A histological examination of the holding sacs and glandular scent organs of some bat species (Emballonuridae, Hipposideridae, Phyllostomidae, Vespertilionidae, and Molossidae)

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Abstract: Using histological techniques at the light-microscope level, we examined and compared structure and sexual dimorphism of the wing sacs and integumentary glandular scent organs of 11 species of microchiropteran bats. The antebrachial wing sacs of the Neotropical emballonurids *Peropteryx macrotis*, *Saccopteryx bilineata*, and *Saccopteryx leptura* differed in size and location but lacked sudoriferous and sebaceous glands, confirming that they were holding sacs rather than glandular scent organs. Glandular scent organs from 11 species consisted of sebaceous and (or) sudoriferous glands in emballonurids (*P. macrotis*, *S. bilineata*, *S. leptura*, *Taphozous melanopogon*, *Taphozous nudiventris*), hipposiderids (*Hipposiderous fulvus*, *Hipposiderous ater*), the phyllostomid *Sturnira lilium*, the vespertilionid *Rhogeessa anaeus*, and molossids (*Molossus ater* and *Molossus sinaloe*). Glandular scent organs were located on the face (*H. fulvus*, *H. ater*), gular region (*S. bilineata*, *P. macrotis*, *T. melanopogon*, *M. ater*, *M. sinaloe*), chest (*T. nudiventris*), shoulder (*S. lilium*), or ears (*R. anaeus*). Glandular scent organs showed greater similarities within than between families, and typically were rudimentary or lacking in females. Scanning electron microscope examination revealed that the hairs associated with glandular areas of male *T. melanopogon* were larger and had a different cuticular-scale pattern than body hairs. These were osmetrichia, hairs specialized for holding and dispersing glandular products. In *S. lilium*, hairs associated with the shoulder scent-gland area were larger than body hairs but similar in cuticular-scale pattern.

Résumé : Nous avons utilisé des techniques histologiques appropriées à un examen au microscope photonique pour examiner et comparer la structure et le dimorphisme sexuel des poches glandulaires du coude et des organes glandulaires intertégumentaires à sécrétions odorantes chez 11 espèces de microchiroptères. Les poches glandulaires antébranchiales des chauves-souris néo-tropicales *Peropteryx macrotis*, *Saccopteryx bilineata* et *Saccopteryx leptura* (Emballonuridae) diffèrent par leur situation et leur taille, mais ne comportent ni glandes sébacées, ni glandes sudoripares, ce qui confirme qu'il s'agit de véritables sacs de rétention plutôt que d'organes glandulaires sécréteurs de substances odorantes. Les organes glandulaires à odeurs de 11 espèces comportent des glandes sébacées et (ou) des glandes sudoripares chez les emballonuridés (*P. macrotis*, *S. bilineata*, *S. leptura*, *Taphozous melanopogon*, *Taphozous nudiventris*), les hipposidéridés (*Hipposiderous fulvus*, *Hipposiderous ater*), le phyllostomidé *Sturnira lilium*, le vespertilion *Rhogeessa anaeus* et les mollosses (*Molossus ater* et *Molossus sinaloe*). Les organes glandulaires à odeurs sont localisés sur la face (*H. fulvus*, *H. ater*), dans la région gulaire (*S. bilineata*, *P. macrotis*, *T. melanopogon*, *M. ater* et *M. sinaloe*), dans la poitrine (*T. nudiventris*), dans les épaules (*S. lilium*) ou dans les oreilles (*R. anaeus*). Les organes glandulaires à odeurs ont plus de similarités au sein d'une même famille que d'une famille à l'autre et de façon générale sont rudimentaires ou absents chez les femelles. L'examen au microscope électronique à balayage a révélé que les poils associés à la région glandulaire chez les mâles de *T. melanopogon* sont plus forts et ont un pattern d'écailles différent de celui que l'on observe sur les poils du corps. Ce sont des osmetrichia, poils spécialisés affectés à la conservation et à la dispersion des sécrétions glandulaires. Chez *S. lilium*, les poils associés à la région glandulaire odorante de l'épaule sont plus gros que les poils du corps mais leur ressemblent par le pattern de leurs écailles cuticulaires.

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Introduction

Bats communicate using a combination of auditory, visual, and (or) olfactory cues, although sound has received the most attention because of the focus on echolocation (Suthers 1970; Fenton 1985; Altringham and Fenton 2001). Olfactory communication probably plays an important role in the everyday lives of bats and can be central to recognition of colonies (De Fanis and Jones 1995) and individuals (Gustin and McCracken 1987). Like other mammals, bats

probably use pheromones to provide specific information about the sender, defuse tension, locate roosts, and maintain social harmony within populations (Ewer 1968; Stoddart 1980; Schmidt 1985). The role of scent in the behaviour of bats is not always clear; for example, we do not know how or why *Myotis lucifugus* use a scent post (Buchler 1980). Many bats have distinctive and pronounced odours (Quay 1970). The strong, penetrating species-specific odours (Quay 1970; Schmidt 1985) of *Noctilio leporinus* (Brooke and Decker 1996), *Taphozous nudiventris* Cretzchmar (Brosset 1962), and *Antrozous pallidus* (Orr 1954), for example, may result from some combination of glandular secretion, diet, and bacterial fermentation, as in other mammals (Gorman and Trowbridge 1989).

The saclike structures in the antebrachial wing membranes of some Neotropical emballonurids are associated with scent-marking behaviour (Bradbury and Emmons 1974; Voigt and von Helversen 1999) and have been called glands (e.g., Stoddart 1980; Eisenberg and Kleiman 1983). Starck (1958), however, found little evidence of typical mammalian scent glands in the wing sacs of *Saccopteryx bilineata* Temminck, indicating that the wing sacs were not glandular organs. Subsequent studies of *S. bilineata* (Voigt and von Helversen 1999) revealed that the exudates from the wing sacs originate elsewhere, as saliva, from the gular glands, and from the genital region.

