

HISTOLOGY OF A SEXUALLY DIMORPHIC INTEGUMENTARY GLAND IN *MACROGLOSSUS LACOCHILUS* (CHIROPTERA: PTEROPODIDAE)

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ABSTRACT.—A sexually dimorphic integumentary gland is described in the pteropodid bat, *Macroglossus lagochilus*. This gland is restricted to males from Central Province (mainland), Papua New Guinea and is not found in either males or females taken from the Bismarck Islands (Manus, New Britain, New Ireland, Duke of York). Histological examination of the glandular structure, which is readily identified externally as a crescent-shaped welt occupying the lower neck and upper chest, reveals that it is comprised of numerous hypertrophied tubular apocrine-type glands. Comparisons of the integumentary gland of *Macroglossus* males with those of other pteropodids that have been reported in the literature document striking differences in the organization and histology of sexually dimorphic glandular structures in Pteropodidae. The absence of the *Macroglossus* chest gland in individuals from the Bismarck Islands is not related to reproductive seasonality or to any apparent biological features of island and mainland populations.

Chest and shoulder glands are found in many species of pteropodid bats. These glands are often associated with specialized hairs or with modified patches of skin and usually are more highly developed in males. Although these facts have been well known for more than a hundred years, few histological studies document the nature of sexually dimorphic integumentary glands in the Pteropodidae (Tomes, 1860; Dobson, 1873; Andersen, 1912; Lang and Chapin, 1917; Quay, 1969, 1970; Mainoya and Howell, 1979).

In the summers of 1979 and 1981, the Natural History Museum of Los Angeles County sponsored expeditions to collect bats in the Bismarck Islands, Papua New Guinea (including Manus, New Britain, New Ireland, and Duke of York). A preliminary report of the 1979 expedition was given by Smith and Hood (1981). Included in these collections was a large sample of the macroglossine bat, *Macroglossus lagochilus*, Matschie, 1899. [This species was placed, without comment, as a junior synonym of *M. minimus* by Lekagul and McNeely (1977); Corbet and Hill (1980) followed this arrangement. We prefer to retain *lagochilus* as a valid species name until such time as a convincing argument to the contrary is presented.] Additional specimens (16 SS, 27 22) of this species were collected in 1981 from Laloki Agricultural Quarantine Station, 9 km NE Port Moresby, Central Province, on the mainland of Papua New Guinea. We were surprised to find that males from this locality possessed a weltlike, crescent-shaped structure across their lower neck and upper chest; this feature was readily noticed by its reddish coloration in live animals (Fig. 1). Although no secretions were observed on the surface of the skin, the structure appeared to be an active integumentary gland. In this paper, we describe

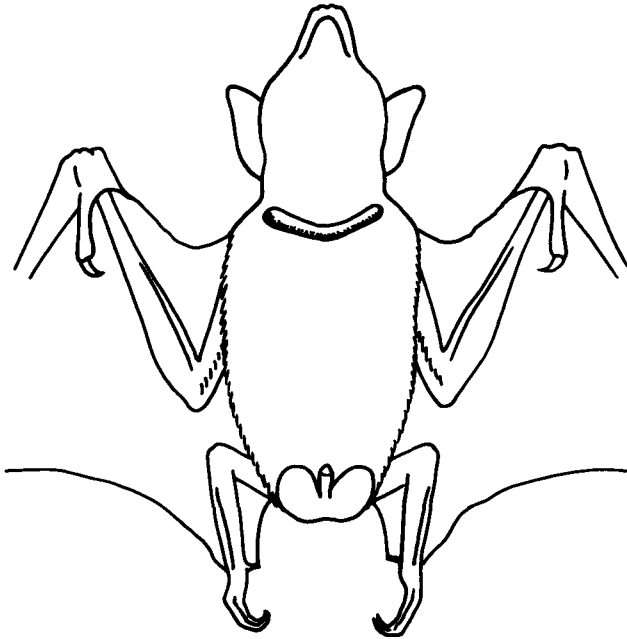


FIG. 1.—Diagrammatic illustration of the externally visible welt-like structure on the lower neck and upper chest of male *Macroglossus* from the Central Province locality.

histological aspects of this apparently sexually dimorphic integumentary gland and discuss these structures within the family Pteropodidae.

