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# Anatomy and histology of the prostate and glands of Cowper in three species of neotropical bats

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## Abstract

The reproductive accessory glands (RAG) are essential components in reproduction because their secretion products ensure survival, viability, and sperm motility. The objective of this study was to characterize and compare the morphological and histological structure of the RAG in three species of bats of the genus *Sturnira* (*S. erythromos*, *S. lilium*, and *S. oporaphilum*). The RAG complex comprise a compact gland (prostate), which surrounds the urethra, and a pair of Glands of Cowper at the base of penis. Anatomical and histologically, the prostate are differentiated in two regions, ventral and dorsal. The dorsal region has tubuloalveolar glands with secretions fine granular or accumulations of a gel-like substance with bubbles and the ventral region, has alveolar glands with secretory cells form a single-layer of small cells. The seminal vesicles are absent. The prostatic morphology of the three species is similar to that of other studied Stenodermatinae and Desmodontinae, but differs from other subfamilies of Phyllostomidae (Carollinae, Glossophaginae, and Phyllostominae) as that of Molossidae and Vespertilionidae. The RAG complex has no annual variation in relation to functionality or size, but it is variable depending on age (subadults and adults). This agrees with the annual reproductive pattern described for these species in these latitudes, where adult males are reproductively active throughout the year.

KEYWORDS

morphology, reproduction, reproductive accessory gland, Yungas forests

## 1 | INTRODUCTION

In mammals, the male reproductive accessory glands (RAG) complex (glandula vesicularis [seminal vesicle], glandula prostatica [prostate], glandula bulbourethralis [bulbouretheral gland or Cowper gland], ampulla ductus deferentis [ampullary gland]) presents variations in location, shape, size, and function. For example, the Artiodactyla have all the glands of the complex, while Carnivora only have the prostate, a gland that is always present in all mammals (Puga et al., 2013; Vásquez & del Sol, 2010). At the same time, the morphology of the prostate is variable among mammals, ranging from a diffuse or spread tissue, in the urethra's stroma (opossums and deer), to an independent compact gland (human, bats, and rodents) that may be organized into one or more lobes, and regions or zones (Chavez et al., 2011; Vásquez & del Sol, 2002, 2010). Each lobe or gland region differs in microscopic anatomy and histology depending on the type of secretion (Pegorin De Campos, Zanetoni, Góes, & Taboga, 2006).

Although the prostate has been studied almost exclusively in males, certainly due to the high incidence of prostatic diseases in mammals, a female equivalent has been described in humans, in some species of rodents, bats, dogs, and rabbits (Biancardi, dos Santos, de Carvalho, Sanches, & Taboga, 2017; Santos & Taboga, 2006; Vásquez & del Sol, 2002). The structure and function of female's prostate (Skene gland) as well as its pathologies, corroborates its homology with the male's prostate (Gross & Didio, 1987; Rochel-Maia et al., 2013; Shinohara et al., 2013; Zaviacic, 1985; Zaviacic & Ablin, 1998, 2000; Zaviacic, Jakubovská, Belošovic, & Breza, 2000), and that both, morphology and function, may vary during the estrous cycle in response to hormonal fluctuations (Fochi et al., 2008). In rodents, the female prostate is homologous to the ventral prostate in males (Biancardi et al., 2017).

The bulbourethral, or Glands of Cowper, is present in the majority of mammals but may be absent, for example, in canids, and their number varies from one to three pairs, depending on the species (Krutzsch, 2000; Vásquez & del Sol, 2001).

  

The importance of the RAG complex secretions lies in the fact that they constitute a large proportion of the volume of ejaculation and in ensuring the survival, viability, and motility of sperm both in the male reproductive tract as well as in the female (Beguelini et al., 2012; Krutzsch, 1979).

The Glands of Cowper secretion has been also associated with the formation of the vaginal plug in some species of rodents (Vásquez & del Sol, 2001). Both, secretory activity as well as development of the accessory gland, depend on several factors such as sexual maturity, hormonal factors, the timing of the reproductive cycle, the absence of any other gland of the complex, environmental factors, and different pathologies (Chaves et al., 2011; Vásquez & del Sol, 2010).

