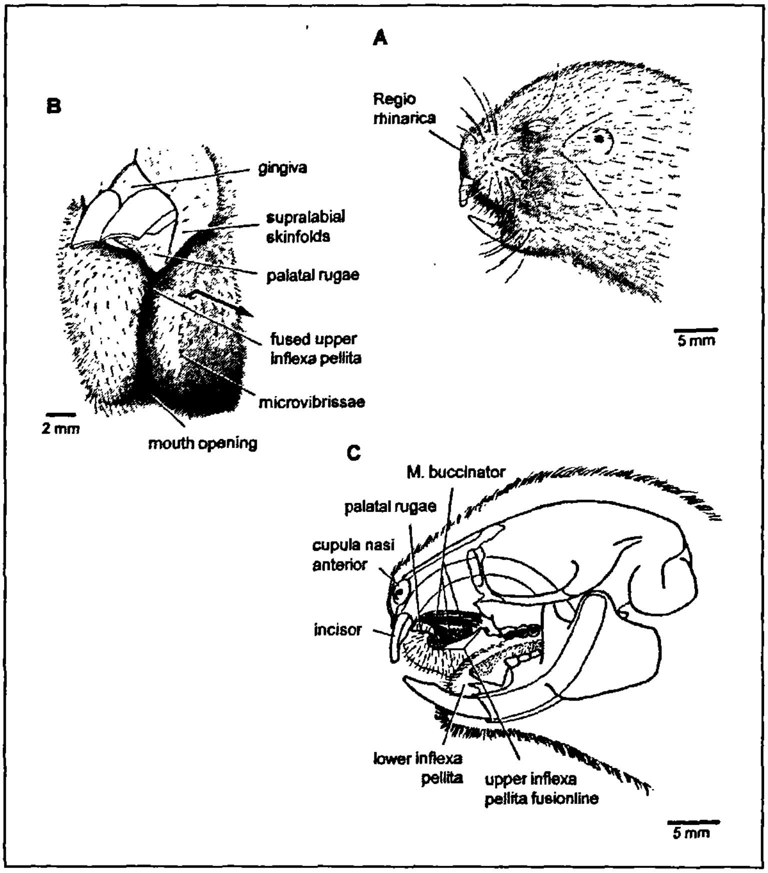


Figure 1
The rostral nasal region of *Cryptomys hottentotus*, rostral view. A, external rostral aspect of the snout; B, *Regio rhinarica* with halfsidely dissected superficial portions of the *M. naso-labialis profundus*, rostral view; C, reconstruction of the rostral nasal skeleton on the base of transverse serial sections, including origins of the *M. naso-labialis profundus*, rostrolateral view.

labialis profundus is not only a *dorsum nasi-* and upper lip-mover, but at the same time a *cupula nasi anterior-* and nasal opening-mover.

The labial complex is strongly developed in *Cryptomys*. Both the upper and lower lip possess the so called *inflexa pellita* (SCHULZE, 1912), i.e., hairy skinfolds that continue medially into the mouth



I Figure 2
The oral region of *Cryptomys hottentotus*. A, external aspect of the head, lateral view, B, external aspect of the fused upper *inflexa pellita*, rostrolateral view, C, internal aspect of the mouth cavity, lateral view.

cavity (figure 1A). In *Cryptomys* the *inflexa pellita* are situated behind the incisors. Thus, the gnawing teeth occupy an extraoral position and the actual mouth opening is situated behind them. Externally the *inflexa pellita* exhibit microvibrissae (figure 2B) crossing each other when the mouth opening is closed. The upper inflexa are especially prominent in *Cryptomys* (figure 2B). They are fused behind the incisors (figure 2B) and occupy the broad diastemal space completely (figure 2C).

Internally, the upper *inflexa pellita* are associated with facial musculature. For the most part it belongs to the *M. buccinator* (figure 2C), which originates along the fusion line of the upper *inflexa pellita* and on the ventral side of the premaxilla, immediately behind the upper incisors. Furthermore, the *M. bucco-naso-labialis* and the *Platysma myoides pars buccalis* insert inside the upper *inflexa pellita*. The former originates on the lateral side of the premaxilla. The latter originates on the skin of the neck region. According to the course of fibres, within these *upper inflexa pellita-movers* (uipm) the *M. bucco-naso-labialis* and the *Platysma myoides pars buccalis* have to be regarded as mouth cavity-openers, while the *M. buccinator* is a mouth cavity-closer. Also inside the lower *inflexa pellita* facial musculature exists that consists of numerous portions of the *M. buccinator* and the *M. mandibulo-labialis.*