METHODS AND MATERIALS

Two hundred and twenty-eight specimens from the Bismarck Islands and 43 from Central Province, Papua New Guinea, were examined for gross external evidence of the gland. Skin samples were taken from males and females of island populations (Manus, 2 M, 2 F; New Britain, 3 M, 2 F; Duke of York, 3 M, 3 F) and from those of the Central Province locality (4 M, 4 F) for histological examination. These tissues were fixed in 10% formalin, processed through cedarwood oil, embedded in Paraplast, serially sectioned at 8-10 Mm, and stained with hematoxylin and eosin, Masson's trichrome, or Gomori's one step trichrome method (Humason, 1972). Voucher specimens are deposited in the Natural History Museum of Los Angeles County and The Museum, Texas Tech University.

RESULTS

Island populations.—Skin samples taken from the neck and upper chest region of *Macroglossus* collected from island localities possessed no qualitative differences compared with skin samples from other body regions in those same specimens. The pelage in this area is extremely fine, with short thin guard hairs. No specialized hairs are found in this region and microscopic structures such as hair follicles, sudoriferous (sweat) glands, sebaceous glands, and arrector pili muscles were readily observed in all specimens. Comparisons of males and females within island localities revealed no qualitative differences, although sebaceous glands appeared slightly more numerous in the males (Fig. 2).

Sweat glands had a simple coiled tubular structure in all specimens examined. The secretory portions of these glands extend deeply into the dermis and consist of cuboidal to columnar cells that have darkly-staining, large round nuclei and lightly-staining cytoplasm. Excretory ducts are distinctly narrower, and are composed of 2 or 3 layers of intensely staining cuboidal cells (acidophilic with hematoxylin and eosin).