The glandular scent organs of mammals typically include sebaceous (flask-shaped) and sudoriferous (tube-shaped) glands that synthesize different odoriferous molecules, and variations in their chemical products can affect both the odour (sweet, musky, spicy) and colour (white, pink) of scent-gland secretions (Albone 1984; Strauss and Ebling 1970; Quay 1972). Depending upon the species, the diets of bats vary from insects to fruit, nectar, animals, and blood (Altringham 1996), and the metabolic transformation of food may produce different odours (Gorman and Trowbridge 1989). Bacterial fermentation can be affected by the environment in which the bat roosts and by the glandular organ itself. The combination of roosting in warm, humid locations and possessing specialized glandular scent organs provides ideal conditions for the proliferation of bacteria, in turn affecting the odour of the secretions.

To humans, many species of bats are sexually dimorphic in odour, with males having a stronger odour than females (e.g., *N. leporinus*; Brooke and Decker 1996). There also are many examples of sexual dimorphism in holding sacs and glandular scent organs, including *S. bilineata* (Bradbury and Emmons 1974; Voigt and von Helversen 1999), *Tadarida brasiliensis* (Davis and Clyde 1960; Gustin and McCracken 1987), *Molossus ater* Geoffroy (Goodwin and Greenhall 1961), *Natalus* species (Dalquest and Werner 1954), hipposiderids, and Old World emballonurids (Brosset 1962). The females of these species and many others have rudimentary holding sacs or glandular scent organs or lack them entirely (Quay 1970).

In mammals, marking behaviour works synergistically with odoriferous secretions to optimize communication (Ewer 1968; Stoddart 1976; Johnston 1983; Walther 1984; Gorman and Trowbridge 1989). An example of specialized marking behaviour is "salting," the wing-shaking used by male *S. bilineata* to mark roosts and females (Bradbury and

Emmons 1974; Voigt and von Helversen 1999). Bats such as *M. ater* and *Molossus sinaloe* J.A. Allen or *Hipposideros ater* Templeton and *Hipposideros fulvus* Gray can evert their gular or frontal glands, respectively, and deposit a thick, strong-smelling secretion (W.M.R.S., unpublished observation). There is a record of a male *Molossus molossus* everting its gular gland and completely soaking a female conspecific (Schmidt 1985). In captivity, male *M. molossus* scent-mark females, subordinate males, and specific areas in the cages (Haussler et al. 1981; Schmidt 1985).

Some mammalian glandular scent organs are associated with specialized hairs, osmetrichia, which tend to be larger in diameter than body hairs and have "pinecone-like" cuticular-scale patterns. Osmetrichia act like paintbrushes, assisting in holding glandular secretion(s) and applying them to objects or conspecifcs (Stoddart 1980; Flood 1985). The osmetrichia of pteropodid and molossid bats may enhance the communicative effect by enriching both olfactory and visual cues (Hickey and Fenton 1987). Bats such as *Sturnira lilium* Geoffroy (Goodwin and Greenhall 1961), *Taphozous melanopogon* Temminck (Brosset 1962), *Epomops* species (Rosevear 1965; Kingdon 1974; Hickey and Fenton 1987), and many molossids (Dalquest and Werner 1954; Hickey and Fenton 1987) have conspicuous hairs associated with scent-gland regions (Haffner 1998).

The purpose of our study was to conduct a histological examination of the holding sacs and glandular scent organs of a selection of bat species from the families Emballonuridae (*S. bilineata*, *Saccopteryx leptura* Schreber, *Peropteryx macrotis* Wagner, *T. melanopogon*, *T. nudiventris*), Hipposideridae (*H. fulvus*, *H. ater*), Phyllostomidae (*S. lilium*), Vespertilionidae (*Rhogeessa anaeus* H. Allen), and Molossidae (*M. ater*, *M. sinaloe*), and to compare glandular sexual dimorphism and the locations of glandular scent organs. We also compared the body and glandular hairs of *S. lilium* and *T. melanopogon* to assess their modifications as osmetrichia. The phyllostomids eat mainly fruit, the other species insects.

Materials and methods

Specimens of *S. bilineata* (4 male; 2 female), *P. macrotis* (4 male; 2 female), *S. lilium* (5 male; 3 female), *R. anaeus* (3 male; 3 female), *M. ater* (3 male; 2 female), and *M. sinaloe* (4 male; 2 female) were collected in the Yucatan peninsula of Mexico in January and June 1996. Wing-sac tissues were preserved with either Bouin's fluid or neutralized buffered formalin. The tissues were dehydrated with increasing concentrations of ethyl alcohol, cleared in toluene, and embedded in paraffin wax. Serial sections were cut at 7 µm thickness and stained with Ehrlich's hematoxylin and an alcoholic eosin counterstain that permits overall examination of tissues. We also used Mallory's Rapid One Step stain for more detailed examination of connective-tissue elements within the tissues (Baker 1963). Other specimens were borrowed from the American Museum of Natural History and the Royal Ontario Museum: *S. leptura* (2 male; 2 female), *S. bilineata* (2 male; 2 female), and *P. macrotis* (2 male; 2 female). These tissues had originally been fixed in formalin and later stored in 70% ethyl alcohol, and the embedding and staining procedures outlined above were conducted. The slides of tissues were examined under the light microscope to determine the histological structure of the wing sacs. Glandular regions were compared for sexual dimorphism and taxon differences.

Taphozous melanopogon (4 male; 2 female), *T. nudiventris* (4 male; 2 female), *H. fulvus* (4 male; 2 female), and *H. ater* (4 male,

2 female) were collected from caves at Keelakuyilkudi, approximately 8 km southeast of Madurai Kamaraj University in India (9°58′N, 78°10′E). The bats in the study were caught at the Keelakuyilkudi caves during emergence and brought back to laboratory facilities at Madurai Kamaraj University. The bats were rendered unconscious with chloroform and cervically dislocated.

