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The structure and distribution of nasal glands in four marsupial species

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The glands which secrete into the nasal cavity in mammals fulfil a number of functions, including humidifying the incoming air, providing an appropriate environment for the olfactory receptor cells, and supplying a moving surface film to trap and remove foreign particles. In addition, they may also play a significant immunological role, since immunoglobulin A forms part of the protein secreted by the lateral nasal gland in the dog (Adams, Deyoung & Griffith, 1981).

The structure and distribution of nasal glands has been studied in the rat and a number of other mammals (Bojsen-Møller, 1964), in the mouse (Cushieri & Bannister, 1974) and hamster (Adams, 1982), revealing an underlying similarity which permits gland classification into broad regional groups. However, there is considerable species variation, presumably since differing life styles place different priorities on the functions served by the glands.

Little has been published on the distribution of nasal glands in marsupials. The present study reports their presence, distribution and structure in four species of different body size, habitat and food selection. *Tarsipes rostratus*, the honey possum, is a blossom and nectar feeder of very small size, average adult male weight about 9 g (Strahan, 1983). The northern brown bandicoot, *Isoodon macrourus*, is a mixed feeder, average male weight about 2·1 kg. The koala, *Phascolarctos cinereus*, average weight about 11·9 kg, is mainly arboreal and feeds on a limited range of eucalypt leaves, and the largest species studied, the agile wallaby, *Macropus agilis*, is a herbivore inhabiting open forest and grassland (average male weight, 19 kg).

MATERIALS AND METHODS

Tissues for light and electron microscopy were obtained from the following: five adult specimens (four males, one female) of *Tarsipes rostratus*; six adult specimens of *Isoodon macrourus* (four males and two females); four adult specimens (three males and one female) and one pouch young of *Phascolarctos cinereus*; three adult specimens (one male and two females) of *Macropus agilis*.

The tissues were fixed by perfusion into the left ventricle in animals under terminal anaesthesia with pentobarbitone sodium. The perfusate was Karnovsky's fixative for *Tarsipes rostratus*; for the other specimens, 1·5 % glutaraldehyde in 0·1 % cacodylate buffer, pH 7·2, containing 4 % polyvinyl-pyrrolidone. The nasal regions were sectioned transversely into slices (2–3 mm for the smaller specimens, 5 mm for the larger) and areas selected for light and electron microscopy. Sections for electron microscopy were decalcified with EDTA, postfixed in osmium tetroxide, and embedded in Araldite. For light microscopy, tissues were decalcified in a solution of

Table 1. *Structure and distribution of glands of the nasal cavity in four marsupial species*

	Tarsipes rostratus	*Isoodon macrourus*	*Phascolarctos cinereus*	*Macropus agilis*
		(A) *Glands of general distribution*		
(*a*) Goblet cells	Characteristic 'goblets' only in epithelium of ventral nasal floor and rostroventral septum. Sparse electron-dense secretion granules in cells on ventral turbinate and lateral walls	Epithelium of ventral floor, rostral and caudoventral septum, ventral surfaces of dorsal- and ethmoturbinates	Epithelium of septum, ventral floor, rostral ventral turbinate, ventrolateral wall. Present but infrequent in maxillary sinus	In *all* areas of ciliated epithelium *except* dorsal and lateral areas of maxillary sinus
(*b*) Olfactory (Bowman's) glands	Simple tubular. Coextensive with olfactory epithelium	Simple tubular. Coextensive with olfactory epithelium (including septal organ)	Simple tubular. Coextensive with olfactory epithelium	Simple tubular. Coextensive with olfactory epithelium
		(B) Glands of the lateral nasal wall		
(*a*) Lateral nasal gland	Compound alveolar. Lateral wall, ventral maxillary sinus. Intercalated, striated and collecting ducts. Single excretory duct opens ventrolaterally in vestibule	Compound alveolar. Rostral ventral and lateral wall, ventrolateral maxillary sinus. Intercalated, striated and collecting ducts. Single excretory duct opens ventrolaterally in vestibule	Absent in adult specimens	Compound alveolar. Rostral ventral and lateral wall, ventrolateral in maxillary sinus, deep to sinus glands. Intercalated, striated and collecting ducts. Single excretory duct opens ventrolaterally in vestibule
(*b*) Maxillary sinus gland	Compound tubular. Dorsal half of maxillary sinus wall. No specialised ducts. Ducts open to epithelial surface	Simple tubular. Medial and dorsal sinus wall. No specialised ducts. Several ducts open dorsally on sinus epithelium	Absent	Compound tubular. Under the whole sinus epithelium. Several ducts discharge dorsally on sinus epithelium
(*c*) Turbinate glands (i) Ventral (maxilloturbinate)	Simple tubular. Few in number, vestibule and rostral cavity only. Ducts open to epithelial surface	Compound alveolar. Numerous rostrally, sparse caudally. Striated and excretory ducts open to epithelial surface	Compound alveolar. Patchy distribution, mainly rostroventrally. Striated and excretory ducts open to epithelial surface	Compound tubulo/alveolar. Numerous rostrally, very sparse caudally. Intercalated and striated ducts open to epithelial surface
(ii) Dorsal (nasoturbinate)	Tubular. Vestibular, forms a dorsolateral vascular/glandular ridge. Striated and excretory ducts, opening to epithelial surface	Compound alveolar (as in [i]). Rostral cavity, extending into vestibule as vascular/glandular ridge. Striated and excretory ducts, opening to epithelial surface	Compound alveolar, on rostral dorsal concha. Myoepithelial cells surround alveoli and ducts. Ducts open to epithelial surface	Compound alveolar. Rostral cavity, extending into vestibule as vascular/glandular ridge. Intercalated and striated ducts open on epithelial surface. Major ducts are secretory