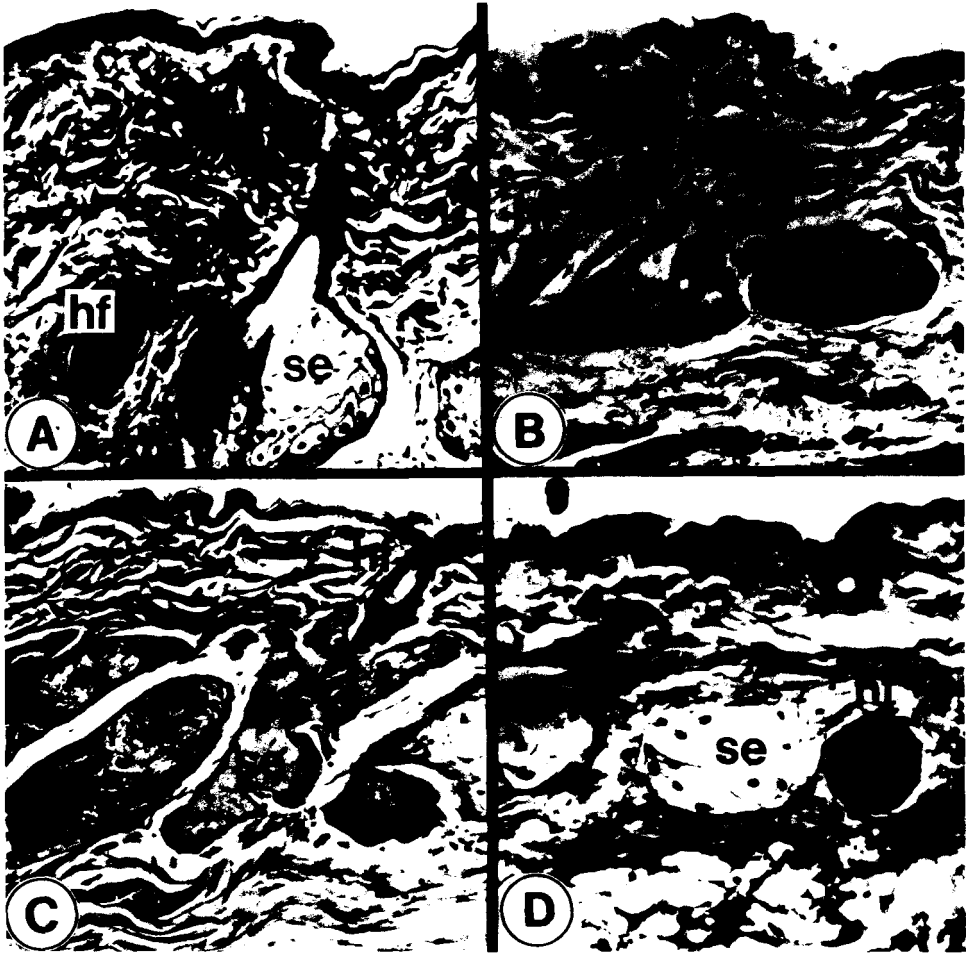


FIG. 2.—Photomicrographs of skin samples of the neck region of *Macroglossus* collected from Bismarck Island populations. Specimens from Duke of York are A, a male, and B, a female, and from Manus Island, C, a male, and D, a female. Abbreviations are, hf, hair follicle, se, sebaceous gland. All photos $\times 125$.

Sebaceous glands contain multiple acini that open by way of short ducts into hair follicles. Cells at the periphery of acini were small and flattened, whereas those occupying central portions of the glands were large, polyhedron-shaped, and pale-staining. Arrector pili muscles, composed of delicate smooth muscle strands inserted in a dense dermis, were associated with the sebaceous glands.

Mainland populations.—Female *Macroglossus* collected at the Central Province locality possessed no qualitative histological differences when compared with both male and female specimens from the island localities (Fig. 3). On the other hand, males from the mainland locality had an integumentary feature that in live animals appeared as a crescent-shaped welt (Fig. 1). Histological examination of this area revealed that the externally visible welt is composed of hypertrophied, tubular glands (Fig. 4).

The glands consist of two histologically distinct regions; an excretory duct system and a multibranching secretory complex. The secretory portions are subdivided into 2 or 3 lobules that are separated from one another by dense connective tissue septa. Each lobule consists of a long



FIG. 3.—Photomicrograph of skin sample of the neck region of female *Macroglossus* collected from the Central Province locality. Abbreviations as in Fig. 1. x125.

secretory tubule lined with tall, simple columnar epithelium. Secretory cells have small round nuclei that are heterochromatic. The cytoplasm is uniformly stained (basophilic with hematoxylin and eosin), and in many cells is displaced by vacuoles that form a network.

A single excretory duct drains the secretory tubules of the gland. Excretory ducts open into hair follicles near the surface of the skin. In some instances, these ducts open directly onto the epidermal surface. There was no evidence of a complex duct system (for example, including intercalary ducts) leading to common central ducts in any of the specimens examined. Cells lining excretory ducts are cuboidal with small, intensely-staining centrally located heterochromatic nuclei. The cytoplasm is strongly acidophilic (with hematoxylin and eosin) and contains many red granules (in samples stained with Masson's and Gomori's trichrome).

Judging from the overall morphology of this glandular tissue and the way by which the excretory ducts open into hair follicles at or near the surface of the epidermis, we conclude that these glands are modified sudoriferous (sweat) or apocrine glands.

Sebaceous glands were conspicuously absent from within the hypertrophied glandular area in males from the Central Province locality. However, large masses of sebaceous tissue with classical histological characteristics were found on the periphery of this complex glandular region (Fig. 4). Sebaceous acini of these particular glands had greatly enlarged cells that were heavily vacuolated (Fig. 5). When stained with Masson's or Gomori's trichrome these cells have a pale-staining cytoplasm and contain red to brown granules that appear to form a reticular network. In comparison with sebaceous glands examined from the islands, these glands appeared to be much more "active." Increased activity is evidenced by an overall enlargement of sebaceous acini, greatly enlarged and vacuolated cells, and the presence of secretory material in the excretory ducts of many glands (see Fig. 5).

