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ORIGINAL RESEARCH

Histological analysis of scent glands in banded mongooses, with implications for chemical communication

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Abstract

Chemical communication is the most ancient and widespread form of communication. In many species, specialised structures called scent glands have evolved to facilitate this communication. These glands vary considerably among species in structure, size, body location and the composition of their secretions. Histological analysis is therefore required to confirm the presence of scent glands, identify secretion types and assess potential roles of the immune system and microbiota in modifying secretions. Here, we investigated the distribution and structure of scent glands in the banded mongoose (*Mungos mungo*), a cooperatively breeding, group-living mammal. We found that individuals possess two large (1.5 cm diameter) anal glands, each consisting of a central sac surrounded by glandular tissue. This in turn is surrounded by a layer of striated muscle, which likely facilitates the deposition of relatively large quantities of odorous chemicals when engaging in deliberate scent marking behaviour. The glands are lined by two different types of epithelia (keratinised and non-keratinised) which may impact how immune genes such as the major histocompatibility complex (MHC) affect the microbiome of the glands, and therefore, the chemicals that are secreted during scent marking. Additionally, we reveal a previously unidentified small (0.75 mm in length) scent gland in the cheek, which may be used for scent marking. We provide evidence that banded mongooses may use their chin and abdomen for scent rubbing, as these regions are often rubbed in odorous substances, but we found no evidence of specialised scent glands in these areas. Our findings highlight the importance of integrating anatomical, behavioural and biochemical approaches to understand the mechanisms and purposes of scent communication. This study serves as a foundation for future research on the interplay between scent marking and rubbing behaviours, and the role of immune genes and microbiota in shaping chemical communication in banded mongooses and other mammalian species.

Introduction

Chemical communication is regarded as the earliest and most extensive form of signalling among animals (Wyatt, 2014). In mammalian communication, chemical signals are commonly conveyed through scent marking, defined as the deposition of an odour into the environment (Johnson, 1973; Reiger, 1979). These odours often come from multiple sources and scent

marking can occur through the deposition of urine, faeces and glandular secretions (Kleiman, 1966; Macdonald, 1980). Although originally thought to solely function as a territorial defence strategy (Gosling, 1982; Hediger, 1949), scent marking has also been observed in non-territorial species (Coombes et al., 2018; Heymann, 2006; Johnson, 1973; Ralls, 1971), suggesting alternative functions. There is growing empirical evidence that the function of scent marking is multifaceted and can communicate substantial information to conspecifics (Ferkin, 2019). For example, studies have shown that scent conveys information regarding the depositor's identity (Kean et al., 2015), the identity of their social group (Vaglio et al., 2016), their sex and age (Linklater et al., 2013), reproductive status (Mitchell, Cant, & Nichols, 2017), social status (Burgener et al., 2009), genetic relatedness (Charpentier et al., 2010), genetic diversity (Stoffel et al., 2015), MHC composition (Radwan et al., 2008) and infection status (Mitchell, Cant, Vitikainen, & Nichols, 2017). Furthermore, the same information can be conveyed from different odour sources and these sources can vary between species. For instance, reproductive status is communicated through urine in house mice *Mus musculus* (Achiraman et al., 2010), vaginal and flank odours in golden hamsters *Mesocricetus auratus* (Johnston, 2003) and anal gland secretions in banded mongooses *Mungos mungo* (Mitchell, Cant, & Nichols, 2017).

For chemical communication to occur, a secretion is usually deposited from the animal into its environment (Johnson, 1973), either by releasing odours into the air, or by employing marking behaviours that involve depositing the odour onto a surface, either through urination/defecation or by rubbing the region of the body in which the odour is located onto an object or conspecific (Gorman & Trowbridge, 1989). Scent marking also includes overmarking, in which the scent mark of one individual is placed directly on top of a scent mark of a conspecific (Johnson, 1973; Ralls, 1971). However, behaviours that appear to be scent marking may, in fact, represent scent rubbing: A less understood action in which animals rub their bodies in odorous substances to acquire scents, rather than deposit them (Alfaro et al., 2012; Gosling & McKay, 1990). For example, cheek and neck rubbing has been documented in several mammalian species (Allen et al., 2017; Charlton et al., 2020; Gosling & McKay, 1990; King et al., 2016) and body rubbing is commonly exhibited by carnivores when individuals collapse their forelegs and push themselves through an odorous substance using their hindlegs (Reiger, 1979). However, it is unclear whether these rubbing behaviours occur purely for the acquisition of odours, or also for their deposition, as abdominal scent glands have been found in several small mammals (reviewed in Bakshi, 2010). Therefore, as scent marking and scent rubbing are observationally similar, anatomical and histological investigations into the presence of scent glands are needed to determine whether a behaviour serves the purpose of depositing or acquiring scents.

Another contributing factor to variation in scent communication is the structure and function of scent-producing glands. Scent glands are exocrine glands that release their secretions onto bodily surfaces such as the skin or through ducts (Freeman et al., 2021). Mammals possess a wide range of such exocrine glands that support diverse communicative functions (see Bakshi, 2010; Thiessen & Rice, 1976). These glands are derived from a variety of skin structures, often comprising both sebaceous (oily) and sudoriferous (sweat) glands (Albone, 1984), and have evolved to produce, deposit, store and modify odours in several ways (Gorman & Trowbridge, 1989). Sebaceous glands produce sebum, a lipid-rich secretion that is deposited on the surface of the skin (Pawlina, 2024) in a holocrine process, during which the cell producing the secretion disintegrates and releases its content into a secretory duct (Schneider & Paus, 2010). Due to their longevity in the external environment, sebaceous secretions are often used for marking objects and conspecifics (Gorman & Trowbridge, 1989). Most sebaceous glands are associated with hair follicles, forming part of a pilosebaceous unit, which consists of the gland, a hair follicle and an associated muscle (Schneider et al., 2009). In this unit, sebum is secreted via the pilosebaceous canal, which transports secretions to the skin (Pawlina, 2024; Schneider et al., 2009). In deer, specialised hairs called osmetrichia have evolved to allow the aggregation of sebaceous secretions within the hair (Ajmat et al., 1999; de la Peña et al., 2021; Müller-Schwarze et al., 1977). However, other sebaceous glands are free from hair follicles and deposit their secretions onto the skin via a distinct secretory duct (Schneider & Paus, 2010). While several functions of sebum have been postulated (reviewed in Smith & Thiboutot, 2008; Vanderwolf et al., 2023), the sebum from some modified sebaceous glands, such as the preputial glands of mice, has been found to contain pheromones (Bronson & Caroom, 1971; Zhang et al., 2008), suggesting these scent-producing chemicals are gland-derived (Wyatt, 2017) and disseminated via the sebum. In contrast to sebaceous glands, sudoriferous glands secrete water-soluble secretions with low durability that are airborne or used to mark objects for short-term chemical communication (Gorman & Trowbridge, 1989). Like sebaceous glands, sudoriferous glands can secrete directly onto the skin (eccrine glands) or through the pilosebaceous canal leading onto the skin (apocrine glands).