(C) Glands of the nasal septum				
(*a*) Anterior medial glands				
(i) Glands opening on 'swell bodies'	Compound alveolar. Rostral septum, under 'swell body', and extending ventrally superficial to vomeronasal glands. Intercalated, striated and collecting ducts. Myoepithelial cells surround alveoli and striated ducts. Major excretory duct opens on ventral vestibular septum. Some ducts open on 'swell body' surface	Compound alveolar. Occupy much of rostral septum. Intercalated and striated ducts. No major duct; several ducts open onto 'swell body' surface	No 'swell body'. Few scattered septal glands resemble dorsal turbinate glands. Ducts open to septal epithelium	Compound alveolar. Form a low 'swell body', and extend to ventral septum. Intercalated, striated and collecting ducts open on 'swell body' and general septal surface
(ii) Ventrolateral septal glands	Compound alveolar. Small group forms a ventral 'swell body' ventrolateral to vomeronasal organ. Duct cells are secretory. Myoepithelial cells surround alveoli and ducts. Ducts open on epithelial surface	Compound alveolar. Small group ventrolateral to vomeronasal organ. Ducts open on epithelial surface towards ventral nasal floor	Compound alveolar. Mainly ventral to vomeronasal organ. Ducts lined by secretory cells, open to epithelial surface	Compound alveolar. Extensive, superficial to vomeronasal glands, extend through whole length of septum. Resemble 'swell body' glands. Intercalated, striated and collecting ducts open on epithelial surface
(*b*) Posterior medial glands				
(i) Vomeronasal glands	Tubulo-alveolar. Extensive, occupying the ventral half of a wide septum. Intercalated and secretory ducts. Single excretory duct lined by cells with long microvilli is continuous rostrally with lumen of vomeronasal organ	Compound tubular. Dorsal to vomeronasal organ on ventral septum. Ducts open dorsomedially into the lumen at junction of sensory and ciliated epithelium. Glands continue on septum caudal to the sensory region	Compound tubular. Dorsal, lateral and ventrolateral to vomeronasal lumen. Duct cells contain secretory granules. Ducts open to the lumen dorso- and ventrolaterally at the junction of sensory and non-sensory epithelium	Compound tubular. Lateral to vomeronasal organ and continuing caudally beyond sensory region. Ducts open to the lumen dorso- and ventrolaterally at the junction of sensory and non-sensory epithelium and into the caudal continuation of the lumen
(ii) Ventral glands of the caudal septum	Absent	Compound alveolar on lateral extensions of ventral septum, deep to olfactory glands under septal olfactory organ. Ducts open to epithelial surface	Compound alveolar, in scattered groups. Ducts lined with secretory cells open on epithelium	No separate group. Some caudal extension of glands in (*a*)(ii)

picric acid, formalin, and formic acid, embedded in paraffin, and serially sectioned at a thickness of 6–10 μm. All *Tarsipes* sections were mounted. For the other species, every tenth section was stained with haematoxylin and eosin. Representative sections were stained with periodic acid–Schiff and alcian blue.

Additional material for light microscopy was obtained from animals perfused with 5% formalin (*Isoodon macrourus*) or by immersion in 5% formalin (pouch young *Phascolarctos cinereus*). Sections were decalcified and prepared as described above.

RESULTS

The distribution and major histological characteristics of the nasal glands in the four species are listed in Table 1. The glands are considered in three general categories:

(A) Glands of wide distribution, associated with particular types of epithelium.

(B) Glands of the lateral nasal wall.