DISCUSSION

Comparisons.—A general understanding of integumentary glands in Chiroptera has been based primarily on descriptions of Microchiroptera (Werner et al., 1950; Werner and Dalquest, 1952; Dalquest et al., 1952; Dalquest and Werner, 1954; Quay, 1970). General microscopic features of the skin in *Macroglossus* are similar to those described for other bats, with two notable exceptions. The simple tubular structure of sweat glands in *Macroglossus* contrasts with

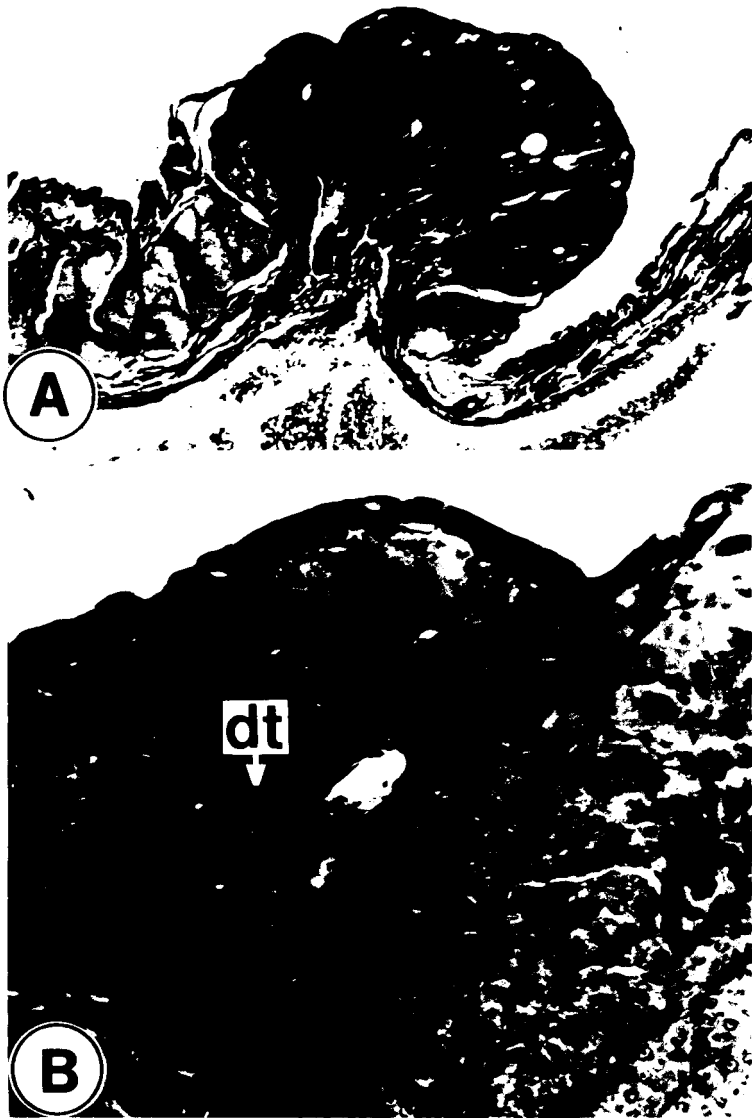


FIG. 4.—Photomicrograph of the integumentary gland of male *Macroglossus* collected from the Central Province locality. A, cross-section of glandular welt with large, hypertrophied masses of sebaceous tissue (SE) at the periphery, x30; B, apocrine-type glands of the glandular welt. Secretory ducts (dt) open into hair follicles (hf) near the epidermal surface, x 100. Arrows point to connective tissue septa.

the complex form described by Wimsatt and Kallen (1952) and Sisk (1957) for sweat glands in *Myotis lucifugus*. However, Quay (1970) has noted that sudoriferous glands are especially variable within bats and that simple to complex forms can be found in different body regions.