The complexity and specialisation of scent glands varies, either occurring in higher numbers in certain regions of the skin or evolving anatomical structures that can store and potentially biochemically alter the secretions (Albone, 1984). For example, anal glands, which are present in many mammal species (McColl, 1965), have evolved from an invagination of the skin to form a sac in which the secretions of associated sebaceous and apocrine glands are stored. These anal sacs provide a moist, warm and often anaerobic environment that facilitates microbial activity (Gorman & Trowbridge, 1989). In line with previous literature in veterinary medicine (Ehrenzweig, 2018), we refer to this entire structure as the anal gland, despite it containing both glandular and non-glandular tissue. In contrast to gland-derived chemicals, the fermentation hypothesis posits that the set of volatiles emitted by an individual—referred to as the volatilome—may be shaped by the microbial modification of odorants and odourless precursors within secretions (Natsch et al., 2003; Schubert et al., 2021). In the anal glands, for example, the microbiota can alter the volatiles emitted through the fermentation of protein and lipid-rich substrates to

produce odorous metabolites (Gorman et al., 1974). Furthermore, variation within the bacterial communities that constitute the microbiota has been found to contribute to variation in odours that can lead to chemical recognition between social groups in the spotted hyena *Crocuta crocuta* (Theis et al., 2012) and between individuals in the Indian mongoose *Herpestes auropunctatus* (Gorman, 1976). Experimentally removing fermentative anaerobic bacteria from the anal glands of Indian mongooses removed the volatile odorous components of their scent marks (Gorman et al., 1974), indicating that, at least in some scent glands, the microbiota is integral to the production of chemical signals used in scent communication.

The microbiome is affected by external factors, such as the microclimate of a body part (Spor et al., 2011), as well as by internal factors, including the host's immune response (Khan et al., 2019). A crucial part of the adaptive immune system is the MHC (Bjorkman et al., 1987). The MHC regulates discrimination between self-derived and foreign peptides and initiates the removal of peptides of pathogenic origin in jawed vertebrates (Kaufman, 2018). Beyond its role in pathogen elimination, the MHC also facilitates tolerance towards commensal microbiota (Khan et al., 2019; Kubinak et al., 2015; reviewed in Schubert et al., 2021). By regulating the immune response to microbiota, the MHC could therefore influence the composition of the commensal microbial community (reviewed in Schubert et al., 2021) and in turn impact the volatilome produced by the microbial community (Singh et al., 1990). Immunological research has thus far mostly focused on investigating interactions of the MHC with microbiota in the gut, but tissue-specific differences between skin and gut (Spor et al., 2011) could impede drawing universal conclusions for skin microbiota. In general, both tissues share characteristics that should enable interactions between the MHC and microbiota on both the skin and gut mucosa similarly (Artis, 2008; Pasparakis et al., 2014). Despite these common mechanisms of MHC interactions with microbiota in gut and skin, histology should aid in identifying the specific cells and therefore potential pathways involved in the immune response towards microbiota within scent glands.

Banded mongooses (*Mungos mungo*) present an excellent opportunity for furthering our understanding of scent communication in mammals. These highly social, cooperatively breeding African carnivores live in social groups of around 20 individuals (Cant, 2000). Banded mongooses are territorial, and their home ranges overlap considerably with neighbouring groups, leading to frequent and violent intergroup conflicts (Cant et al., 2013; Müller & Manser, 2007). While previous studies have found that scent marking is used for communication both within and between groups (Müller & Manser, 2008), scent marking appears to play a greater role in intrasexual competition than in territorial defence (Jordan et al., 2010; Jordan, Mwanguhya, Furrer, et al., 2011). Banded mongooses rely on multiple sources for scent communication, with scent presentation experiments conducted in the wild demonstrating that faeces, urine and anal gland secretions convey information (Jordan et al., 2010; Müller & Manser, 2008). However, other body locations that may be used in scent communication include the cheeks, chin and abdomen (Fig. 1).

Like many other mammals (McColl, 1965), banded mongooses are known to possess anal glands (Fig. 2). Multiple studies have analysed anal gland marking behaviour (Mitchell, Cant, & Nichols, 2017; Müller & Manser, 2007, 2008) and the chemical profiles of their anal gland secretions (Jordan et al., 2010; Jordan, Manser, et al., 2011; Jordan, Mwanguhya, Furrer, et al., 2011; Jordan, Mwanguhya, Kyabulima, et al., 2011). Anal gland marking in banded mongooses involves rubbing or dragging the anal region horizontally across a substrate (Fig. 1a) and anal gland secretions are the most commonly deposited odour cue (Mitchell, Cant, & Nichols, 2017). The anal glands are located either side of the anus, with the secretory ducts releasing their products either side of an anal pouch (Fig. 2, Mitchell, 2017). While cats and dogs possess anal glands that are involuntarily emptied during defecation (Ehrenzweig, 2018), behavioural observations of banded mongooses suggest that anal gland secretions are, at least in part, deposited actively as a result of anal rubbing on the ground without simultaneous defecation (Jordan et al., 2010 and personal observation by NS), although passive secretion may also occur during defecation.

Previous studies of banded mongooses have categorised cheek rubbing (Fig. 1b) as a marking behaviour based on behavioural observations (Jordan et al., 2010) and have described cheek marks as 'glandular secretions' (Jordan, Manser, et al., 2011), although neither glands nor secretions have been formally identified. A distinct 'spot' is visible in both cheeks of banded mongooses, defined by a small, round patch of lighter skin surrounded by lighter and sparser fur (Fig. 3). Similar potential cheek glands have also been anecdotally described in dwarf mongooses *Helogale parvula* (Christensen et al., 2016; Rasa, 1973), with Rasa (1973) having obtained an opaque secretion when the cheeks of dwarf mongooses were stroked with a glass slide, although this secretion appeared odourless to the human nose. Furthermore, potential cheek marking has been observed in the yellow mongoose *Cynictis penicillata* (Le Roux et al., 2008), with dominant males increasing their cheek marking rates during the breeding season, indicating this behaviour has a potential role in olfactory mate guarding. However, without histological confirmation of the presence of a scent gland, it is not possible to discriminate scent marking from scent rubbing behaviour.