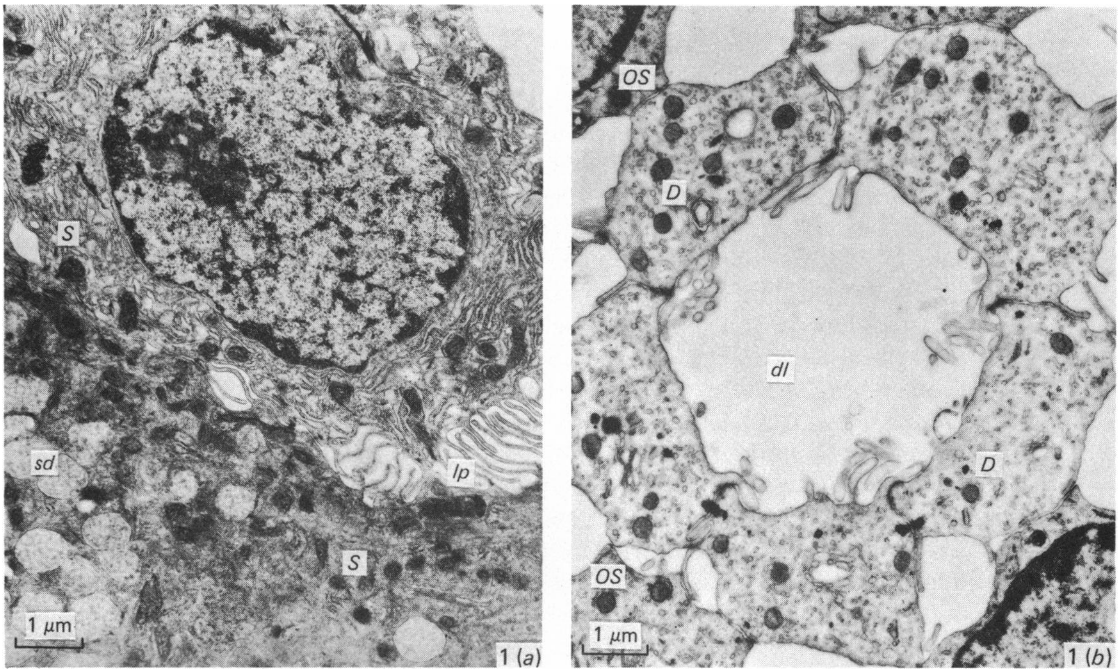
(C) Glands of the nasal septum (medial nasal glands).

Glands of general distribution included mucous goblet cells and olfactory (Bowman's) glands. While goblet cells were a general component of ciliated respiratory epithelium, their distribution varied throughout the nasal cavity, being most frequent rostrally and ventrally. They were absent in the maxillary sinus, except in the koala, where scattered goblet cells provided the only secretion discharged onto the sinus epithelium. Where typical goblet cells did not occur in respiratory epithelium, non-ciliated cells occasionally contained a few secretion droplets, frequently seen in the honey possum.

Large areas of epithelium on the turbinates and lateral wall showed no evidence of secretion in the bandicoot. Scattered goblet cells occurred in the vomeronasal non-sensory epithelium in the agile wallaby, but not in other species. Simple tubular olfactory glands (Bowman's glands) in the underlying lamina propria secreted onto the olfactory epithelium, including that of the septal organ in the bandicoot. Fine structural characteristics included abundant granular endoplasmic reticulum, secretion granules of varying density, and numerous fine basal and lateral cell processes. Ducts were short and non-secretory (Fig. 1*a*, *b*).

Glands of the lateral wall. The lateral nasal gland (Stensen's or Steno's gland) was not found in the adult koala but was well developed in the other three species, where secretory alveoli formed a dense mass under the lateral wall, extending into the ventral aspect of the maxillary sinus. In the bandicoot and agile wallaby they also occupied the floor of the nasal cavity. Secretory cells had extensive fine granular reticulum basally and secretion droplets of very variable electron density apically. Nerve endings containing light- and dense-cored vesicles were often seen close to the basal lamina. In the honey possum, the alveolar lumen was irregular and invaginated deeply into the secretory cells. Short intercalated ducts lined by cuboidal epithelium led to striated ducts whose bases were frequently indented by fenestrated capillaries (Fig. 2*a*, *b*). A series of collecting ducts led to the major excretory duct which opened laterally in the vestibule caudal to the opening of the nasolacrimal duct.

Maxillary sinus glands were absent in the koala, present in the other species, and most extensive in the agile wallaby. The tubular alveoli were formed by cells with extensive granular endoplasmic reticulum, electron-dense secretion droplets, and smooth basal and lateral surfaces. In the agile wallaby, the lumen extended deeply into the cell surface (Fig. 3). There were no striated or secretory cells in the ducts, several of which opened on the dorsal sinus epithelium.