Quay (1969) examined the histology of arrector pili muscles in Chiroptera, and reported that whereas all Microchiroptera have highly modified, striated muscle arrector pilori, most Mega-

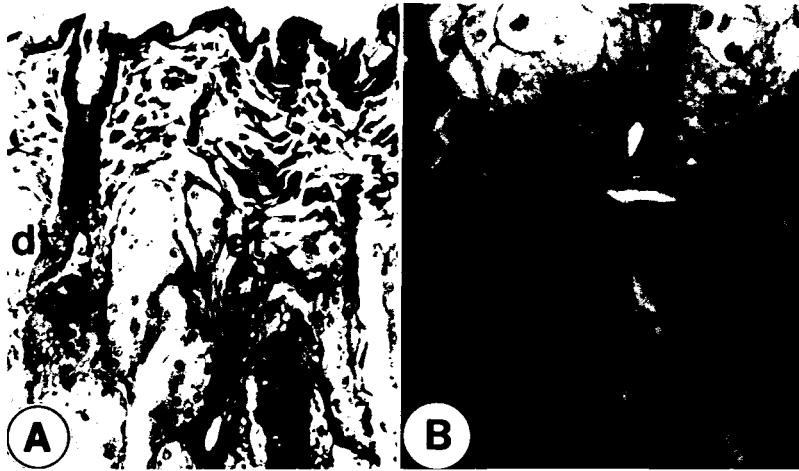


FIG. 5.—Photomicrograph of sebaceous glands at the periphery of the glandular welt from the specimen in Fig. 4. A, x95; B, holocrine-secreting cells of sebaceous glands, x240.

chiroptera have predominantly smooth muscle fibers. In *Macroglossus* this muscle is composed entirely of smooth muscle; this complements Quay's (1969) observations on other pteropodid bats.

Although special integumentary glands, including neck, throat, and chest glands, are well known in a variety of microchiropteran species (Werner and Lay, 1963; Valdivieso and Tamsitt, 1964; Kitchener, 1976; Dapson et al., 1977; Hall and Gordon, 1982), few examples of Megachiroptera have been examined histologically for these structures. Mainoya and Howell (1979) presented detailed histological observations on sexually dimorphic integumentary glands in three pteropodid bats. *Eidolon helvum*, *Rousettus aegyptiacus*, and *R. angolensis*. These three species have prominent, sexually dimorphic neck and shoulder regions. These areas are characterized on the basis of external morphology by the occurrence of longer brushlike hair, which usually is differentially colored in males. This general area also possesses a "glandular" appearance that has been noted by numerous authors (Dobson, 1873; Andersen, 1912; Lang and Chapin, 1917; Rosevear, 1965; Mutere, 1967; Kingdon, 1974). Mainoya and Howell's (1979) histological examination revealed that the glandular skin patches of two of these species (*E. helvum* and *R. aegyptiacus*) are generally similar.

In *Eidolon helvum*, the glandular tissue of the skin patch consists of a multilobulated sebaceous glands with excretory ducts that open into hair follicles well below the surface of the skin

TABLE 1.—Pregnancy data for female *Macroglossus lagochilus* collected from four Bismarck Islands, and from the Quarantine Station locality (Central Province). Size classes of embryos are in mm (crown-rump).

Locality	N	No. pregnant*	Embryo size classes				
			5.9	6.0-10.9	11.0-15.9	16.0-20.9	21.0>
New Ireland	38	30	14	1	5	5	5
New Britain	15	11	3	2	3	0	3
Duke of York	51	35	17	3	5	6	4
Manus	9	2	2	0	0	0	0
Quarantine St.	27	16	8	0	3	3	2

* All pregnant females carried but a single fetus.

in the deeper portions of the dermis. The glandular skin patches in *Rousettus aegyptiacus* are similar to those of *Eidolon* in being sebaceous and located deep within the dermis. However, the sebaceous complex of *aegyptiacus* consists of large hypertrophied masses of sebaceous tissue rather than being lobulated.

Rousettus angolensis males possess a collar or ruff or specialized hairs on the upper chest and lower neck region. In their study, Mainoya and Howell (1979) were surprised to find no evidence of special glandular development in this area. Their data seem to contradict observations reported by Kingdon (1974:137) and Rosevear (1965:85) in which a glandular secretion was indicated by a sticky substance on the specialized hairs of the chest region. If glandular development and activity is a seasonal phenomenon as Kingdon (1974) suggested, possibly the specimens examined by Mainoya and Howell (1979) were simply atrophied or inactive and the glands were not really absent, as they supposed. Therefore, we must regard their observations concerning the presence or absence of these glands as inconclusive.