Glandular and nonglandular hairs were collected from *T. melanopogon* and *S. lilium*. The hairs were attached to stubs using double-faced sticky tape, and were sputter-coated with a thin layer of 60/40 gold/palladium for 2 min using the Hummer IV Sputtering System. Each sample was observed with a Hitachi 5-520 scanning electron microscope (operating at 20 kV) and photographs were taken for comparative purposes.

Results

Emballonuridae

In male *S. bilineata* and *S. leptura* the antebrachial wing sacs (Figs. 1*a*, 1*b*, 3*b*) have many infoldings that are lacking in *P. macrotis* (Fig. 1*c*). There are short, stiff hairs within the wing sacs of all species but the wing sacs lack the abundance of sudoriferous and sebaceous glands typical of other mammalian scent glands. The few sebaceous glands scattered throughout the sacs are associated with the short, stiff hairs of the sac. The greatest abundance of glandular tissue occurs where the sac meets the propatagial membrane, and here sebaceous glands encapsulated in connective tissue have ducts that lead to hair follicles. The wing sacs appear to have a thick layer of cornified epidermal tissue that is easily detached from the upper epidermis of the sac (Figs. 1*a*–1*c*). Scattered throughout the tissue are blood vessels, nerves, connective tissue, and striated muscle. The wing sacs of female *P. macrotis*, *S. bilineata*, and *S. leptura* are smaller than those of males but similar in histological and overall structure, showing a low abundance of sebaceous and sudoriferous glands. Although the details of opening and location of wing sacs vary among species, these structures are virtually the same histologically in males and females.

The glandular scent organs of the emballonurids showed many similarities in morphology, and histology, but those of *T. melanopogon* differed from the others, for in some males there was a black beard under the chin associated with the gular glandular organ (Fig. 1*d*). The long hairs of the beard were coated with a waxy secretion. To us, the odour from the bearded region was musky and unpleasant. The beards varied in size in males and were entirely absent in females. in The beards of male specimens stored in 70% ethanol showed no evidence of the black colour. Scanning electron microscope examination revealed that the beard hairs were larger in diameter than the body hairs and had more cuticular scales (Figs. 2*b* and 2*a*, respectively).

The gular glandular organ associated with the beard (Fig. 1*d*) had an abundance of sebaceous glands with low cuboidal cells around its periphery. Towards its center the sebaceous cells had proliferated and become large and spherical, containing many lipid droplets. Many cells appeared to have released their contents and cell remnants into the ducts leading to hair follicles (= holocrine secretion). There were very few sudoriferous glands in this tissue, and the parenchyma contained numerous fibroblasts, collagenous fibers, elastic fibers, nerves, and blood vessels. Female

T. melanopogon had numerous sebaceous glands associated with hair follicles but lacked the beard.

In the gular area, male but not female *T. nudiventris* had a sac rather than a dark-coloured beard and gular glandular organ. Very little hair covered the gular region compared with the rest of the body, and none was visible in the interior of the sac. In male *T. nudiventris* (Fig. 1*e*) the sac showed very little glandular material, but the few sebaceous glands in the tissue above it were associated with the pilosebaceous canals of hair follicles. No sebaceous glands were apparent in the sac. Within the dermis, a large bed of highly coiled sudoriferous glands extended the length of the tissue and was encapsulated by connective tissue. The sudoriferous cells consisted of low cuboidal epithelium with myoepithelial cells around the periphery of the chest glands. In females, the gular region resembled that of males and sebaceous glands were associated with hair follicles.

Male *T. nudiventris* had a chest glandular organ whose outer surface was covered by hair. This chest glandular organ had numerous sebaceous glands encapsulated in connective tissue and associated with the hair follicles (Fig. 1*f*). Deeper within the dermis was a large bed of sebaceous glands surrounded by connective tissue, and large ducts extended from them to the opening of the chest gland. A large bed of sudoriferous glands within the dermis was encapsulated by connective tissue. A smaller duct led from the sudoriferous glands to the opening of the chest gland.

Among New World emballonurids, male *S. bilineata* and *P. macrotis* had gular glandular organs (Figs. 1*g* and 1*h*, respectively), but *S. leptura* did not. Male *S. leptura* did have two small pores in the gular region. The gular glandular openings in *S. bilineata* and *P. macrotis* were densely covered with hair and located at the base of the chin. Preserved specimens of male and female *Balantiopteryx plicata*, *Rhychonycteris naso*, and *Diclidurus scutatus* lacked gular glands.

Gular glandular organs in *S. bilineata* and *P. macrotis* (Figs. 1*g* and 1*h*, respectively) had numerous sebaceous glands around their periphery. The sebaceous glands appeared to be encapsulated by connective tissue and had ducts leading to the pilosebaceous canals of hair follicles. Within the dermis of the opening to the gland was a large bed of sudoriferous glands encapsulated by connective tissue, and around the periphery of the glands were numerous myoepithelial cells. A large, obvious duct extended from the bed of sudoriferous glands through the center of the opening to the surface of the gland but was not associated with hair follicles. Scattered throughout were connective tissue, blood vessels, and nerves. Sectioning problems prevented our examining the gular tissue in *S. leptura*.