Other body parts potentially involved in scent marking behaviour include the chin (Fig. 3b) and the abdomen (Fig. 1c). Scent glands in the chin are well documented in the European rabbit *Oryctolagus cuniculus* (Hayes et al., 2002; Mykytowycz, 1965) and scent marking using the chin has also been observed in male greater sac-winged bats *Saccopteryx bilineata* (Caspers & Voigt, 2009). However, to the best of our knowledge, there has been no anatomical or histological investigation confirming the presence of scent glands within the facial region of any mongoose species. Moreover, abdominal rubbing has been observed in banded mongooses but has not yet been described, to the best of our knowledge, or linked to scent marking behaviour in this species, nor its close relatives.

Fuelled by these behavioural observations, we explored the location and histology of known and as yet undescribed scent

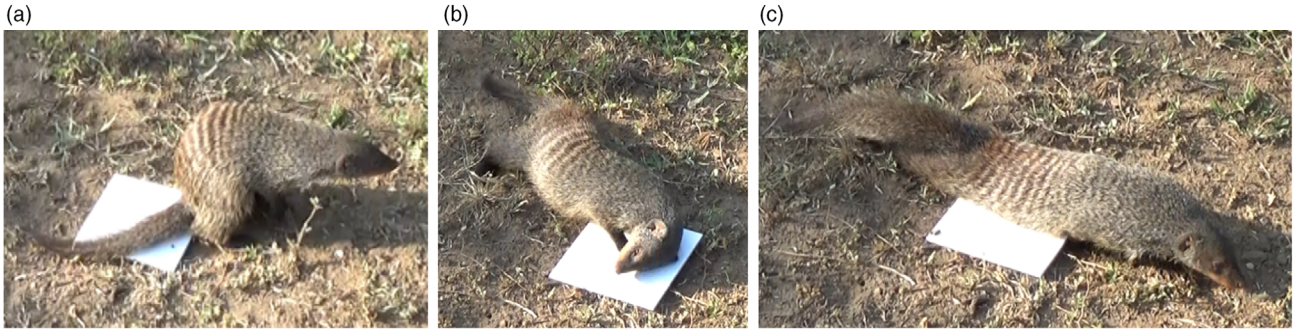

Figure 1 Potential scent marking behaviours of banded mongooses, observed during a scent presentation trial (Schubert et al., 2024), in which banded mongooses were individually presented with anal gland secretions of another individual on a white tile. (a) Anal marking, whereby the individual rubs its anal region across the surface of the tile. (b) Facial rubbing, in which both cheeks and the chin are wiped across the tile. (c) Body rubbing, where the front legs are used to drag the body forward across the tile, with the abdomen maintaining the largest area of contact with the surface of the tile. Photo credit: Nadine Schubert.

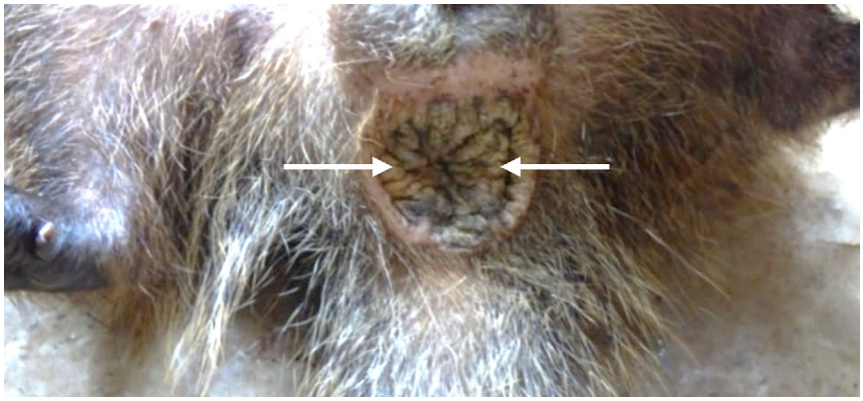

Figure 2 Anal region of a male banded mongoose. Arrows show the openings of the secretory ducts that lead from each sac of the anal glands and terminate on either side of the anus within the anal pouch. Photo credit: Hazel Nichols.

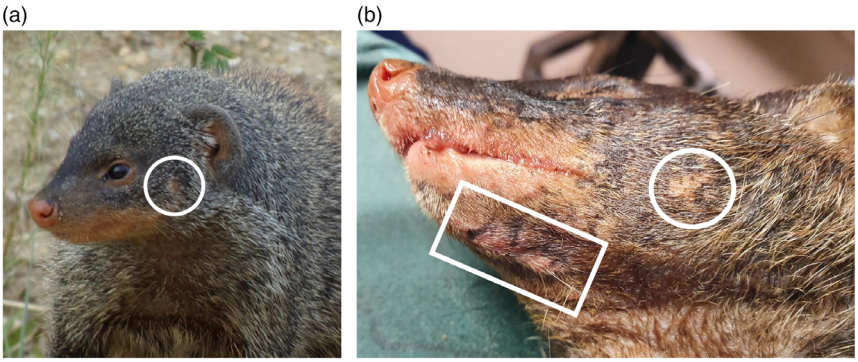

Figure 3 The cheek and chin regions of banded mongooses. (a) The cheek spot of a wild banded mongoose (circle). (b) The cheek spot (circle) and chin region (rectangle) of one of the euthanised adult females used in this study, prior to tissue sampling. Photo credit: Nadine Schubert.

glands in banded mongooses. The presence of anal glands in this species has already been established (Jordan et al., 2010; Mitchell, Cant, & Nichols, 2017; Müller & Manser, 2007), but nothing is yet known about their internal structure. We therefore investigated the overall histological structure of the anal glands, identified glandular structures and determined the mode of secretion. We also evaluated the potential for interactions between the microbiota present in the anal gland and the

immune system, particularly the MHC. We predicted that anal glands would be relatively large, contain both sebaceous and apocrine glands and have associated striated muscle to allow voluntary contractions of the gland. We also predicted blood vessels would be present in close proximity to the anal glands if immune regulation was to occur. In addition, we conducted histological examinations to search for previously unidentified scent glands, focusing on the cheeks, chin and abdomen. Our aim was to determine whether the use of these regions is more indicative of scent marking or scent rubbing, with the presence of scent glands suggesting the former, and an absence of scent glands suggesting the latter.

Materials and methods

Sample acquisition

Four adult female banded mongooses, obtained from the Biobank of Odense Zoo (Odense, Denmark), were used for this study. The individuals were aged between 2 and 11 years and were captively bred, having been born in Odense Zoo or other Danish zoos. Since the individuals were non-CITES listed surplus animals, they were euthanised according to Danish law and the tissue was made available for scientific research. The animals were frozen immediately after death and removed from the freezer the day before dissection. They were then slowly thawed at room temperature and remained cold during dissection.