Among mammals, Chiroptera are special because of their adaptations to flight and their peculiar way of living. The taxonomic diversity of bats is also reflected in the diverse reproductive patterns, which vary with latitude, with abiotic factors, and food availability. Because of their wide geographical distribution, from temperate to tropical regions, bats experience considerable effects of abiotic factors in their reproductive strategies. Although neotropical bats have no hibernation, many reproductive characteristics vary depending on the season, mainly due to the availability of food (Altrigham, 1996; Krutzsch, 1979).

Despite the large number of species and the great diversity of life styles, some aspects of reproductive biology of bats are still poorly understood, especially those related to reproductive cyclicity of males, and functional relationships of the secondary sexual glands with seasonal variations. RAG have been studied in a few species of bats, showing a great variation in morphology, ultrastructure, and volume of secretions between species (Beguelini et al., 2012; Krutzsch, 1979, 2000; Krutzsch, Fleming, & Crichton, 2002; Puga et al., 2013). The prostate and Glands of Cowper are present in all species of bats for which information is available, while the seminal vesicle may be absent in some species or higher taxonomic units (Krutzsch, 2000).

In bats, the prostate varies in the gross anatomy and morphology at family and subfamily level. In Phyllostomidae and Noctilionidae it is a compact gland with two or three regions while in Vespertilionidae it is a lobular gland and in Molossidae it shows an intermediate degree of lobulation (Beguelini, Puga, Morielle-Versute, & Taboga, 2016; Beguelini et al., 2012; Christante et al., 2013; Martins et al., 2014; Negrin et al., 2013).

Studying the microstructure of the RAG in bats, we explore further the interspecific variation and add morphological data for evolutionary and phylogenetic interpretations.

In Argentina three sympatric species of bats of the Genus *Sturnira* can be found in the Yungas Forests. *Sturnira lilium* is the most common, followed by the also common *S. erythromos*, and by the rare but widely distributed *S. oporaphilum* (Barquez, Mares, & Braun, 1999; Díaz, Solari, Aguirre, Aguiar, & Barquez, 2016). Although these species have been widely studied in Argentina with respect to distribution and some aspects of its natural history, virtually nothing is known about their reproduction (Autino & Barquez, 1994; Contreras, 1994; Crespo, Vanella, Blood, & De Carlo, 1961; Delpietro & Russo, 2002; Pearson & Pearson, 1989).

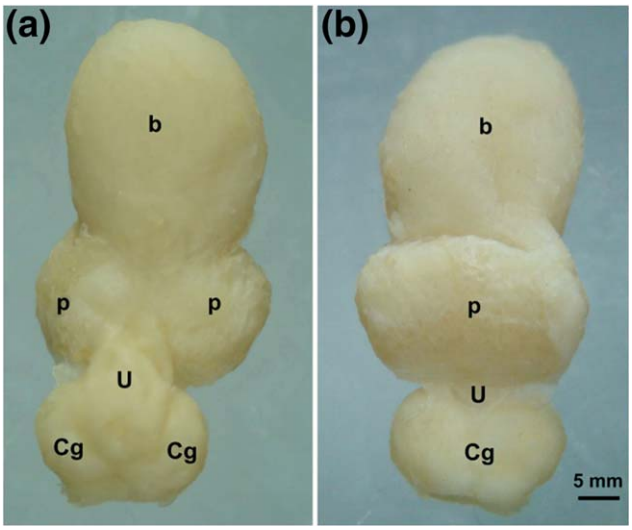


**FIGURE 1** *Sturnira lilium*: gross anatomy of the accessory reproductive glands of an adult male. (a) Ventral view; (b) Dorsal view. b bladder; Cg Cowper's gland; p prostate; u: urethra

The aim of the present study was to characterise the histology and morphology of the prostate and Glands of Cowper for these three neotropical bats and to evaluate the seasonal functional variations of the prostate gland.

## 2 | MATERIAL AND METHODS

Prostates of 65 specimens, including adults and sub-adults of 27 *Sturnira erythromos* (Tschudi, 1844), 13 adults, 14 subadults, 34 *Sturnira lilium* Geoffroy St.-Hilaire, 1810 (24 adult,10 subadult), and 4 *Sturnira oporaphilum* (Tschudi, 1844), 3 adults, 1 subadult, were studied.