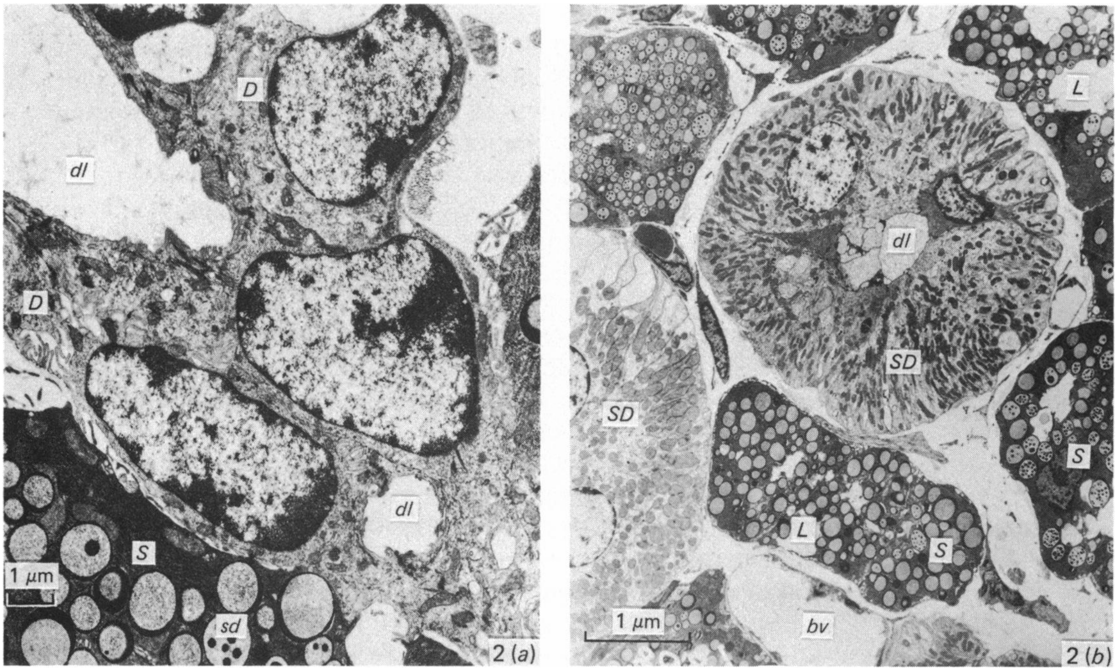


Fig. (1*a–b*). Olfactory gland secretory cells, ***Phascolarctos*** (*a*) and duct, ***Isoodon*** (*b*). Adjacent secretory cells (*S*) have interdigitating lateral processes (*lp*) and pale secretion droplets (*sd*) of variable electron density. Intraepithelial duct cells (*D*) seen in horizontal section are surrounded by olfactory supporting cells (*OS*). *dl*, duct lumen.

Fig. 2 (*a–b*). Lateral nasal gland, *Tarsipes*. Secretory cells (*S*) have electron-dense cytoplasm with abundant granular reticulum and secretion droplets (*sd*) of very variable density; cuboidal cells (*D*) line an intercalated duct (*a*). Alveoli (*b*) have an irregular lumen (*L*) extending deeply into secretory cells. Striated ducts (*SD*) have deeply folded basal membranes and numerous mitochondria. *bv*, blood vessel; *dl*, duct lumen.

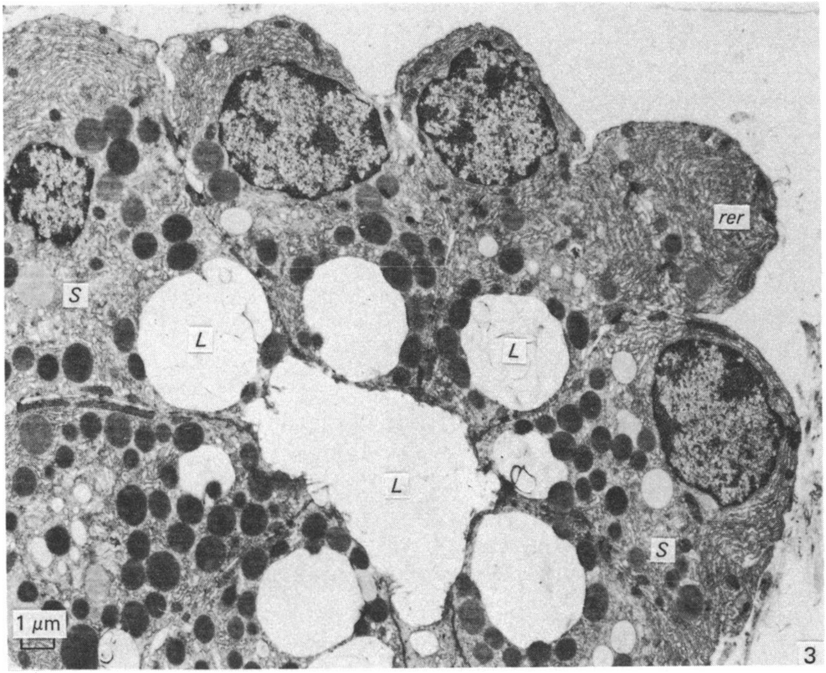
Turbinate glands were unevenly distributed on the conchae. While there was glandular tissue deep to the respiratory epithelium on the dorsal and ventral concha, it was sparse, except rostrally, though well developed on the vestibular extension of both conchae. Alveoli with intercalated and striated ducts resembled those of the lateral nasal gland, but secreted directly to the epithelial surface. These glands were best developed and more widely distributed in the bandicoot. In the other species, most of the conchal lamina propria was occupied by vascular tissue and glands were rare beyond the vestibule. In the honey possum, simple tubular glands without striated ducts occurred on the ventral concha close to the opening of the incisive duct which was widely patent in this species. In the koala, the dorsal conchal glands lacked striated ducts, but alveoli and ducts were surrounded by myoepithelial cells (Fig. 4). In the agile wallaby, the excretory ducts were lined by secretory cells and small nerve endings were frequent at the base of the ducts (Fig. 5).