Dissection and sample preparation

A CT and MRI scan were performed on one individual to identify the exact location and size of the anal glands before dissection (see Figure S1). This was done to identify their *in situ* placement and minimise the risks of destroying the glands during the dissection itself. Glandular structures in the head region or the abdomen could not be identified on the scans (Figure S2), so the dissections were approached with extra care. Both anal glands and tissue encompassing the cheek spot from both cheeks were excised from all four individuals (Fig. 3a). Abdomen tissue was excised from two individuals and chin tissue from one individual. Due to the large area of the abdomen, samples were taken from five locations following an X-shaped pattern and avoiding the mammary glands. All samples were stored in 10% formaldehyde solution for 48 h and were then embedded in paraffin according to the protocol described in the Appendix S1 (Table S1). The anal glands were kept intact or opened laterally to allow us to view the interior of the anal sac before embedding.

Microtomy

The prepared paraffin blocks were serially cut using a rotary microtome. Cheek, chin and abdominal tissue sections were cut to a thickness of 6 µm. Anal gland sections were cut to 10 µm due to the increased fragility of the tissue resulting from the large lumen of the anal sac. Approximately every third section was retained for microscopic analysis. Retained sections were relaxed in a warm water bath heated to 42°C before being placed onto glass slides that had been prepared with a thin layer of protein glycerine (Morphisto, Germany) to enhance adhesion of the tissue to the glass slides. Two sections were mounted on each slide. The tissue sections were then incubated overnight at 58°C to further fixate the tissue sections on the glass slides. A total of 1134 sections were cut from seven of the blocks containing anal gland tissue across all four individuals; 403 sections were cut from six cheek samples across all four individuals; 188 sections were cut from a single chin; and 860 sections were cut from nine abdomen samples across two individuals.

Histological staining and light microscopy

Sections on approximately every third slide from all tissue samples were stained with haematoxylin and eosin (H&E) to provide a general overview of tissue structures. Stained sections were covered with cytoseal XYL (Thermo Scientific). Details of the staining procedure can be found in the Appendix S1 (Table S2). Approximately every third stained section (every 90 µm for anal glands and every 54 µm for all other tissue types) was initially examined. Where potential glands were identified, samples from consecutive slides were stained for further examination. Images were captured using the light microscopic settings of the BZ-X800 fluorescence microscope (Keyence, Neu-Isenburg, Germany).

Results

Anal glands

MRI and CT images of the anal gland can be found in the Appendix S1 (Figure S1). All four individuals possessed two anal glands dorsal to the anus, located either side of the anal canal and measuring approximately 1.5 cm in diameter (Fig. 4).

An overview of the general histology of the anal glands is shown in Fig. 5. Each anal gland consisted of a single anal sac with a large central lumen which serves as a reservoir for secretory products. The anal sac was lined with keratinised stratified squamous epithelium (Fig. 6a) and was connected directly to the anal pouch via a single duct. This duct appeared to be an extension of the anal sac wall and was therefore also lined with keratinised epithelium. The anal sac was surrounded by connective tissue, within which sebaceous and apocrine glandular tissues occurred around the circumference of the anal sac (Fig. 6b). Ducts were present within these glands in all individuals and were found to have a smaller secretory duct directly linking them to the anal sac (Fig. 6b). Unlike the epithelium lining the anal sac, the epithelium lining the intraglandular ducts was non-keratinised stratified squamous epithelium. A thin layer of striated muscle surrounded the periphery of the anal glands following the distribution of the glandular tissue but did not occur between the anal sac and

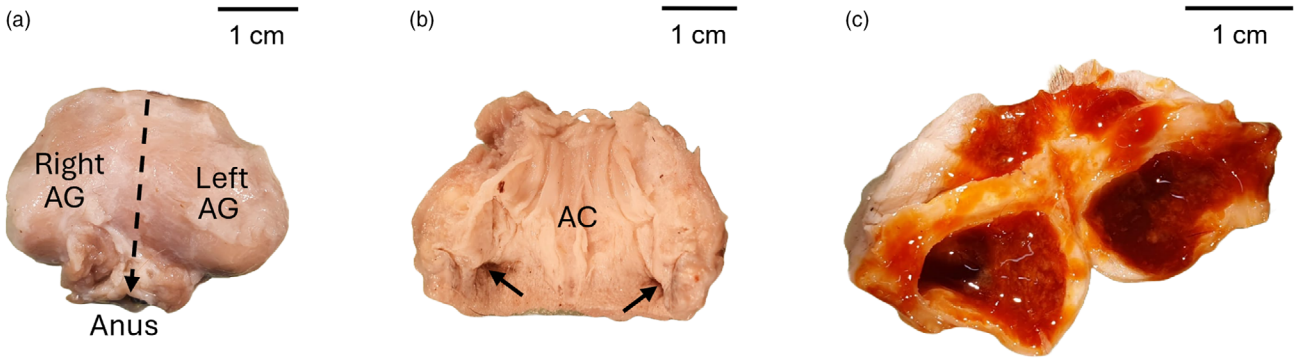

Figure 4 Dissection of the anal glands. (a) The position of the anal glands (AG) at either side of the anal canal (dashed arrow). (b) Midline section of the anal canal (AC) showing a single secretory duct (arrows) leading from each anal sac and terminating either side of the anus within the anal pouch. (c) Midline section of an anal gland showing the lumen of an anal sac containing secretory products from the glands. Scale bars: 1 cm. Photo credit: Nadine Schubert.

