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The rostral nasal anatomy of two elephant shrews

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INTRODUCTION

The common name of elephant shrews for the Macroscelididae clearly stems from their long mobile snout. Their taxonomic relations are uncertain and they have been variously associated with insectivores, ungulates, tree shrews, primates and lagomorphs (McKenna, 1975; Rathbun, 1984). They have been traditionally placed in the order Insectivora (Kingdon, 1974; Nowak & Paradiso, 1983) but they have many differences from other insectivores, such as the presence of a caecum, and some authorities favour the creation of a monotypic order for them, the Macroscelidea (McKenna, 1975; Rathbun, 1984).

Modifications of nasal anatomy have been put to specialised uses in a number of the insectivores. Some of these may be sensory, involving tactile or olfactory senses which are well developed in many members of the group. Others, such as the golden mole, have altered the shape of the nose for better physical adaptation to burrowing. Kingdon (1974) suggested that the role of the organ in the elephant shrews is that of a mobile probe. Although some features of nasal anatomy in this group have been studied (Broom, 1902; du Toit, 1942), its general structure in the adult has received little attention. This study describes the structure of the rostral nasal cavity in two species, *Elephantulus brachyrhynchus* and *Elephantulus myurus*.

MATERIALS AND METHODS

The specimens for study were taken from two specimens each of *E. brachyrhynchus* and *E. myurus* captured in the wild in 1985 in the Pilanesberg and northern Transvaal regions of South Africa respectively. Tissues were fixed by perfusion with glutaraldehyde under terminal anaesthesia for electron microscopy or by immersion in glutaraldehyde for light microscopy. For light microscopy, the decalcified nasal area was embedded in paraffin in two (*E. brachyrhynchus*) or three (*E. myurus*) blocks, and sectioned at 5–6 μm. Every tenth section was picked up, stained with haematoxylin and eosin and examined.

For electron microscopy the rostral nasal cavity of *E. brachyrhynchus* was decalcified in ethylenediaminetetraacetic acid (EDTA), sectioned transversely into 5 regions, and the appropriate areas for study selected under a dissecting microscope. Specimens were embedded in Araldite, and stained with lead citrate and uranyl acetate; 1 μm sections stained with toluidine blue were used for orientation.