Our findings on the sexually dimorphic integumentary gland in *Macroglossus lagochilus* document strikingly different histological features compared to those described above. The pelage of the neck and chest area in *Macroglossus* is not noticeably specialized, although somewhat sparser, when compared to other areas of the body. The externally visible welt found in males from the mainland had no associated specialized hairs or other unusual surface features. This is not particularly surprising because macroglossines (except *Megaloglossus*) do not possess sexually dimorphic integumentary features (Andersen, 1912; Benedict, 1957). Histologically, the neck and chest gland was of an apocrine-type as opposed to the sebaceous-type found in *Eidolon* and *Rousettus*. These apocrine glands have ducts that open near or at the surface of the skin. Additionally, the glandular complex of *Macroglossus* occupies a broad expanse in the middle to upper portions of the dermis. The sebaceous tissue surrounding the sudoriferous core of the *Macroglossus* chest gland appears to be similar to the sebaceous tissues reported in *R. aegyptiacus* by Mainoya and Howell (1979).

Biological implications.—The presence of special integumentary glands on males from the mainland population of *Macroglossus* and their apparent absence on those of the Bismarck populations raises the question—what are the biological implications of these observations? Three interesting alternatives are apparent. First, the glands may be seasonally developed and we simply have missed them in the Bismarck specimens, as we suspect was the case when Mainoya and Howell (1979) failed to find sebaceous glandular development in *R. angolensis*. Second, these curious glands may be seasonal or persistent only in males of mainland populations, which represent a different species from the Bismarck populations. Third, these glands may be a geographic feature of the mainland population.

Because our collecting efforts were restricted to June through August, we obviously cannot support or refute the possibility that these male chest glands are a seasonal phenomenon. We can, however, present an argument that would suggest their absence in Bismarck populations is not an artifact resulting from the time of collection.

A possible rationale for a seasonal, sexually dimorphic gland would seem to concern reproduction either in the form of sexual recognition, male territoriality, or perhaps, a combination of these (Bradbury, 1977; Mainoya and Howell, 1977; Mainoya, 1979). Table 1 shows the incidence of pregnancy in female *M. lagochilus* from four Bismarck Islands, captured June through August 1979 and in 1981, and pregnancy of females from the Quarantine Station (Central Province) locality, captured in August 1981. Also shown in Table 1 are size classes of embryos from these pregnant females. Except for Manus Island, a large proportion of the females captured in all populations were pregnant. Also, the distribution of size classes of embryos is relatively proportional. Manus Island was visited early in June 1981 and this population may have been in the early stages of reproduction. In addition, the sample size is small. The mean length, (range), and sample size of the testes in males from these same localities were as follows (in mm): New Ireland, 5.5(1.9-8.4), 55; New Britain, 5.6(2.2-7.5), 12; Duke of York, 6.6(2.0-9.0), 38; Manus, 5.8(2.3-7.5), 6; and Central Province, 5.2(3.0-7.2), 14. A single classification

ANOVA found no significant differences among these means. Thus, these populations seem to be generally in the same state of reproduction and "seasonably." We would expect the glands to be equally developed in males of both island and mainland populations if their presence were tied in some way to reproduction.

The last two alternatives present some difficulty. At this point, we have not found other evidence that would support recognition of the mainland *Macroglossus* as a species or subspecies distinct from the island populations. Further investigation may indeed reveal such evidence. Other investigators who have collected *Macroglossus* have not reported the occurrence of these strikingly visible glands but their presence (or absence) might not arouse the interest of a field collector who was not aware of their absence (or presence) in other geographic areas. For example, we have handled several hundred individuals of *Macroglossus* from the islands and would not have been aware of the existence of the glands had we not fortuitously sampled the mainland of New Guinea. The chances of observing these glands would be further reduced if they are truly seasonal in their development. The external characteristics of the glands are modified in fluid-preserved and dried specimens.

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