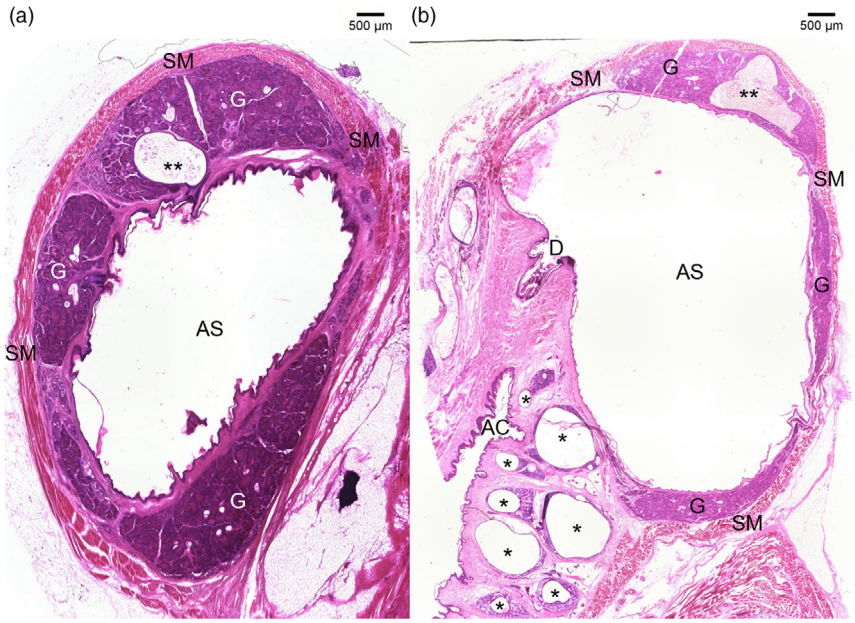

Figure 5 An overview of the histology of the right (a) and left (b) anal glands from two adult female banded mongooses; stained with H&E, original magnification ×2. Each anal gland consists of a large central anal sac (AS) surrounded by glandular tissue (G). This glandular tissue is directly surrounded by a layer of striated muscle (SM) that surrounds the anal sac and the glandular tissue. Multiple secretory ducts are shown that are located within the gland tissue (**) or between the anal sac and anal canal (AC) (*) and protrude directly from the anal sac towards the anal canal (D). Scale bars: 500 µm.

the anal canal. This area was comprised of connective tissue that contained multiple ducts that were observed in all four individuals (Fig. 7a) and the striated muscle layer was found to surround the anal sac and around the posterior of these ducts. Sebaceous glands were located around the periphery of each duct, which release holocrine secretions into the lumen through gaps in the non-keratinised stratified squamous epithelium (Fig. 7b). Despite the ubiquity of these ducts, we were unable to determine whether they are directly linked to the anal sac and the anal canal. Multiple blood vessels were found close to this ductal region between the anal sac and the anal canal (Fig. 7c).

Cheek gland

We found evidence of a free modified sebaceous gland within the dermis of a cheek from a single individual (Fig. 8). This cheek gland was larger than the pilosebaceous complexes and exhibited more irregular-shaped lobules than the comparatively more defined sebaceous glands that partly constituted the surrounding

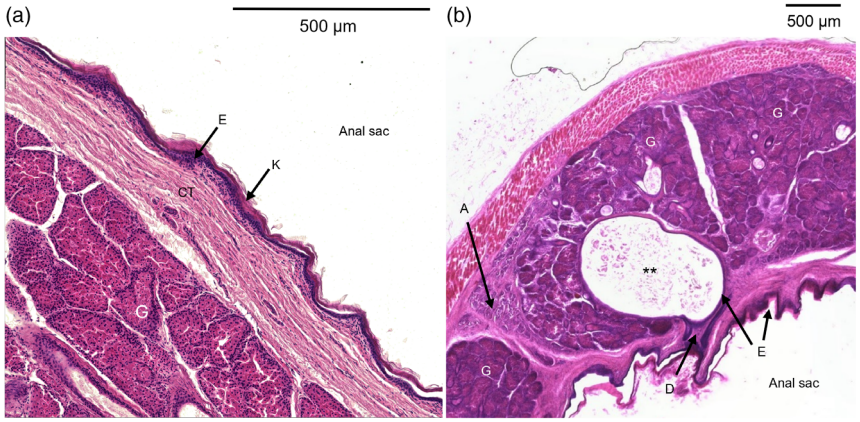

Figure 6 The glands and epithelium of the anal glands; stained with H&E, original magnification (a) ×2 and (b) ×40. (a) The keratinised layer (K) of the epithelium (E) of the anal sac is shown at higher magnification. The surrounding connective tissue (CT) and gland tissue (G) are also present. (b) A small number of apocrine glands (A) are interspersed among more abundant sebaceous glandular tissue (G). The duct within this gland tissue (**), in which traces of secretion can be seen, is connected to the anal sac via a smaller secretory duct (D). Unlike the anal sac, the intraglandular duct is lined with non-keratinised epithelium. Scale bars: 500 µm.

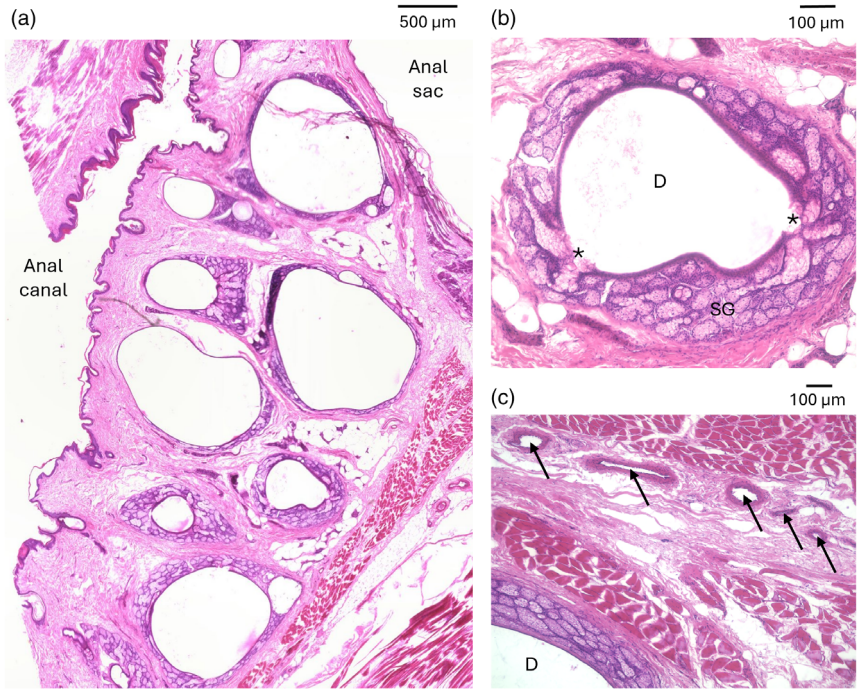

Figure 7 Secretory ducts located between the anal sac and anal canal; stained with H&E, original magnification (a) ×2, (b, c) ×10. (a) An overview of the ducts and the sebaceous glands that surround them. (b) The holocrine secretions of the sebaceous glands (SG) appear to empty directly into the ducts (D) via gaps within the epithelial lining (*). (c) Multiple blood vessels (marked with arrows) are present within the connective tissue surrounding the ducts (D). Scale bars: 500 µm and 100 µm.

pilosebaceous units (Fig. 8a). Rather than secreting sebum directly into the hair follicle, as pilosebaceous glands do, this modified sebaceous cheek gland had a distinct duct lined with potentially non-keratinised stratified squamous epithelium that transports the holocrine secretion directly to the surface of the skin (Fig. 8b).