Discussion and conclusions

In the rostral head region of *Cryptomys* the gnawing teeth form a suitable digging tool, because of their extraoral and prominent rostral position (comp. BOLLER, 1970). The *Regio rhinarica* and the underlying *cupula nasi* anterior are situated behind the gnawing teeth. As the latter therefore come into contact with the substrate more often than the rostrum, the incisors also seem to be an important rostral instrument for gathering tactile information from the environment (comp. ADE, 1999). This is most likely the reason that the narial pads, i.e., tactile elements of the nose tip of rodents, are hardly represented in the examined juveniles of *Cryptomys*. That the indistinct pairy elements in the internaric region have to be regarded as narial pads at all is finally supported by ADE (1998), who provides ontogenetic evidence for narial pads in *Cryptomys mechowi*.

In *Cryptomys* the *Regio supralabialis* is continuous with the oral region. In the sense of a broad contact, the supralabial skinfolds of the *Regio rhinarica* can therefore be regarded as a link between the external nose tip and the oral region. Most likely, secretions produced by the nasal glands are transported to the oral region along these supralabial skinfolds. Though such a link has been never mentioned as explicitly as in the present paper, it is indirectly confirmed by photographs and illustrations of further representatives of the

The facial musculature of the nasal region enables *Cryptomys* both to modify the entrance of the nasal opening and to move the skin of the rostrum backwards and forwards, i.e., the *dorsum nasi* including the adjacent supranaric part of the *Regio rhinarica* and the upper lip together with the lateral aspect of the *Regio supralabialis*. Two more aspects are probably important with regard to moving the nasal region. Firstly, due to the absence of an anterior wall of the *cupula nasi anterior*, which is regarded as an apomorphic character within hystricognath rodents occurring in all Bathyergidae investigated so far (MESS, 1997, 1999), the dorsal margin of the nasal opening is shifted upwards. Secondly, the lack of the *M. dilatator nasi* in *Cryptomys* most likely causes a high flexibility of the *dorsum nasi* in rostral direction. To date, a comparable condition is only known for the naked mole-rat *Heterocephalus glaber*, where the *M. dilatator nasi* is either strongly reduced or lacking (MEINERTZ, 1951). Taken together, these aspects indicate that the rostral protrusion of the *dorsum nasi* is unlikely to be without influence on the nares, i.e., the forward-movement of the *dorsum nasi* seems to be a covering mechanism of the nasal openings. This mechanism is interpretated as protecting the nasal cavity from penetration by the substrate while digging. This hypothesis is supported by behavioural observations of the naked mole-rat, which is able to cover the nares by an integument fold (STARCK, 1957; HILL *et al.*, 1957).

In *Cryptomys* the *cupula nasi anterior* is ventrally almost completely supported by the premaxilla. It is interpretated as a stabilizer of the rostral nasal cartilage. During digging powerful mechanical forces fused upper *inflexa pellita* have to be regarded as an apomorphic char-

[illegible]

them (TULLBERG, 1899/1900). However, it is yet to be determined if this fusion is either an autapomorphic character of *Cryptomys* or a mole-rat defining condition within hystricognath rodents.

In conclusion, with regard to fossorial lifestyle the gnawing teeth form a suitable digging tool in the rostral head region, particularly due to their extraoral position. Based on the flexible *dorsum nasi* and the differentiation of the cartilaginous nasal skeleton, the nares can be almost completely closed during digging. The *inflexa pellita* form a mobile oral instrument that protects the actual mouth cavity from irritating substrate during digging.

Prospectively, further examinations within the Bathyergidae and the Rodentia are necessary, especially with regard to the distribution of the following character states: 1) indistinct narial pads; 2) continuation of the *Regio supralabialis* into the oral region; 3) lack of an anterior wall of the *cupula nasi anterior*; 4) lack of the *M. dilatator nasi*, and 5) fusion of the upper *inflexa pellita*. Moreover, future research should be aimed at homologizing the various portions of the *M. nasolabialis profundus* within rodents in order to allow phylogenetic interpretations.

References

ADE M., 1998 —
Makroskopische Untersuchungen am Rhinarium der Glires (Rodentia und Lagomorpha). Eine Studie zur evolutiven Differenzierung des Rhinariums auf phylogenetisch-systematischer Grundlage. Berlin, Wissenschaft and Technik Verlag, 150 p.