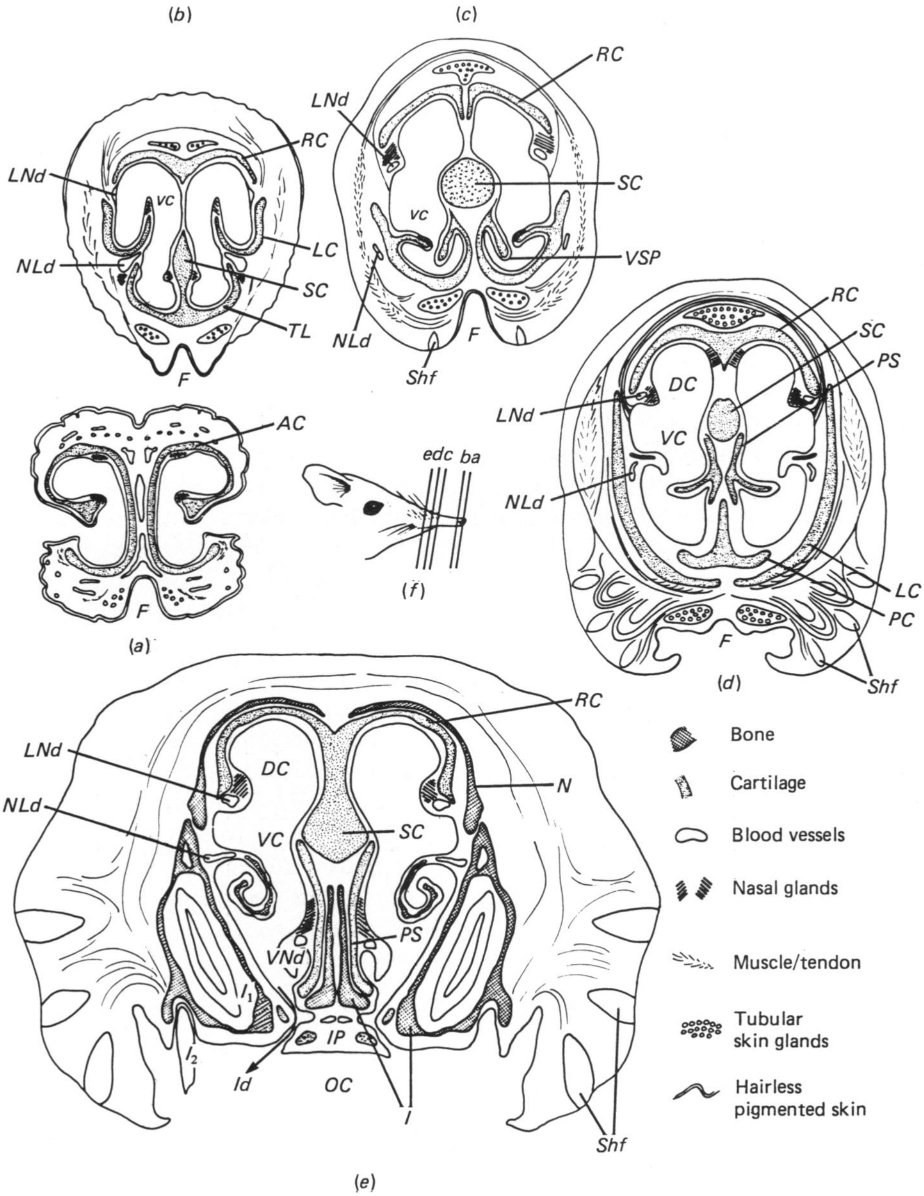

Fig. 1(*a–f*). Diagrammatic transverse sections of the rostral nasal cavity of ***Elephantulus brachyrhynchus***. The position of each section is indicated on Fig. 1(*f*). *AC*, alar cartilage; *DC*, dorsal concha; *F*, ventral furrow; *I*, incisive bone; $I_{1,2}$, incisor teeth; *Id*, incisive duct; *IP*, incisive papilla; *LC*, lateral cartilage; LNd, duct of lateral nasal gland; *N*, nasal bone; *NLd*, nasolacrimal duct; *OC*, oral cavity; *PC*, pre-incisive cartilage; *PS*, paraseptal cartilage; *RC*, roof cartilage; *SC*, septal cartilage; *Shf*, sinus hair follicle; *TL*, transverse lamina; *VC*, ventral concha; *VNd*, vomeronasal duct; *VSP*, ventral septal process.

RESULTS

Of the two species studied, the snout is longer in *E. myurus* than in *E. brachyrhynchus*, but in most aspects the anatomy is very similar. The following description is based on that seen in the smaller specimen, and differences between the two are noted where they occur. The main features of the snout of *E. brachyrhynchus* are shown diagrammatically in Figure 1(*a–f*).

Cartilaginous skeleton

The structural framework consists of a series of cartilages which effectively, if not completely, separate the air passages from the muscular and cutaneous components. The cartilages resemble the rostral part of the embryonic chondrocranium in *E. myurus* described by du Toit (1942); the major components are the septum, roof (tectum nasi) and ventral transverse laminae (laminae transversales anteriores). Associated with the latter are the paraseptal cartilages, extending from near the tip to the caudal extent of the vomeronasal organ.

For a short distance at the rostral tip the external nares are separate, each supported by a C-shaped alar cartilage formed by the dorsal, septal and ventral cartilages. Caudally, each alar cartilage develops a re-entrant hook dorsolaterally, which comes into close association with the ventral cartilage as the caudal boundary of the nares is reached and forms the structural basis of a vestibular concha.

Caudal to the nares, the relationship of the cartilages to one another is variable. There are a number of fenestrae in the septal cartilage, and in some areas it lacks continuity with the dorsal cartilages (Fig. 1*b*, *c*, *d*). A lateral cartilage is separated from the dorsal roof by the insertion of a transverse band of striated muscle and becomes increasingly associated with the ventral cartilage, though separated from it by the terminal part of the nasolacrimal duct (Fig. 1*b*). The ventral cartilages and ventral septum are continuous for some distance caudal to the nares, forming an expanded ventral septum with a pair of ventrolateral processes (Broom's (1902) septal turbinates) (Fig. 1*c*). Further caudally, the septal and ventral elements in this area separate, the cartilages of the septal processes remain with the central part of the ventral cartilages, and lose continuity with the transverse part of the ventral cartilage to become the paraseptal cartilages (Fig. 1*d*, *e*). Modifications and reductions of the paraseptal cartilages occur in the region of the incisive duct, and caudally they become the vomeronasal cartilages. A central cartilage extends rostral to the incisive bone and lies between the two vomeronasal cartilages (Fig. 1*d*).