Chin and abdomen

We found no histological evidence of any scent glands in the chin (Fig. 9) or the abdomen (Fig. 10). Both locations contained multiple pilosebaceous units, which were expected due to hair being prominent in both locations.

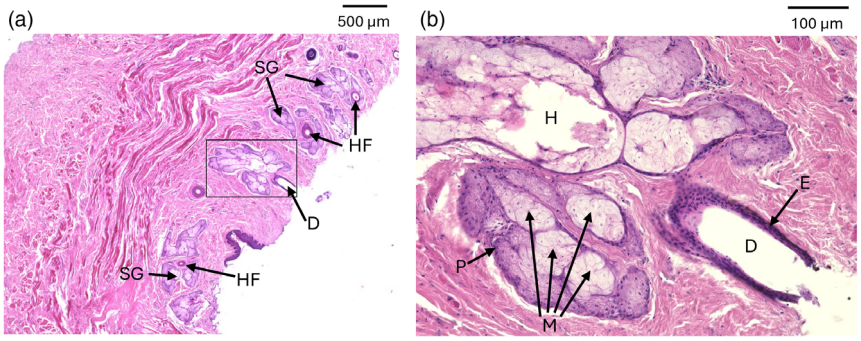

Figure 8 A free modified sebaceous gland found in the cheek of an adult female banded mongoose; stained with H&E, original magnification (a) ×2 and (b) ×20. (a) The cheek gland (boxed area) positioned within the dermis with a distinct secretory duct (D). Notice the cheek gland presents larger, irregular-shaped lobules compared to the surrounding sebaceous glands (SG) associated with a hair follicle (HF). (b) The secretory components of the cheek gland from (a) shown at higher magnification. Proliferating sebocytes (P) replenish the maturing sebocytes (M), which undergo holocrine secretion (H) at the centre of the gland. The secretion is carried from the gland directly to the surface of the skin via a duct (D), lined with stratified squamous epithelium (E). Scale bars: 500 μm and 100 μm.

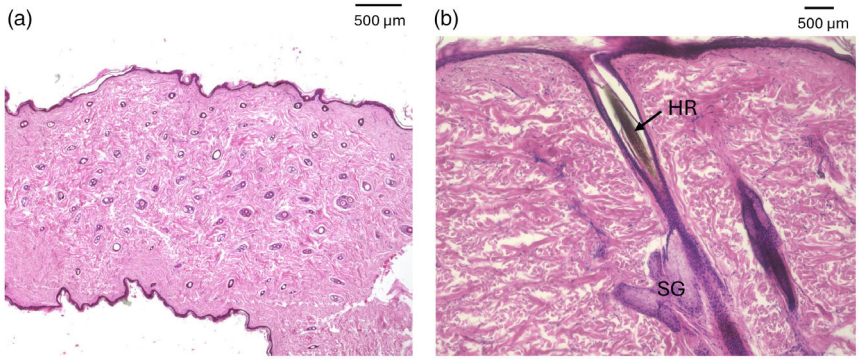

Figure 9 Sections of the dermis from the chin of an adult female banded mongoose; stained with H&E, original magnification (a) ×2 and (b) ×10. (a) A transverse section of the chin showing numerous pilosebaceous units throughout the dermis. (b) A longitudinal section showing the hair root (HR) and its associated sebaceous gland (SG). Scale bars: 500 μm.

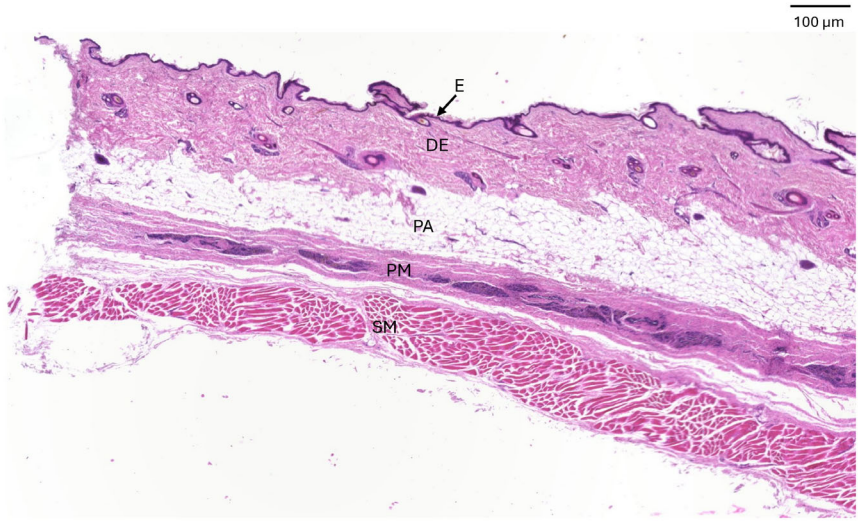

Figure 10 Section of abdominal tissue showing the epidermis (E), dermis (DE), panniculus adipose (PA), panniculus muscle (PM) and striated muscle (SM); stained with H&E, original magnification ×10. Numerous pilosebaceous units are present throughout the dermis. Scale bar: 100 μm.

Discussion

The aim of this study was to explore the locations, histological structures and the mode of secretion of scent glands in banded mongooses. We examined the histology of the anal glands, which are known to have a role in chemical communication, and explored the histology of the cheeks, chins and abdomens of adult female banded mongooses. Consistent with our predictions, the anal glands were relatively large and contained both apocrine and sebaceous glands. The layer of striated muscle surrounding the anal sac aligns with our prediction that banded mongooses may voluntarily excrete anal gland secretions. The epithelium lining the anal sac was keratinised, while the secretory ducts were lined by non-keratinised epithelium, suggesting that the potential for the immune system to regulate the microbiota within the anal gland may vary depending on the gland location in which the microbiota is found. We also observed several blood vessels close to the anal gland, which may increase the potential for immune regulation of the microbiota. Histological analysis confirmed the presence of a yet undescribed sebaceous scent gland in the cheek of the banded mongoose, suggesting that cheek rubbing behaviour is likely involved in scent marking, while the absence of scent glands in the chin and abdomen suggests these locations are involved in scent rubbing.

The anal glands of banded mongooses were relatively large (1.5 cm diameter) compared to their body size (1–1.6 kg and 30–45 cm in length excluding the tail, Stuart & Stuart, 2015), allowing them to store and secrete a large amount of secretion at any given time. Accordingly, a mean of 0.35 g (± 0.034 g SE) of secretion was previously extracted from both glands of 21 live females, with a maximum extraction of 1.10 g (HJN, unpublished data). Jordan, Manser, et al. (2011) found adult banded mongooses preferentially overmarked scents from anal gland secretions from the same sex, and this was driven by the sex of the most recent overmark. Furthermore, males with higher overmarking scores begin mate-guarding at an earlier age, a behaviour which secures males the majority of the matings (Jordan, Mwanguhya, Furrer, et al., 2011). Therefore, producing larger quantities of anal gland secretion may enhance mating success by providing a competitive advantage during intrasexual competition.