Hipposideridae

In front of the noseleaf, eversible frontal glandular organs in male but not female *H. ater* and *H. fulvus* secreted a waxy substance. A pouch-like layer of skin overlaid the midventral portion of the glandular organ and a transverse slit led to the glandular tissue. Hairs were visible on the surface of the glandular sac. In both species the frontal glandular organ (Figs. 1*i*, 1*j*) had a large bed of sebaceous glands around its periphery, and sebaceous glands were encapsulated in connective tissue and appeared to have ducts leading to the
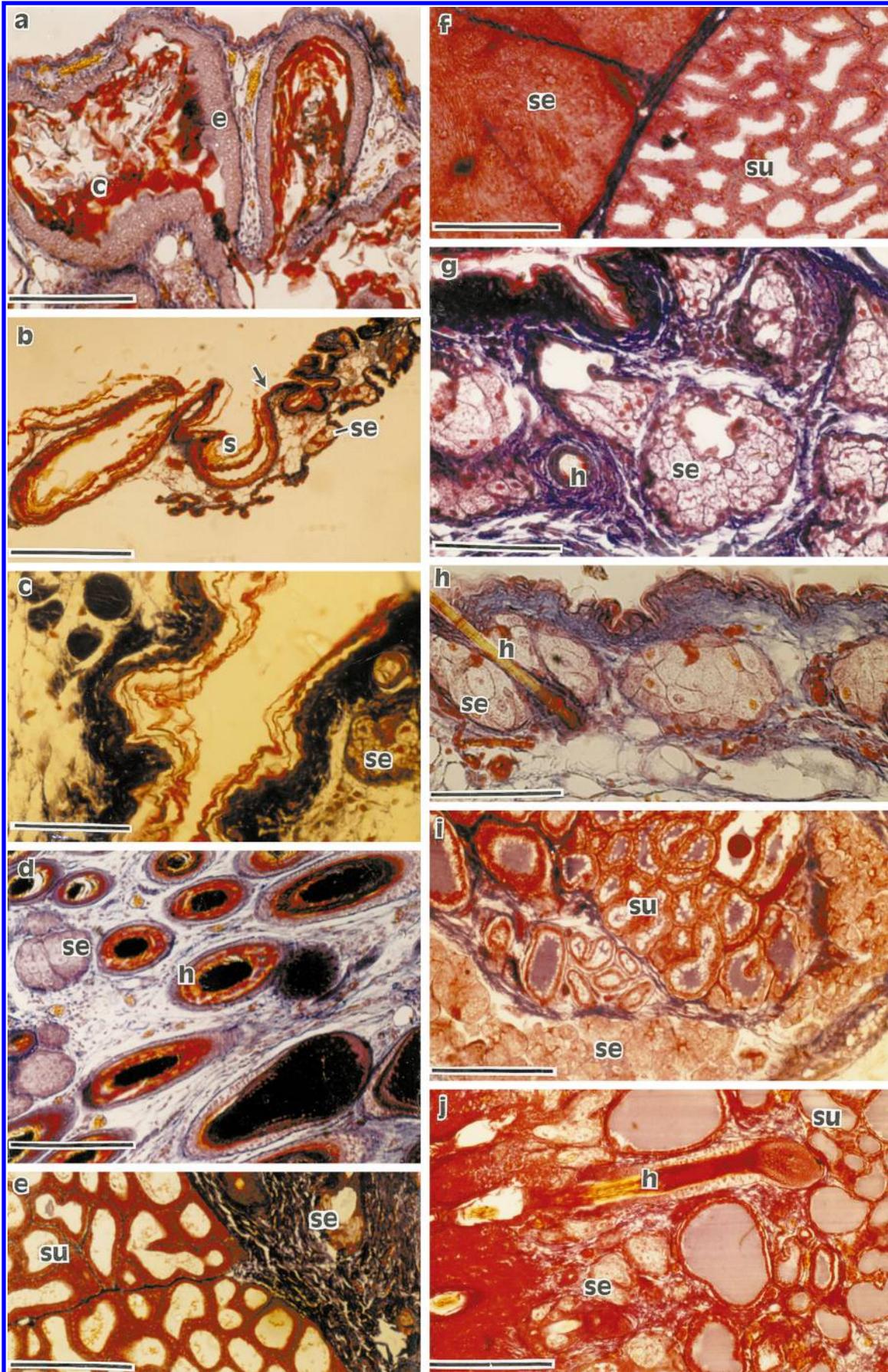
Fig. 1. Histological sections of the holding sacs and glandular scent organs of a selection of bat species. (*a*) A antebrachial wing sac of a male *Saccopteryx bilineata*, showing no glandular tissue and the thick cornified layer of epidermis. Scale bar = 200 μm. (*b*) Antebrachial wing sac of a male *Saccopteryx leptura*, showing no glands in the antebrachial wing sac but sebaceous glands where the sac meets the wing membrane (arrow). Scale bar = 500 μm. (*c*) Antebrachial wing sac of a male *Peropteryx macrotis*, showing no glands in the antebrachial wing sac but sebaceous glands where the sac meets the wing membrane. Scale bar = 200 μm. (*d*) Gular gland of a male *Taphozous melanopogon*, showing hairs and sebaceous glands. Scale bar = 200 μm. (*e*) Gular gland of a male *Taphozous nudiventris*, showing the large area of sudoriferous glands and few sebaceous glands. Scale bar = 200 μm. (*f*) Chest gland of a male *T. nudiventris*, showing the large area of sebaceous glands and sudoriferous glands. Scale bar = 500 μm. (*g*) Gular gland of a male *S. bilineata*, showing hairs and sebaceous glands. Scale bar = 200 μm. (*h*) Gular gland of a male *P. macrotis*, showing hairs and sebaceous glands. Scale bar = 200 μm. (*i*) Frontal gland of a male *Hipposideros fulvus*, showing sebaceous glands associated with hair, and sudoriferous glands. Scale bar = 200 μm. (*j*) Frontal gland of a male *Hippisideros ater*, showing sebaceous glands associated with hair, and sudoriferous glands. Scale bar = 200 μm. *c*, cornified layer; *e*, epidermis; *h*, hair; *s*, wing sac; *se*, sebaceous glands; *su*, sudoriferous glands.

pilosebaceous canals of hair follicles. Deep within the dermis of the frontal gland was a large bed of sudoriferous tissue. There, the sudoriferous glands were surrounded by connective tissue and myoepithelial cells were associated with each one. There were blebs at the apex of each sudoriferous cell. Smaller sudoriferous ducts extended to the surface of the gland, and several blood vessels and muscle fibers were scattered throughout the glandular tissue.