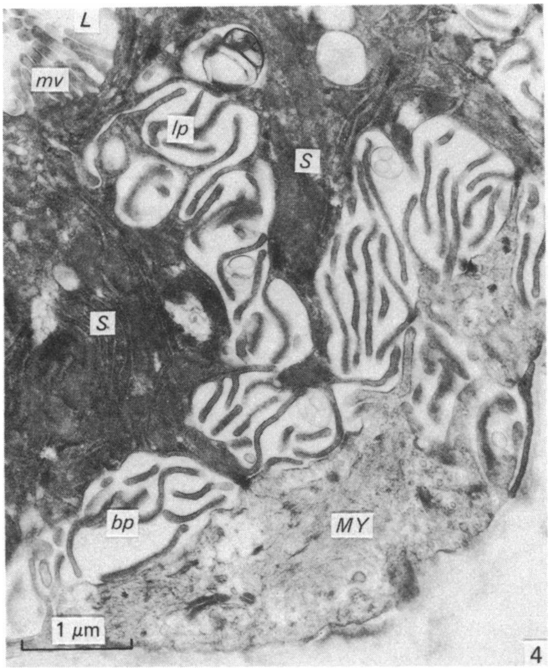
Glands of the nasal septum have been grouped as anterior or posterior medial glands to permit comparison with the findings of other authors, but the groups overlapped anatomically, especially in the ventral part of the septum. The anterior group included those associated with 'swell bodies' and a ventolateral group superficial to the vomeronasal organ. The posterior medial glands included those of the vomeronasal organ, and other glands of the ventral septum in the caudal part of the nasal cavity.

In the bandicoot, the honey possum and, to a lesser extent, the agile wallaby, the rostral third of the septum bore bilateral 'swell bodies' formed by a concentration of vascular and glandular tissue. The secretory cells and ducts of these glands generally resembled those of the lateral nasal gland (Fig. 6). They were extensively developed in the honey possum, with myoepithelial cells surrounding alveoli and ducts. Some short ducts opened along the surface of the 'swell bodies', but the major duct opened ventrally on the septum just inside the anterior nares. In the bandicoot and the wallaby there was no major duct, but a series of short ducts secreted directly to the epithelial surface along the elevated 'swell bodies'. In the wallaby, where the 'swell bodies' were poorly developed, scattered glands occurred under the whole septal epithelium, and there was no clear distinction between 'swell body' and ventral septal glands in the rostral septum. In the koala, the septum was very slender, without 'swell bodies', and the few scattered glands resembled those on the dorsal concha.

In all the species studied there were aggregations of glandular tissue ventral or ventrolateral to the vomeronasal region. They were most extensively developed in the agile wallaby, where they lay superficial to the main mass of the vomeronasal glands, separated from them only by part of the septal lamina propria. In structure, they resembled the septal 'swell body' glands. They were poorly developed in the koala; in the bandicoot and the honey possum they were ventrolateral to the vomeronasal organ. In these three species there were no striated ducts, but duct cells contained a few secretion droplets. In the honey possum, alveoli and ducts were surrounded by myoepithelial cells, and with the surrounding vascular tissue they helped to form small ventral 'swell bodies' lateral to the vomeronasal organ.

Vomeronasal glands have been classified as posterior medial nasal glands, but usually began well forward in the cavity. In all species they were compound tubular in form and lacked striated ducts. Duct cells often contained secretion droplets, and the main collecting ducts were lined by cells with long microvilli (Fig. 7*a*, *b*). These glands were most extensively developed in the honey possum, beginning caudal to the sensory epithelium. The non-sensory continuation of the lumen of the organ