We identified both sebaceous and apocrine glands in the anal glands of banded mongooses, supporting previous findings in several mammalian species (McColl, 1965). Similarly, sebaceous and apocrine glands have been found in the preorbital glands of ungulates (Moawad, 2016) and canines (Ehrenzweig, 2018), which also play a key role in olfactory communication, suggesting that these glands likely serve a similar function in the anal glands of banded mongooses. Furthermore, sebaceous and apocrine secretions have been found in the anal gland secretions of Indian mongooses, which contribute to distinct odours used by conspecifics for individual recognition (Gorman, 1976). Our histological analysis found that the sebaceous glands, which produce lipid-rich secretions that increase the longevity of scent marks (Gorman & Trowbridge, 1989), were notably larger and more abundant than the apocrine glands. This aligns with observations of banded mongoose marking behaviour, in which anal gland secretions are frequently used to mark surfaces (Jordan et al., 2010) and therefore must endure in the environment for long enough for conspecifics to find them (Gorman & Trowbridge, 1989; Gosling & Roberts, 2001). Our results also support previous gas chromatography–mass spectrometry analysis of anal gland secretions of banded mongooses, which found an abundance of cholesterol, a relatively heavy molecule with low volatility (Mitchell, Cant, & Nichols, 2017; Mitchell, Cant, Vitikainen, & Nichols, 2017).

Regarding the method of excretion of the anal gland products, we found a layer of striated muscular tissue surrounding the anal sac, a component generally associated with voluntary control. However, the presence of striated muscle does not negate the possibility of involuntary control, as observed in the oesophagus, where striated muscle involved in swallowing initiates subsequent involuntary peristaltic contractions (Goyal & Chaudhury, 2008). While dogs can only passively excrete from their anal glands as a result of pressure created during defecation (Aronson, 2003), behavioural observations indicate that banded mongooses can deposit anal gland secretions independently of defecation (Jordan et al., 2010 and personal observation by NS). A similar situation occurs in spotted hyenas, whereby the gland is protruded to deposit odorous paste (Burgener et al., 2009). Nevertheless, given that voluntary and involuntary control mechanisms can coexist, further investigations into the muscular control of the anal glands of banded mongooses and other mammals are necessary to confirm the extent of voluntary excretion.

Previous work has suggested that odours can be influenced by the microbiome (Costello et al., 2009; Song et al., 2013), in addition to internal factors such as an individual's immune response (Bard et al., 2000; Willse et al., 2006). Furthermore, immunological evidence from medical research hints at a potential interaction between immune genes, the microbiome and the chemical composition of scents (reviewed in Schubert et al., 2021). However, there are tissue-specific factors affecting the cells involved in the immune response towards microbiota (Spor et al., 2011), that may lead to different relationships in different tissues. For example, the gut is lined by a mucosa with a non-keratinised epithelium and contains excessive lymphatic tissue (reviewed in Artis, 2008), whereas skin is mostly formed of keratinocytes and specialised immune cells such as the Langerhans cells and dendritic epidermal T cells (reviewed in Pasparakis et al., 2014). As the histology of the anal gland of banded mongooses had not been previously investigated, potential immunological similarities with other tissues remained unclear.

Our analysis of the anal gland in banded mongooses revealed two distinct types of epithelia. The anal sac, in which the secretion is presumably stored until excreted through secretory ducts, was lined with keratinised epithelium, whereas the secretory ducts found in the periphery of the anal gland were lined with non-keratinised epithelium. This difference in epithelial structure may result in variation in MHC–microbiota interactions within the anal gland compared to other tissues,

such as the gut, in addition to variation within the anal gland itself. The MHC has the potential to eliminate or induce tolerance towards the microbiota, and this could be mediated by immunoglobulins like IgA on non-keratinised mucosal surfaces (Cullender et al., 2013; Pabst, 2012; Peterson et al., 2007), such as those lining the secretory ducts. Whether this mechanism similarly applies to keratinised, non-mucosal epithelium within the anal sac remains unclear. Furthermore, blood vessels were found in closer proximity to the secretory ducts than the anal sac. This may contribute to potential variation in the immunoregulation of the microbiota in different regions of the anal gland as MHC-carrying cells and antibodies may be able to access secretory ducts more readily. Further research is needed to determine whether differences in epithelial structure affect MHC-driven responses and therefore microbial colonisation. Future studies could explore the types of immune cells present within the anal gland and compare microbial communities found within the anal sac versus the secretory ducts to provide deeper insights into how immune function and anal gland microbiota interact in banded mongooses.

Banded mongooses have been observed rubbing their cheeks against surfaces and this behaviour has been interpreted as a form of scent marking (Jordan, Manser, et al., 2011), despite the lack of an anatomical confirmation of scent glands in the cheeks. Our histological analysis confirmed the presence of an irregularly lobulated sebaceous gland exiting in a small secretory duct in the cheek spot of one adult female. The overall appearance of this gland is comparable to that of the abdominal gland of Mongolian gerbils *Meriones unguiculatus*, which also consists of irregular lobules (Deutschland et al., 2011). As the gland was only observed in one cheek in a single individual, it is possible that the gland was present in other samples but was missed due to its small size (750 μm in length). However, this seems unlikely given that we inspected approximately 134 sections of the cheek area (sampled every ~54 μm) from three further individuals and did not find any evidence of a cheek gland. Nevertheless, while tissue samples were placed in paraffin blocks at different orientations to try and maximise the chances of finding a gland, it is possible that structures in transverse sections may have been less obvious compared to longitudinal sections (see Fig. 9 for comparison) and therefore could have been missed during analysis.