ADE M., 1999 —
External morphology and evolution of the rhinarium of Lagomorpha. With special reference to the Glires hypothesis. *Mitteilungen aus dem Zoologischen Museum, Zool. Reihe,* 75 (2): 191-219.

ADE M. and ZIEKUR I., 1999 —
The Forepaws of the Rodents *Cryptomys hottentotus* (Bathyergidae) and *Nannospalax ehrenbergi* (Muridae, Spalacinae): Phylogenetic and Functional Aspects. *Mitteilungen aus dem Zoologischen Museum Naturkunde in Berlin, Zoologische Reihe,* 75 (1): 11-17.

BANKE J., 1999 —
Morphoökologische Untersuchung der vorderen Kopfregion von Cryptomys hottentotus (Bathyergidae, Rodentia). Dipl. arbeit, Humboldt-Univ., Berlin, 72 p.

BOLLER N., 1970 —
Untersuchungen an Schaedel, Kaumuskulatur, und aeusserer Hirnform von *Cryptomys hottentotus* (Rodentia, Bathyergidae). *Zeitschrift für wissenschaftlische Zoologie,* 181 (1/2): 7-65.

FRAHNERT S., 1998 —
Zur Stellung des Bibers (Castoridae: Castor) im System der Nagetiere (Rodentia). Eine craniogenetische Studie zur Ethmoidalregion sciurognather Rodentia. Berlin, Wissenschaft and Technik Verlag, 150 p.

GAMBARYAN P. P., 1989 —
Evolution of facial musculature of Mammals. Leningrad, Nauka, Acad. Sci. URSS, Zool. Institute: 1-148. (in russian)

HILL W. C. O, PORTER A., BLOOM R. T., SEAGO J. and SOUTHWICK M. D., 1957 —
Field and laboratory studies on the naked mole rat, *Heterocephalus glaber. Proceedings of the Zoological Society, London,* 128: 455-514.

JARVIS J. U. M. and BENNETT N. C., 1991 —
In SHERMAN P. W., JARVIS J. U. M., ALEXANDER R. D. (eds): *The biology of the naked mole-rat.* Princeton, Princeton University Press: 66-96 .

MAIER W., SCHRENK F., 1987 —
The hystricomorphy of the Bathyergidae, as determined from ontogenetic evidence. *Zeitschrift für Säugetierkunde,* 52: 156-164.

MEINERTZ T., 1942 —
Das oberflächliche Facialisgebiet der Nager. *Zoologische Jachbucher Abteilung für Anatomie,* 67: 119-270.

MEINERTZ T., 1951 —
Das Facialisgebiet der Nager. VIII. Bathyergini Winge, sowie einige Bemerkungen über *Pedetes caffer* (PALL.). *Morphologisches Jahrbuck,* 90: 105-147.

MESS A., 1997 —
Ontogenetische und phylogenetisch-systematische Studie zur Ethmoidal- und Orbitalregion der Hystricognathi (Rodentia). Berlin, Wissenschaft and Technik Verlag, 110 p.

MESS A., 1999 —
The rostral nasal skeleton of hystricognath rodents: Evidence on their phyologenetic relationships.

Mitteilungen aus dem Zoologischen Museum Naturkunde in Berlin, Zoologische Reihe, 75 (1): 19-35.

SABAN R., 1970 — "Musculature peaucière de la tête du cou". *In* GRASSÉ P. P. (ed.): *Traité de Zoologie*, 16 (3): 480-680.

SHERMAN P. W., JARVIS J. U. M. and ALEXANDER, R. D. (eds), 1991 — *The biology of the naked mole-rat.* Princeton, Princeton University Press.

SCHULZE F. E., 1912 — Die Erhebungen auf die Lippen- und Wangenschleimhaut der Säugetiere. I. Ruminantia. *Sitzungberichte der Königlischen Preussigen Akademie de Wissenschaften*, 25 (3): 510-521.

STARCK D., 1957 — Beobachtungen an *Heterocephalus glaber* Rüppel 1842 (Rodentia, Bathyergidae) in der Provinz Harar. *Zeitschrift für Zaugetierkunde*, 22: 50-56.

STARCK D. (ed.), 1995 — *Lehrbuch der Speziellen Zoologie. II/V/I - Säugetiere.* Jena, Stuttgart, New York, Fischer, 694 p.

TULLBERG T., 1899/1900 — *Ueber das System der Nagethiere. Eine phylogenetische Studie.* Upsala, Akademie Buchdruckerei, 514 p.