Phyllostomidae

A glandular area on the top of the shoulder of male *S. lilium* sometimes extended onto the neck (Fig. 3*a*). Here, black hairs with a waxy secretion on their surface had a pleasant, sweet-smelling, spicy odour. Scanning electron microscope examination of the hairs from the shoulder region of adult males revealed no difference in cuticular-scale pattern from body hairs, but gland hairs tended to be larger in diameter than body hairs (Figs. 2*c*, 2*d*). The size of the neck–shoulder glandular region varied between males and females, the latter entirely lacking both the odour (to us) and coloured hairs. Only hairs in the center of the neck–shoulder region were dark over the entire length of their shaft; those at the periphery were dark at the tips of the follicles only. The neck–shoulder hairs of museum specimens preserved in ethanol were lighter in colour and in this respect were more similar to body hairs.

The shoulder glandular region of males (Fig. 3*a*) had numerous hair follicles and associated with each were numerous sebaceous glands encapsulated in connective tissue. Deeper within the dermis was a layer of adipose tissue containing scattered small sudoriferous glands along with blood vessels, connective tissue, and nerves. There was no large bed of either sudoriferous or sebaceous glands. Tissue from the shoulder region of females (Fig. 3*b*) had the same glandular elements as that from the shoulder region of males, with numerous sebaceous glands associated with hair follicles.

Vespertilionidae

Male but not female *R. anaeus* had a large glandular area on the dorsal surface at the base of each ear (Fig. 3*c*). A white sticky substance was exuded when the glandular area on the ear of the male was squeezed. No hair was apparent on the surface of the glandular area. The upper epidermis of the male ear glands (Fig. 3*c*) was typically mammalian and was underlain by a thin layer of connective tissue (Fig. 3*d*). Deeper within the dermis was a thick bed of sebaceous

glands, each surrounded by connective tissue. There was degeneration of the cells in the center of the alveoli. Ducts from the sebaceous mass led directly to the dorsal surface of the ear and did not appear to be associated with hair follicles. However, other smaller regions of sebaceous glands were associated with hairs. Under the large bed of sebaceous glands was a thick bed of sudoriferous glands surrounded by connective tissue and associated with myoepithelial cells. Under this region was a layer of hyaline cartilage and then the epidermis of the ventral surface of the ear. Scattered throughout the tissue were blood vessels, connective tissue, and nerves. The ears of females (Fig. 3*e*) lacked the thick bed of sebaceous glands, and the layer of sudoriferous glands was greatly reduced compared with that of males.

Molossidae

Male but not female *M. ater* and *M. sinaloe* had a large gular glandular organ at the base of the neck where the throat meets the chest. This structure was oval and flattened dorsoventrally, with its main axis at right angles to the anterior–posterior axis of the bat. The glandular mass was covered by a pouch-like recess with an opening that allowed eversion of the gland. Some small hairs extended from the glandular mass, but most of the area was naked compared with the rest of the body. The gular gland (Figs. 3*f*, 3*g*, 3*h*) in both species was encapsulated in connective tissue. The glands had numerous sebaceous glands around the periphery, each apparently with a duct leading to the pilosebaceous canals of hair follicles. Deeper in the parenchyma was a large bed of sebaceous glands, with striated low cuboidal epithelium and alveoli showing the greatest degeneration at the center. Large ducts extended from the large bed of sebaceous glands to the surface of the tissue. The glands may release their secretions directly to the surface because they were not associated with the pilosebaceous canals of hair follicles. Within the parenchyma was a large bed of sudoriferous glands surrounded by connective tissue whose cells appeared to have been low cuboidal epithelium; there were myoepithelial cells around the periphery of the ducts that extended to the surface of the tissue. Within the stroma of the gular gland were blood vessels, connective tissue, and fibrocytes. Muscle tissue within the dermis was associated with the gular gland. Tissue removed from the gular region of females of both species showed no indication of a gular gland, although numerous sebaceous glands were associated with numerous hairs (Fig. 3*g*).