Alternatively, and possibly more plausibly, the presence, absence and detectability of cheek glands may vary among individuals depending on life-history traits such as age, reproductive status and/or sex. While Rasa (1973) documented cheek rubbing in dwarf mongoose pups as early as 30 days old, which may be indicative of the presence of a scent gland, Swanson and Norman (1978) found marking behaviour to be independent of scent gland development in Mongolian gerbils. Regardless, as all the banded mongooses in our study were adults, age is unlikely to have influenced the presence of cheek glands. However, scent glands may develop or enlarge in response to reproductive status (Kumari & Prakash, 1983; Tomiyasu et al., 2025). For example, yellow mongooses have been observed to engage in cheek scent marking which increases in frequency during the breeding season, suggesting that the secretions in this species might be involved in olfactory mate guarding (Le Roux et al., 2008). If scent glands in banded mongooses also respond to reproductive status, this may affect their conspicuousness in the dermal tissue. Furthermore, gland size may be related to sex. All individuals in our study were female, but males may have larger and therefore more detectable sebaceous scent glands if their size is modulated by testosterone, as previously found in male goats (Iwata et al., 2000) and male brown bears *Ursus arctos* (Tomiyasu et al., 2018, 2025). As our study sample is constrained to adult females of unknown breeding status (e.g. whether they were in oestrous at the time of death), further studies are required to determine the source of variation in the presence or absence of cheek glands across individuals. Furthermore, neither histological nor behavioural observations alone are sufficient to determine the function of a gland and further analyses of the cheek glands of banded mongooses are needed. Behavioural experiments should aim to identify the context in which cheek marking is used to help determine the purpose of the signals conveyed through the secretion. This could be supported by chemical analyses of cheek gland secretions, for example, using gas chromatography–mass spectrometry, which could help to identify the subsets of the volatilome that may be associated with factors such as sex, reproductive state, genetic makeup and age.

We did not find any evidence of specialised scent glands in the tissue samples from the chin or abdomen. Both locations exhibited a high volume of hair follicles, and while hair may function in dispersing chemical signals produced by the associated sebaceous glands (Albone, 1984), this function cannot be deduced through the histology of the pilosebaceous unit alone. Although banded mongooses have been observed to rub their chin and abdomen on surfaces, the absence of histological evidence for specialised scent glands or osmetrichia in these areas suggests that these behaviours may serve as scent rubbing rather than scent marking. Moreover, the belly is an ideal part of the body for picking up scent as central body regions are warmer than the extremities (Costa et al., 2018) and should therefore aid in distributing volatiles effectively. This interpretation aligns with findings from studies of yellow mongooses. Pocock (1916) hypothesised that yellow mongooses do not deposit scent, but acquire odours in a self-anointing manner, as they exhibit rubbing behaviour similar to banded mongooses and lack scent glands in their flanks. Similarly, banded mongooses have been observed to roll in their own scent markings as well as those of other group members (Cant et al., 2002). Since banded mongooses are highly social, live in groups consisting mostly of relatives (Cant et al., 2016; Wells et al., 2018) and react aggressively towards intruders (Cant et al., 2002), acquiring odours that signal relatedness or group membership may be beneficial. Banded mongooses have been observed to respond to relatedness in anal gland odours (Mitchell et al., 2018; Schubert et al., 2024) and females preferentially evict females that are more closely related to themselves (Thompson et al., 2017). Picking up odours of other related individuals might signal relatedness and thereby trigger acceptance, while at the same time disguise exact relatedness levels. The resulting uncertainty about relatedness levels might facilitate cooperation, aid in-group cohesion and increase

individual fitness (Frank, 2003; Marshall et al., 2021; Okasha, 2012; Queller & Strassmann, 2013).

Our study was able to (1) examine the structure of banded mongoose anal glands from a morphological to a cellular level, (2) identify a likely scent gland in the cheek and (3) show that banded mongooses appear to lack specialised scent glands in the chin and abdomen. However, our results should be treated with some caution as (due to the availability of tissues stored in the biobank) we were only able to investigate these structures in up to four adult female banded mongooses. Future studies would benefit from investigating potential scent glands in males, as previous research has shown that scent marking can differ between the sexes (Johnson, 1973; for banded mongooses, see Mitchell, Cant, Vitikainen, & Nichols, 2017), although Müller and Manser (2008) observed only marginal differences between male and female banded mongooses. Including more individuals would also allow us to quantify individual variation in scent gland location and structure, while examining a broader range of age classes would further our understanding of the ontogeny of scent glands, as scent marking behaviours often increase with the onset of sexual maturity (Woodmansee et al., 1991), and associated physiological changes in scent glands are likely. Finally, further investigations could explore the potential involvement of microbiota and immune genes in generating odours. Bacteria-specific staining techniques could be employed to detect the presence of microbiota within the glands, and 16S rRNA sequencing could help characterise bacterial communities and determine whether aerobic or anaerobic microbes dominate. Analysis of the microbiota would be highly feasible in the short term through the collection of anal gland secretions from a habituated population of wild banded mongooses that have been part of a long-term study in Queen Elizabeth National Park, Uganda (Cant et al., 2013). To further examine the role of the MHC, immunohistochemistry techniques could be used to selectively stain MHC-carrying immune cells. Although species-specific antibodies for banded mongooses are not yet available, future studies could test commercially available antibodies from related species for cross-reactivity to visualise MHC-carrying cells in the glands. Importantly, a cross-disciplinary approach is likely to be highly beneficial to moving this field of research forward, combining histological, chemical and genomic techniques with behavioural observations (e.g. see Caspar et al., 2022; Charpentier et al., 2010; Schubert et al., 2021).

Conclusion

Our study provides novel insights into the scent marking mechanism of banded mongooses. We characterised the histological structures of the anal gland, which include both apocrine and sebaceous glands, and epithelial variation that may influence immune–microbiota interactions. We confirmed the presence of a previously undescribed sebaceous cheek gland, which may be used to deposit lipid-rich secretions capable of producing long-lasting odorous volatiles, indicating that cheek rubbing functions as scent marking. In contrast, we found no evidence of specialised scent glands in the chin or abdomen, suggesting these body locations play a role in scent rubbing rather than deposition. However, the precise mechanisms underlying scent marking behaviours and the formation of chemical cues that can be detected and interpreted by conspecifics remain unclear. Given the complex interplay of internal factors, gland structures and environmental influences, future research should adopt an integrative approach. By combining behavioural experiments with anatomical and histological analyses, chemical profiling of odour composition, genetic studies examining links to immune genes like the MHC, and functional analyses investigating microbiota's role in producing odorous compounds, we can develop a more comprehensive understanding of the mechanisms underlying chemical communication through scent marking.

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Author contributions

NS conceived the study. NS, AKOA and BS designed the methodology. MHN, NS, AKOA and FH collected the data. MHN, NS, AKOA and OLN analysed the data. BS provided resources for data collection and analysis. JIH, JCW, BAC and OK provided funding. MHN and NS wrote the initial manuscript. AKOA, OLM, JIH, BAC, OK, HJN and JCW edited the manuscript. All authors approved the final manuscript for publication.

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Conflict of interest

The authors declare that there are no conflicts of interest.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Paraffin embedding protocol.

Table S2. H&E staining protocol.

Figure S1. MRI and CT scan of banded mongoose anal glands.

Figure S2. MRI and CT scans of banded mongoose head and abdomen.