Cutaneous and muscular features

For a short distance the rostral snout is covered with non-hairy pigmented and keratinised skin divided by a pattern of ridges and furrows resembling that in the rhinarium of the dog. The dermis is highly vascular, with thin-walled veins, and contains tubular glands which open on to the surface (Fig. 1*a*). Hairy skin replaces pigmented skin rostral to the caudal narial wall, at first dorsally but spreading ventrally until only the ventral furrow, extending from the rostral tip to the entrance to the oral cavity, is lined by non-hairy skin. Primary hair follicles are of several sizes and are associated with large sebaceous glands and sparse tubular glands. The latter appear to be distinct from the tubular glands associated with non-hairy skin (Fig. 1*b*), which extend deep into the dermis under the hairy skin forming three major aggregations, one dorsal and two ventral (Fig. 1*b*, *c*, *d*). The fine structure of the glands is similar in both locations, consisting of long tubules formed by cuboidal cells with deeply infolded basal cytoplasm and numerous mitochondria (Fig. 2). The secretory cells are surrounded by myoepithelial cells and a fine but distinct envelope of connective tissue. Rostrally, the single dorsal gland spreads across the dorsum but is restricted to a mid-dorsal position more caudally, and ends about the level of the first incisor. The ventral glands lie on either side of the ventral groove and end rostral to the incisive. Each glandular area is accompanied by a large blood vessel and nerve.

Longitudinal muscle bundles extend to the tip of the nostrils, curving round the


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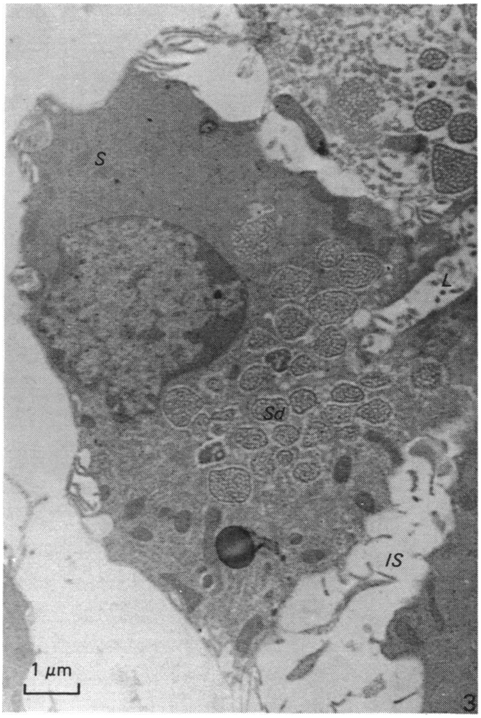
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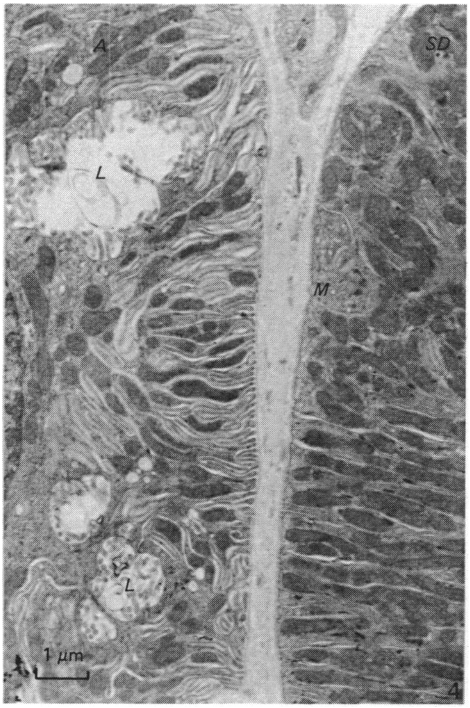
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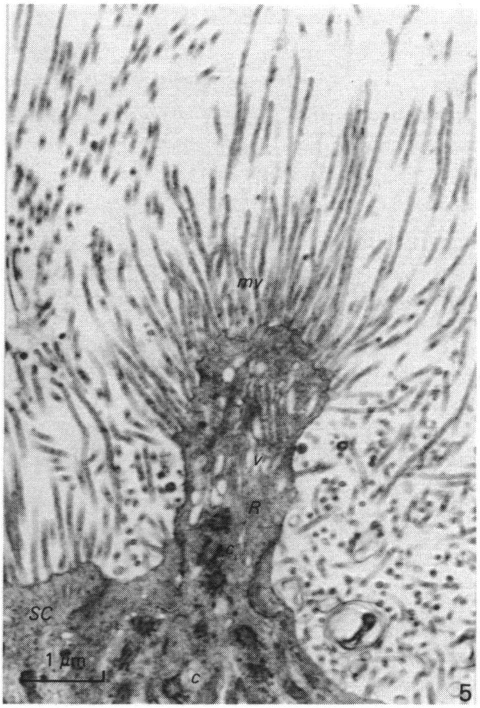
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ventrolateral edge of the alar cartilages (Fig. 1*a*). A thin sheet of transverse fibres lies across the dorsum of the snout, separating the dorsal glandular area from the dermis of the hairy skin. This muscle sheet inserts to the dorsal tip of the lateral cartilages (Fig. 1*b*), medial to a bundle of longitudinally orientated fibres. A dorsoventrally orientated sheet of fibres extends from the vestibular concha to the thick dermis lateral to the ventral groove, and separates each ventral glandular area from the sebaceous glands and hair follicles. This muscle slip is reinforced by fibrous connective tissue more caudally, forming a strong tendinous capsule around the gland.