Fig. 2. Scanning electron micrographs of a body hair from a male *Taphozous melanopogon* (*a*); a beard hair from a male
T. melanopogon, which has more numerous modified scales and a thicker diameter (*b*); a body hair of a male *Sturnira lilium* (*c*); and a
shoulder gland hair of a male *S. lilium* that is thicker in diameter than a body hair (*d*).
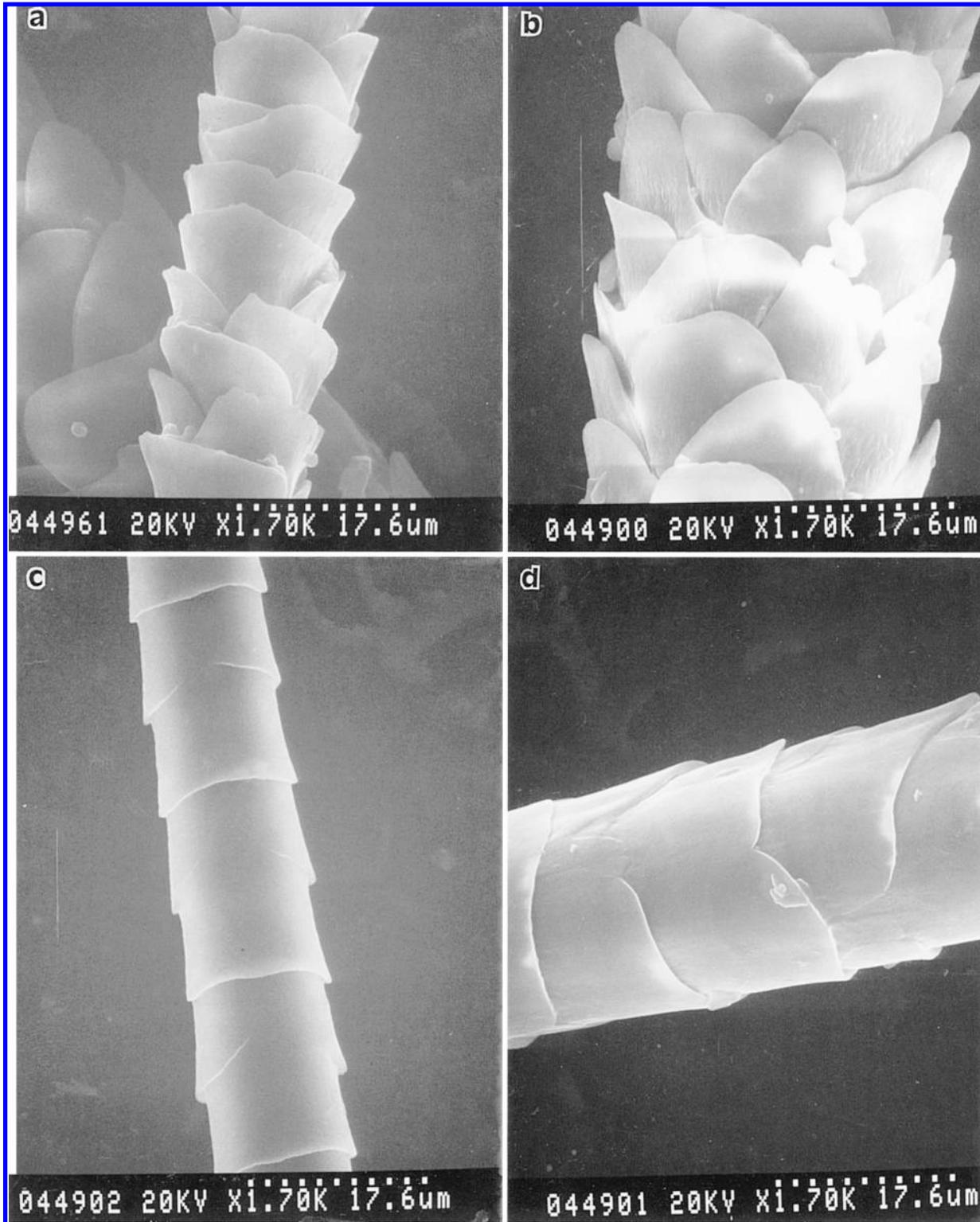
Discussion

Like others (reviewed in Quay 1970), we found that bats
have typically mammalian integumentary glandular scent or-
gans composed of sebaceous and sudoriferous glands (Quay
1970, 1972; Strauss and Ebling 1970; Albone 1984; Haffner
1998) and the integumentary glandular scent organs of bats
tend to be similar across species. Among emballonurids,

P. macrotis, *S. bilineata*, and *T. nudiventris* gular glands resemble the situation in *Taphozous flaviventris* (Hall and Gordon 1982) or *Taphozous georgianus* (Kitchener 1976), whose gular glandular organs consist of a large bed of sudoriferous glands in the dermis connected to ducts leading to the surface of the throat. The large, eversible gular glandular organs of *M. ater*, and *M. sinaloe* are histologically similar to the chest gland of the emballonurid *T. nudiventris*. In these three species the parenchyma primarily consists of sebaceous glands with some sudoriferous glands and skeletal muscle, allowing eversion of the scent gland. Similar glandular components have been found in the gular area of *M. ater* (Werner and Lay 1963), *Molossus bondae* (Dapson et al. 1977), *T. brasiliensis* (Dapson et al. 1977; Gutierrez and Aoki 1973), *Tadarida cynocephala* (Werner et al. 1950), and *Phyllostomus discolor* (Valdivieso and Tamsitt 1964). Many hipposiderids have eversible frontal glands that produce a waxy secretion (Rosevear 1965), and in male *H. ater* and *H. fulvus* the situation resembles that described for others (e.g., *Hipposideros commersoni*, *Hipposideros ruber*, and *Triaenops persicus*; Mainoya and Howell 1977). Although the location of the ear glands of *R. anaeus* is unique among vespertilionids, they are similar in morphology and histology to those of other vespertilionids such as *Antrozous pallidus*, *Lasiurus borealis*, *Lasiurus floridanus*, and *Nyctalus noctula* (Walton and Siegel 1966; Dalquest 1950; Werner and Dalquest 1952).

Our findings support the earlier conclusion that the wing sacs of *S. bilineata* are not glandular organs but holding sacs (Starck 1958; Voigt and von Helversen 1999) and we extend this finding to other taxa (*S. leptura*, *P. macrotis*). Although the wing sacs are largest, with the greatest abundance of infoldings, in *S. bilineata*, they are similar in cellular composition across species. More numerous infoldings could provide more storage area for secretions, and the skeletal muscle could assist in opening and closing the wing sacs (Starck 1958; Voigt and von Helversen 1999). The wing sacs are sexually dimorphic, being larger in males than in females (Reid 1997). In the field, a sweet-smelling pink exudate is associated with the glands in just-caught male but not female *S. bilineata* (Bradbury and Emmons 1974). The location of the holding sacs on the wings may facilitate scent-marking during wing-flapping (Bradbury and Emmons 1974; Voigt and von Helversen 1999) while minimizing the weight associated with an actual gland. The utility of antebrachial wing sacs as a diagnostic feature (Reid 1997) reflects the fact that they have evolved more than once among Neotropical emballonurids. Wing sacs occur in the genera *Saccopteryx*, *Peropteryx*, *Balantiopteryx*, and *Cormura*, the latter genus apparently representing a different lineage (Dunlop 1998).

We found two kinds of hairs associated with scent glands, those differing from body hairs in size and cuticular-scale pattern (*T. melanopogon*) and those differing only in size (*S. lilium*). Only the former should be called osmetrichia. Sometimes the glands of males and females show little difference in glandular structure, but odoriferous secretions that colour the hairs occur only in adult males (*T. melanopogon* and *S. lilium*). In these species, the disappearance of the distinctive hair colour in fluid preservative is a good indication that it is derived from glandular activity. Between-male vari-

ation in the appearance of the beard (*T. melanopogon*) or neck–shoulder area (*S. lilium*) indicates that males vary in glandular activity.