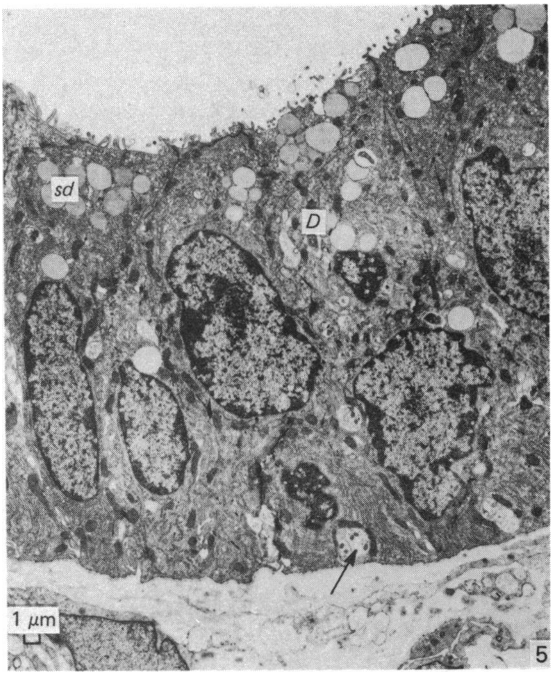
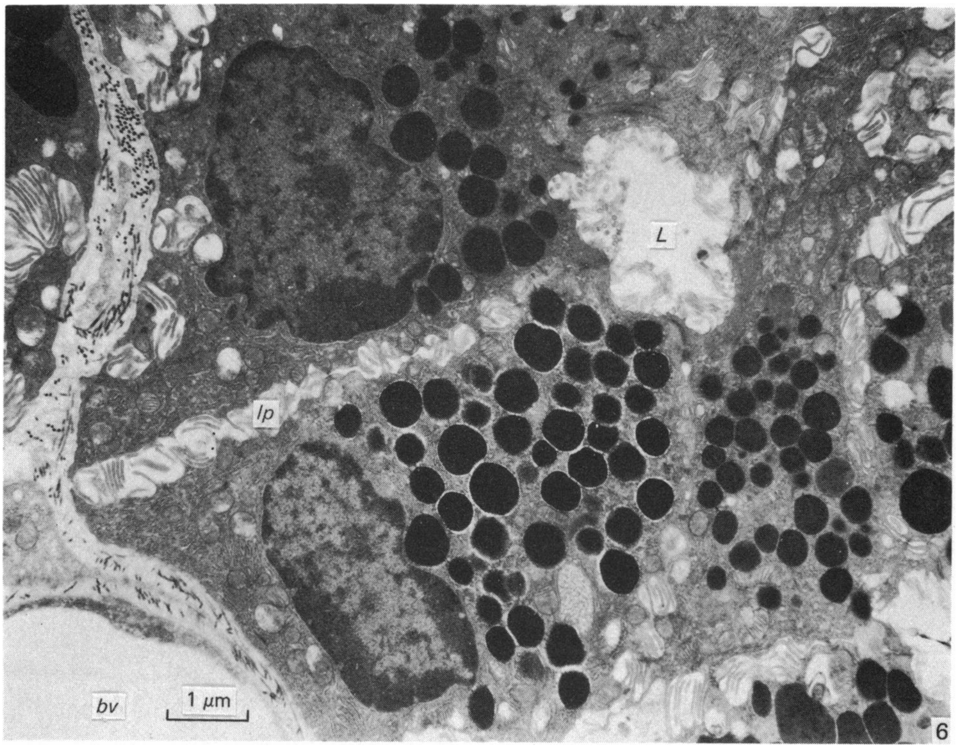


Fig. 3. Maxillary sinus gland, *Macropus*. Secretory cells (*S*) have smooth basal and lateral borders, abundant granular reticulum (*rer*) and electron-dense secretion droplets. The alveolar lumen (*L*) is large and extends deeply into the cytoplasm.

Fig. 4. Dorsal turbinate gland, *Phascolarctos*. Secretory cells (*S*) have extensive lateral (*lp*) and basal (*bp*) processes. Myoepithelial cells (*MY*) surround the alveolus. Microvilli (*mv*) extend into the lumen (*L*).

Fig. 5. Duct of dorsal turbinate gland, *Macropus*. Duct cells (*D*) have extensive granular endoplasmic reticulum and pale secretion droplets (*sd*). Note the small nerve ending (arrow) at the base of the epithelium.