Nasal features

A low stratified squamous epithelium and thin propria line the internal aspect of the alar cartilages in the vestibule. The first glands opening into the air passages are a small group on the dorsal wall with another on the upturned edge of the lateral wall (Fig. 1*a*). More glands become evident on the ventral angle of the dorsal alar cartilage, and as the nostril becomes a closed tube a small group of glands opens on the ventral septum. The nasolacrimal duct opens medially on the vestibular concha and a large group of glands with a series of openings on the apex of the concha add to the secretions delivered into the ventral nasal cavity. A little further caudally, the duct of the lateral nasal gland (Steno's duct) opens on the dorsolateral wall under the insertion of the transverse muscle band (Fig. 1*b*).

For most of the snout the main glandular areas are septal and conchal. Septal glands include those of the swell body rostrally (Fig. 1*b*) and the vomeronasal glands more caudally. Conchal glands include those of the ventral concha and others on the dorsolateral wall around Steno's duct in an area which becomes increasingly prominent caudally and is continuous with the dorsal concha. Rostrally, glands in this region (Fig. 3) open on to the surface, but more caudally a few alveoli of the lateral nasal gland (Fig. 4) are evident. Throughout most of the snout, a low stratified epithelium lines the air passages except over the glandular areas of the septum and conchae where a higher ciliated epithelium develops, spreading over the dorsal and lateral walls more caudally. Goblet cells are infrequent except over the glandular regions. A low stratified epithelium covers the mid-ventral floor of the nasal cavity for the full length of the snout and lines the incisive and vomeronasal ducts.

There is no chemosensory epithelium in the nasal passages rostral to the oral cavity. Olfactory epithelium extends rostrally on the dorsal septum and dorsolateral wall to the level of the opening of the incisive duct into the nasal cavity. The extent of sensory epithelium increases caudally until it lines the dorsolateral wall and dorsal septum. The fine structure of the epithelium does not differ significantly from that described in

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Fig. 2. Dorsal tubular skin gland. Secretory cells (*S*) have deeply indented basal cytoplasm and numerous mitochondria, and are surrounded by myoepithelial cells (*M*). Collagen fibres (*Col*) and fibroblasts (*f*) form a fine capsule around the tubule.

Fig. 3. Dorsal conchal gland. Secretory cells (*S*) are separated by wide intercellular spaces (*IS*) except at the lumen (*L*). Much of the cytoplasm is occupied by secretion droplets (*Sd*) of variable density.

Fig. 4. Lateral nasal gland. The section shows part of a secretory alveolus (*A*) and of a striated duct (*SD*). Both cell types have deeply indented basal cytoplasm and numerous mitochondria. The alveolar lumen (*L*) is irregular and extends well into the cytoplasm. Myoepithelial cells (*M*) surround striated duct cells.