The location of glandular scent organs on a mammal's body reflects its habitat, behaviour, and size. For example, in both terrestrial voles (lateral glands) and arboreal voles (sternal glands), the glands are well positioned to mark accessible surroundings (Müller-Schwarze 1983). The scent glands of bats show a similar correlation with behaviour (Quay 1970) and our data support this view. The gular–chest region is a common one for scent glands in bats that roost with their venter against a surface (*P. macrotis*, *S. bilineata*, *S. leptura*, *T. melanopogon*, *T. nuiventris*, *M. ater*, *M. sinaloe*). In bats that hang free of the surface while roosting, neck–shoulder glands (*S. lilium*) and frontal glands (*H. ater* and *H. fulvus*) readily allow marking, as is evident in some pteropodids (Schmidt 1985). The day-roost posture of *R. anaeus* is not known, but these bats have been found roosting in the hollows of trees, in attics, in thatched roofs, between boards of houses, and under palm fronds (Goodwin 1946; Goodwin and Greenhall 1961; Eisenberg 1989).

Integumentary glandular scent organs in mammals are often sexually dimorphic, reflecting differences in breeding activity and responses to sex steroid hormones (Mykytowycz 1965; Ewer 1968; Quay 1970; Quay and Müller-Schwarze 1970; Strauss and Ebling 1970; Eisenberg et al. 1971; Kingdon 1974; Kitchener 1976; Stoddart 1976; Hosken et al. 1998). Sexual dimorphism in bats is evident in body size and secondary characteristics. Although females tend to be larger than males, their scent glands tend to be smaller or show decreased glandular activity compared with males; this was evident in all of our study species (*P. macrotis*, *S. bilineata*, *S. leptura*, *T. nudiventris*, *H. ater*, *H. fulvus*, *M. ater*, *M. sinaloe*, *R. anaeus*, *T. melanopogon*, and *S. lilium*). Changes in hormone levels can contribute to differences in glandular appearance in bats (e.g., *T. brasiliensis*, Gutierrez and Aoki 1973; *T. georgianus*, Kitchener 1976) as they do in other mammals (hamsters, Montagna and Hamilton 1949; *Oryctolagus cuniculus*, Mykytowycz 1965; *Elephas maximus*, Eisenberg et al. 1971). The situation is complex, however, for in both *T. melanopogon* and *S. lilium* the scent glands (gular and shoulder, respectively) in males and females are similar in overall histology and structure but, as noted above, apparently differ in level and (or) timing of activity.

The scent glands of other mammals show the greatest amount of glandular activity during the breeding season, when androgen levels are high (Ralls 1971; Albone 1984; Hosken et al. 1998). Seasonality affects scent glands with respect to the amount of secretory tissue, hypertrophy of individual sebaceous cells, and changes in excretory ducts, synthesis and accumulation of sebum, as well as the chemical composition of the secretory droplets (Albone 1984). High levels of androgens in the bloodstream also affect behaviour (Ewer 1968; Eisenberg and Kleiman 1972) as well as prostate and seminal vesicle activity (Montagna and Hamilton 1949; Davis et al. 1962; Thiessen et al. 1968). The glandular scent organs of other bats show seasonal differences in activity (Kitchener 1976; Hosken et al. 1998), with the timing of spermatogenesis (Courrier 1927; Nakano 1928; Mainoya 1979) reflecting seasonal increases in hormone levels. Seasonal changes in behaviour also indicate the impact
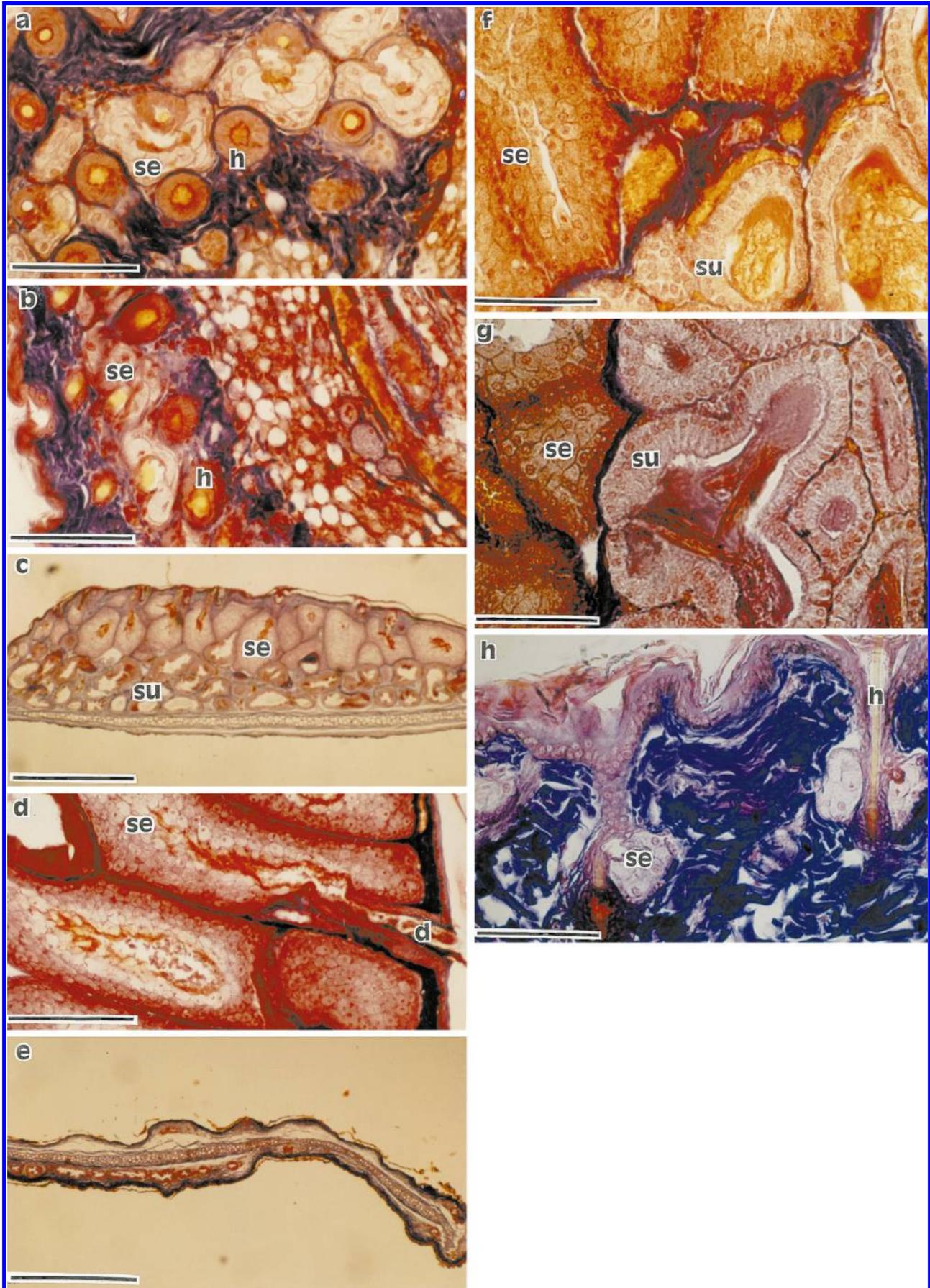
Fig. 3. Histological sections of the glandular scent organs of a selection of bats. (*a*) The neck–shoulder glandular region of a male *S. lilium*, showing sebaceous glands associated with hair. Scale bar = 200 μm. (*b*) Tissue from the neck–shoulder area of a female *S. lilium*, showing sebaceous glands associated with hair. Scale bar = 200 μm. (*c*) Ear gland of a male *Rhogeessa anaeus*, showing the large bed of sebaceous glands on the dorsal surface and numerous sudoriferous glands. Scale bar = 200 μm. (*d*) Ear gland of a male *R. anaeus*, showing the large bed of sebaceous glands with ducts leading directly to the dorsal surface. Scale bar = 50 μm. (*e*) Ear of a female *R. anaeus*, showing that the large bed of sebaceous glands is missing and the layer of sudoriferous glands is reduced. Scale bar = 500 μm. (*f*) Gular gland of a male *Molossus ater*, showing sebaceous and sudoriferous glands. Scale bar = 200 μm. (*g*) Gular gland of a male *Molossus sinaloae*, showing sebaceous and sudoriferous glands. Scale bar = 200 μm. (*h*) Tissue from the gular region of a female *M. sinaloe* at higher magnification. Scale bar = 200 μm. *e*, epidermis; *h*, hair; se, sebaceous glands; *su*, sudoriferous glands.