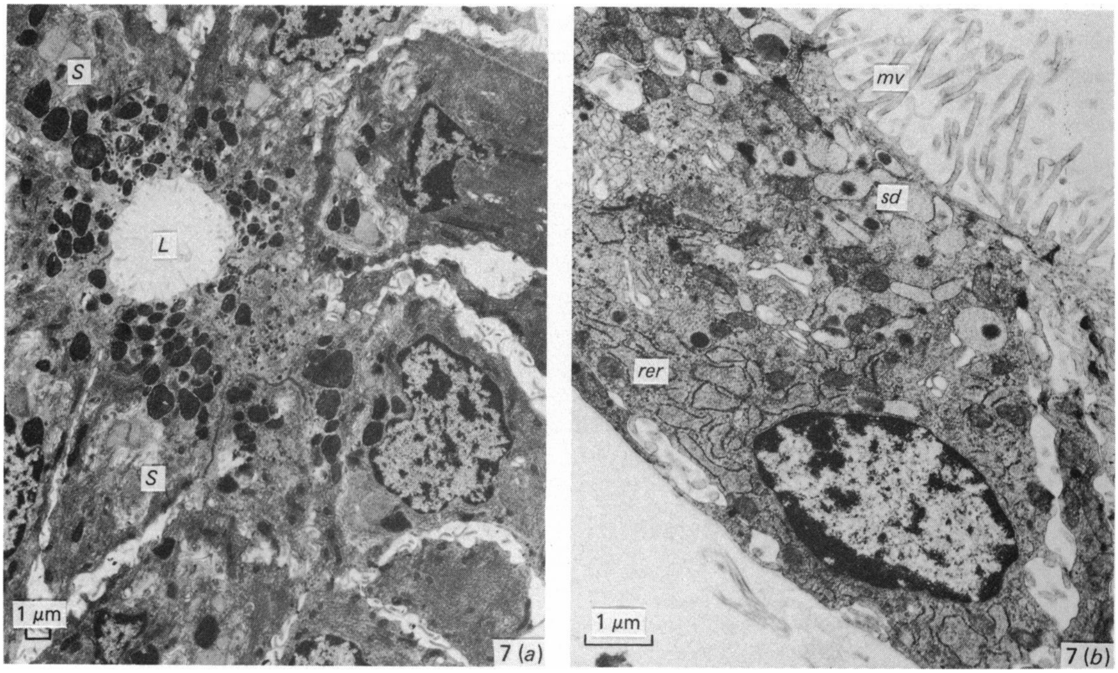


Fig. 6. Septal 'swell body' gland, *Isoodon*. Secretory cells have smooth basal borders but wide intercellular spaces with fine lateral processes (*lp*). Electron-dense secretion droplets are abundant above the nucleus. *bv*, blood vessel; *L*, lumen.

Fig. 7 (*a–b*). Vomeronasal gland secretory cells, *Phascolarctos* (*a*) and collecting duct, *Tarsipes* (*b*). Secretory cells (*S*) have dense, fine granular endoplasmic reticulum and electron-dense secretion droplets. Fine lateral processes extend into wide intercellular spaces. Duct cells (*b*) have granular endoplasmic reticulum with dilated cisternae (*rer*) and secretion droplets of variable density (*sd*). Long microvilli (*mv*) extend into the lumen.

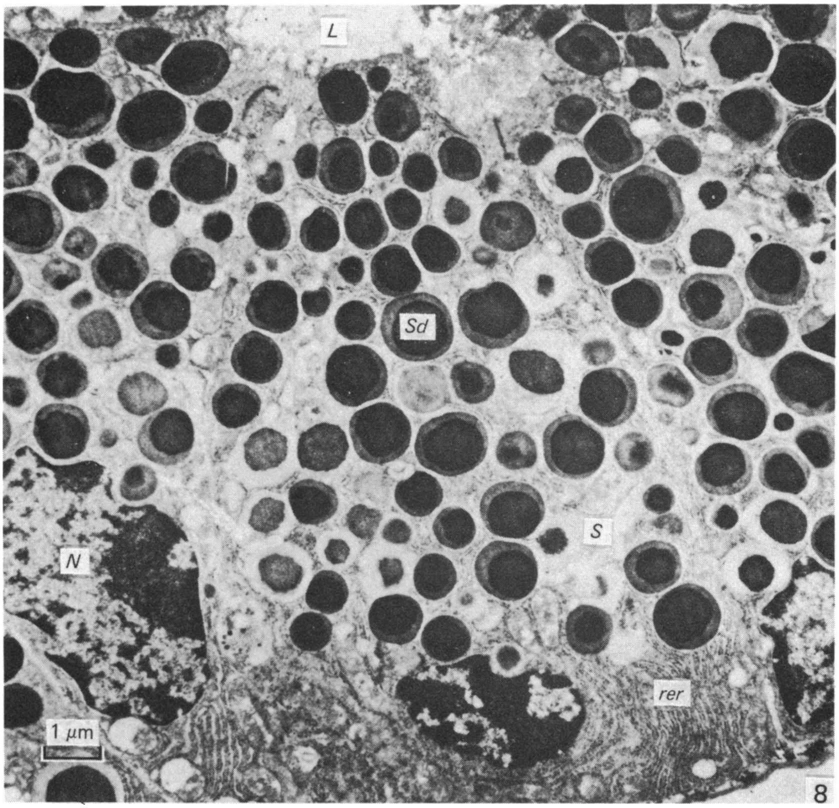


Fig. 8. Caudal ventral septal gland, *Isoodon*. Secretory cells (*S*) have basal nuclei (*N*) and granular endoplasmic reticulum (*rer*). Apical cytoplasm contains electron-dense secretion droplets (*Sd*) with denser cores. *L*, lumen.

acted as a collecting duct for the whole secretory region. A similar extension of the lumen acted as a major collecting duct in the bandicoot and the wallaby but in addition a series of ducts opened into the lumen dorsoventrolaterally at the junction of sensory and non-sensory epithelium. In the koala, all ducts opened in this fashion and the glandular area was less extensive.

The ventral glands of the caudal septum were variable in extent. They were absent in the honey possum, but in the koala there were scattered groups of alveoli with secretory ducts, and in the agile wallaby the glands of the rostal septum extended into the middle third of the nasal cavity. In the bandicoot the caudal two thirds of the septum did not reach the floor of the cavity and the free end was widened laterally to an inverted T shape to carry the septal olfactory organ. Secretory alveoli of the caudal ventral septal glands underlay the olfactory glands of the septal organ and extended under the respiratory epithelium of the ventral septum (Fig. 8).

DISCUSSION

The distribution of nasal glands in the four marsupials resembles the mammalian pattern described by Bojsen-Møller (1964) though there are some variations. In functional terms, the glands fit into two main categories – those which humidify and control the temperature of the incoming air, and those which provide an immediate environment for the epithelial surfaces.