Fig. 5. Surface of vomeronasal neuroepithelium. A receptor cell (*R*) ends in a rounded process with numerous microvilli (*mv*). Centrioles (*c*) and vesicles (*v*) lie in the receptor cytoplasm. The supporting cell (*SC*) surface also carries microvilli.

other mammals. Tubular olfactory glands and bundles of olfactory nerve fibres occupy the dermis. Where fenestrae occur in the septal cartilage, only a thin line of fibrous tissue separates the olfactory membrane on each side of the septum.

The ducts of the vomeronasal organ open to the nasal cavity at (*E. myurus*), or just caudal to (*E. brachyrhynchus*: Fig. 1 *e*) the opening of the incisive ducts. A short length of the organ extends rostral to the duct, receiving secretions from the most rostral part of the extensive vomeronasal glands. For most of their length, the tubules of the organ are U-shaped in cross section. Chemosensory epithelium lines the U, and ciliated epithelium roofs its dorsal aspect. A large blood vessel lies immediately dorsal to the ciliated epithelium, surrounded by glands which extend caudal to the sensory part of the organ. The main features of the vomeronasal sensory cells resemble those described in other mammalian species, though their distal processes extend further beyond the epithelial surface and carry more microvilli than those of most mammals (Fig. 5).

Communication between rostral oral and nasal cavities

A pair of incisive ducts provides open communication between oral and nasal cavities at the level of the second incisor (Fig. 1 *e*). The ducts open orally into the sulcus that surrounds the mid-line incisive papilla rostral to the first palatal ridge. In the nasal cavity the ducts open close to the vomeronasal ducts, though there is no direct continuity between the two structures. The incisive papilla has a core of fibrous tissue reinforced by a curved cartilaginous rod, and is separated from the palatine process of the incisive bone by an area of vascular tissue. Keratinised epithelium lines the papilla and its sulcus. In *E. myurus*, but not in *E. brachyrhynchus*, taste buds are located on the tip of the papilla and on the medial aspect of the sulcus. The papilla begins rostrally at a central point behind the first incisors, and the sulcus which surrounds it is in continuity with the ventral furrow of the snout. As the oral cavity is reached, the furrow widens slightly but continues without interruption between the first pair of incisors, and ends at the sulcus of the incisive papilla. Thus a system of grooves or furrows links the ventral snout, sulcus and incisive duct.

DISCUSSION

The structural features of the long nose of *Elephantulus* suggest an organ which is flexible and reasonably mobile but not unduly specialised for physical strength or sensory function. Rather, it extends over a longer area the features of the rhinarium and nasal vestibular area found in other species. The supporting cartilages form a continuous ring for only a short distance from the nostrils. For most of the snout separate septal, dorsal, lateral and ventral cartilages allow lateral or dorsoventral movement. Muscles which achieve this belong to two main groups, a lateral, mainly longitudinal group, and a dorsal transverse group. Some of the longitudinal fibres extend to the tip of the alar cartilages, but most are inserted on the ventral cartilages (Fig. 1 *d*). The dorsal fibres are inserted to the tip of the lateral cartilages and to the propria underlying the lateral nasal wall. Contraction of these would appear to be able to modify the shape of the nasal cavity, exert pressure on the duct of the lateral nasal gland, and on the dorsal tubular skin glands. In the same way, fibres inserted near the ventral furrow may modify its shape and apply pressure to the ventral pair of tubular glands. The complex array of striated muscle fibres lateral to the furrow is associated with the large and numerous sinus hairs.

Most of the snout is covered with hairy skin well provided with sebaceous glands but with only a few small tubular sweat glands associated with the hair follicles. Sinus hairs are ventrolateral in position and increase in size and number towards the oral cavity. There is no area of hairless skin on the dorsum of the snout as in *Solenodon* (Hofer, 1982*b*). The bare pigmented skin of the tip is well provided with Merkel cells but does not appear to have any unusual sensory features. The lining of the ventral furrow is non-glandular stratified squamous epithelium throughout its length.