of these factors on marking behaviour (Hosken et al. 1998), an example of which is the establishing of territories and scent-marking of roosts by male *Pteropus poliocephalus* (Schmidt 1985).

Some of the glandular scent organs we studied are situated so as to attract immediate attention from conspecifics. In *T. melanopogon* and *S. lilium* the prominent gland hairs were soaked with and coloured by glandular secretions, enhancing their visual contrast with body hair. *Taphozous melanopogon* roost with their heads tilted upwards, making it easy for a human observer to distinguish mature males from females and subadults even at a distance of several metres (W.M.R.S., personal observation). The variability in size of the beard and neck–shoulder glands could provide a visual clue as to status and fitness. In *Oryctolagus cuniculus*, the chin and anal glands of older, heavier dominant males are larger than those of young, smaller subordinates (Mykytowycz 1965). Striated muscle associated with the glandular scent organs (e.g., in male *M. ater*, *M. sinaloae*, *H. ater*, and *H. fulvus*) allows the bats to evert the glands, potentially attracting attention to themselves and providing information about their reproductive condition (Mainoya and Howell 1977). Hipposiderids use their frontal glands to anoint themselves with odoriferous secretions (Leen and Novick 1969; Kingdon 1974), enhancing the conspicuousness of other displays. The ear glands of male *R. anaeus* swell and exude a white, milky secretion (Audet et al. 1993), also potentially indicating male reproductive status to females.

The social behaviour of most bats is unknown, making it difficult to determine in detail the function of glandular scent organs in their everyday lives. Like most other mammals, bats appear to make extensive use of chemical signals in a range of situations. Differences in the location of scent glands appear to reflect roosting behaviour, but the overall similarity in glandular structure suggests prevalent common themes. Furthermore, the high level of olfactory acuity known from some bats (e.g., *Carollia perspicillata*; Laska 1990) and their use of olfactory cues in choosing ripe fruits (Rieger and Jakob 1988) demonstrate their potential for using olfactory cues. Differences in the arrangement and quantities of sebaceous and sudoriferous glands may reflect some blend of habitat and the persistence of glandular secretions. For example, the secretions from one gland type may survive better under humid conditions, those of another under dry conditions (Ralls 1971). The oily secretions of sebaceous elements tend to be long-lasting, releasing their volatiles slowly, while the watery, volatile secretions of sudoriferous elements are more useful in short-term signaling (Gorman and Trowbridge 1989). Most of the glandular scent

organs we observed have both sebaceous glands and sudoriferous glands, indicating complex and multiple functions for the secretions they produce. Furthermore, the potential synergistic effects of signals in different media (acoustic, olfactory, and visual; Hessel and Schmidt 1994), known from mother–young interactions (Gustin and McCracken 1987; McCracken and Gustin 1991; Balcombe and McCracken 1992), remind us that bats are not one-channel animals.

Acknowledgements

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