Bojsen-Møller (1964) suggested that the humidification of inspired air is best achieved by secretions which are delivered with a nozzle effect at the nasal vestibule. In the species studied, in addition to a number of smaller secretory areas, the vestibule receives the secretions of the lateral nasal gland in all but the koala, the septal 'swell body' glands in the honey possum, the lacrimal and other orbital gland secretions in all species. The nasolacrimal duct opens a little more medially and rostral to the opening of the duct of the lateral nasal gland. Although not a nasal gland, lacrimal secretion must make a considerable contribution to humidification of inspired air and to the moist nature of the pigmented nasolabial skin. The nasolacrimal duct lies in a bony canal at the base of the ventral concha for most of its length, and is surrounded by a network of blood vessels; it is a striated duct in the honey possum, and a small group of glands open into it just before it opens at the vestibule.

The fine structure of secretory cells of the lateral nasal gland resembles that described in the rat (Moe & Bojsen-Møller, 1971), dog (Adams *et al.* 1981) and that of the major acinar cell type in the hamster (Adams, 1982). Intercalated and striated ducts also resemble those in the dog, but lack the myoepithelial cells reported in rat intercalated ducts. In the dog, the secretions contain sialic acid, and some immunoglobulins, and a protective role has been postulated in addition to that of temperature control. In the koala, the absence of the gland is part of a general reduction in nasal secretory tissue; the duct and a few alveoli have been seen in sections of a pouch young specimen (Kratzing, 1984).

Within the nasal cavity proper, several groups of glands are well placed to assist humidity and temperature control as well as contribute to the mucous layer over the epithelium. They are usually associated with vascular tissue of an erectile nature which can modify the direction of airflow by a variable degree of obstruction to the lumen. The septal 'swell bodies' and the glandular ridge on the dorsolateral wall belong to this category. In the absence of 'swell bodies', the koala may achieve a similar control by the glandular areas on the ventral face of the ventral concha (Kratzing, 1984). In all species studied, there is provision for secretory activity at the nasal opening of the incisive duct. Where this is a wide opening, as in the honey possum, there may be considerable air movement in the region. One further gland in this category surrounds the septal olfactory organ in the bandicoot. Here, some extra secretion may be needed to protect this strip of sensitive tissue exposed to the respiratory air stream in the ventral meatus.

Much of the mucous layer over the respiratory epithelium comes from the goblet cells but varies in amount in different areas. The bandicoot has two distinct types of ciliated epithelium, only one of which contains goblet cells (Kratzing, 1982*a*). Their presence in the non-sensory epithelium of the vomeronasal organ in the agile wallaby is unusual, though cells with goblet-like apical protrusions have been seen in the mouse (Naguro & Breipohl, 1982). They are often absent from the greater part of the maxillary sinus epithelium. Here, glands in the lamina propria provide a secretory cover, and glands resembling those in the bandicoot, honey possum and agile wallaby have been reported in other species (Vidić & Greditzer, 1971; Adams, 1982). Their absence in the koala may be a contribution to water conservation in this animal. The immediate environment of the olfactory epithelium in all species is provided by the underlying olfactory glands. Despite their presence in all terrestrial mammals, their role in the olfactory process has not been clearly established, though the significance of sulphomucins in their secretion has been discussed by Cushieri & Bannister (1974). Secretion for the vomeronasal sensory epithelium is provided by the vomeronasal glands which must provide sufficient fluid to remove surface debris from this blind ended tubular organ. The duct of the organ opens into the nasal cavity in the koala and agile wallaby, and into the incisive duct, and thus indirectly towards the oral cavity, in the bandicoot and the honey possum. Vomeronasal glands are most extensively developed in the honey possum. Here, the incisive ducts open on either side of an incisive papilla which is strongly curved ventrally (Kratzing, 1982*b*), and it seems probable that the secretion of the vomeronasal glands is poured onto the dorsal surface of the spiny tongue as it moves through the groove of the incisive papilla.

SUMMARY

The structure and distribution of nasal glands in four marsupial species were studied by light and electron microscopy. The species studied were the honey possum (*Tarsipes rostratus*), the bandicoot (*Isoodon macrourus*), the koala (*Phascolarctos cinereus*) and the agile wallaby (*Macropus agilis*). Glands were grouped and described according to their location. Those of general distribution (goblet cells and olfactory glands) were similar in structure and distribution in all specimens. Glands of the lateral nasal wall include the lateral nasal, maxillary sinus and turbinate glands. The lateral nasal and maxillary sinus glands were absent in the adult koala but occupied large areas in the other species. Turbinate glands were best developed rostrally and ventrally in the nasal cavity.

On the nasal septum, *Tarsipes* and *Isoodon* had well developed glands associated with vascular 'swell bodies'. These were poorly developed in *Macropus* though septal glands were abundant. 'Swell bodies' were absent in *Phascolarctos* and glands were sparse. Tubular vomeronasal glands were present in all species and most extensive in *Tarsipes*. In *Isoodon*, there was a posterior ventral septal gland associated with the septal olfactory organ.

The fine structural features of secretory cells and ducts are described and their potential role discussed in terms of chemoreception and temperature and humidity control.

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