The most unusual feature of the skin is the development of the dorsal and ventral tubular glands. Although the secretory areas extend the whole length of the snout, the ducts open only to the smooth skin of the tip, and provide secretions here to which the products of the nasolacrimal and lateral nasal gland ducts would be added, since both of these open close to the nostrils. These elephant shrews feed largely on ants and termites (Smithers, 1983) and many of these social insects have a wide range of chemical defences which are injected into or sprayed on to predators (Brian, 1983). The soldier caste of some termites spray attackers from a distance with complex mixtures of mono- and di-terpenes (Baker & Walmsley, 1982), which function as entangling agents, irritants and topical poisons (Prestwich, 1983). Some termite-eating mammals avoid termites with this form of defence (Redford, 1984), but others do feed on them including *Tamandua* anteaters (Lubin & Montgomery, 1981) and the aardwolf *Proteles cristatus* (Richardson, 1987), while elephant shrews *Elephantulus* spp. will feed on these species in captivity (Nasutitermitinae: *Trinervitermes*: P.F.W., personal observations), although they often rapidly withdraw their snout after first approaching the termites. The secretions released at the tip of the elphant shrew's snout may serve to protect the rostral epithelium from this chemical assault.

The extended nasal cavity in the long snout does not contribute to the special chemosensory functions of the nose. The opening of the incisive duct marks the transition from the vestibule to the nasal cavity proper, and the extent and organisation of the olfactory and vomeronasal neuroepithelia within the cavity present no unusual features. The anatomy of the oronasal region, the structure of the vomeronasal organ and the relationship between its duct and the incisive duct have been examined in a number of insectivores and prosimian primates, in the expectation that they may provide clues to affinities in problematical classifications (Hofer, 1977, 1982*a*, *b*; Hedewig, 1980). The results remain inconclusive, complicated by the diversity of structures which serve several functions and by the development of an elongated rostrum or a longer proboscis in a number of groups. Within the tenrecs, considered by some an archaic group of insectivores, Hofer (1982*a*, *b*) found major differences in the anatomy of the incisive (nasopalatine) ducts and the palatine papilla. He concluded that the organisation of these structures in *Setifer* and *Echinops*, though not in other Tenrecinae, differed from that in the tree shrews and lemuriform primates. Hedewig (1980) found that the anatomy of the cartilages in the vomeronasal and incisive ducts linked the prosimians *Nycticebus coucang* and *Galago crassicaudatus* with other insectivores rather than with the tree shrew *Tupaia*, but the structure of the vomeronasal organ itself in *Nycticebus* was closer to that of *Tupaia* than to its fellow prosimian *Galago*. Broom (1902) examined the vomeronasal organ of *Macroscelides proboscideus* and concluded that its characteristics linked it with the marsupials. His observations, based on a fetal specimen, noted that the vomeronasal duct opened directly to the incisive duct, a condition which he claimed to be characteristically marsupial. More recent investigations of nasal and palatal anatomy in marsupials and megachiroptera show that the arrangement of the ducts varies from one species to another, and no one condition can be described as characteristic of the group (Kratzing, 1987). Variability is seen in the two species studied here, since the vomeronasal duct opens to the nasal cavity caudal to the incisive duct in *E. brachyrhynchus* but to both the nasal cavity and the incisive duct in *E. myurus*. Variability is also evident in the presence of taste buds on the incisive papilla in *E. myurus* but not in *E. brachyrhynchus*. The occurrence of taste buds on the papilla or at the oral entrance to the incisive ducts has been noted in a variety of mammals (Kolmer, 1927; Hofer, 1977, 1980; Wohrmann-Ripenning, 1978; Miller & Smith, 1983; Kratzing, 1987), but a specific role for their unusual location remains to be identified.

SUMMARY

The nasal anatomy of *Elephantulus brachyrhynchus* and *E. myurus* shows adaptations needed for a long, mobile snout with no special chemosensory features. Olfactory and vomeronasal neuroepithelia do not extend rostral to the nasal opening of the incisive ducts. Their fine structure presents no unusual features. Separate dorsal, lateral and ventral cartilages and fenestrations in the septal cartilage permit snout flexibility.

Dorsal and ventral tubular glands extend the whole length of the snout under the dermis but only release their secretions at the tip, together with the products of the nasolacrimal and lateral nasal gland ducts. These secretions may protect the bare rostral epithelium from the chemical defences of termites and ants, which are major food items.

A ventral groove in the snout communicates directly with the sulcus of the incisive papilla on the rostral palate. The oral openings of the incisive ducts also lie within the sulcus.

Variability in the relation of the vomeronasal duct to the incisive duct and in the presence of taste buds on the incisive papilla in the two species of *Elephantulus* studied here limit their value as evidence of relationships between elephant shrews and other insectivores and prosimians.

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