The bats were obtained at several localities of the Yungas forests of northwestern Argentina, in the provinces of Jujuy, Salta, and Tucuman between 22 and 28 degrees South Latitude. Bats were collected for projects on "Diversity of Birds and Mammals of Northwestern Argentina 1998–2008" directed by one of us (RMB) and granted by CONICET PIP N 4963, and CIUNT 26/Z103 and 26/G207, with authorizations issued and supported by the provincial authorities for administration of the natural resources: Dirección de Recursos Naturales Renovables de la Provincia de Jujuy (CONST 06.WPS), Dirección Provincial de Medio Ambiente y Recursos Naturales de Salta (authorization to RMB issued June 1998) and Secretaría de Estado de Agricultura y Ganadería de la provincia de Tucumán ((authorization to RMB issued June 1998). The specimens were captured with mist nets and the age was defined in the field, as adults and subadults, based on their fur color, degree of ossification of the metacarpal epiphyses and tooth wear (Dinerstein, 1986; Hutson & Racey, 2004; Racey, 1988). Also, the age was later corroborated in the laboratory by the presence or absence of spermatozoa inside the testicles, the tail of the epididymis (Beguelini et al., 2013), urethra and accessory hypertrophy of the sex gland. The capture and euthanasia procedures for bats followed the guidelines given by the Ethics Committee of SAREM (Argentine Society for the study of Mammals). Individual organs were measured (usually

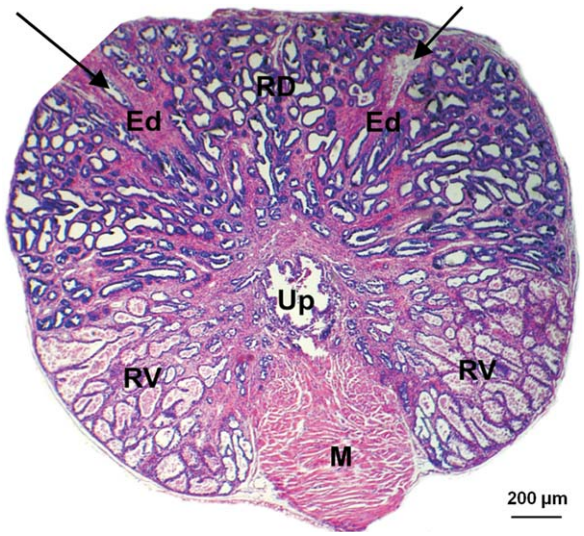


**FIGURE 2** *Sturnira lilium*: adult male prostate. The two regions, dorsal and ventral and the ejaculatory ducts are clearly visible. Ed ejaculatory ducts (arrows); M muscular tissue; RD dorsal region; RV ventral region; Up Prostatic urethra. Hematoxylin and eosin staining

greatest length and width) and in the case of prostate, high by width, with dial calipers to the nearest 0.10 mm. For each species a complete reproductive tract was studied in order to describe the gross anatomy (Figure 1).

The entire reproductive tracts were prepared for light microscopic examination, by immersion in 10% neutral formalin, dehydration in graded ethyl alcohol, clearing in xylene, and embedding in paraffin wax. Tissues were sectioned at 6 µm (serial or semiserially) and stained with Ehrlich's hematoxylin and eosin (McManus & Mowry, 1968) for general analysis of glandular structure, and with periodic acid-Schiff (PAS) to assess the overall activity of the gland secretion (Pearse, 1960). The micrographs were taken with a digital camera AxioCam ERC5S and processed with Microscope Imaging software ZEISS ZEN 2012-Blue edition (Germany).

The bats carcasses were preserved in ethanol 70% or prepared following Díaz, Flores, and Barquez (1998) and deposited in the Colección Mamíferos Lillo (CML), Universidad Nacional de Tucumán, Tucumán, Argentina. Histological slides were also deposited at the CML annexes.

Specimens examined: *Sturnira erythromos* (13 subadults): CML 10271, 10274, 10280, 10284, 10295, 10321, 10322, 10323, 10325, 10326, 10330, 10331, 10878; (14 adults) CML 10269, 10292, 10294, 10298, 10299, 10300, 10307, 10312, 10314, 10319, 10881, 10882, 10885, 10889. *Sturnira lilium* (10 subadults) CML 10342, 10343, 10348, 10351, 10354, 10355, 10357, 10363, 10436, 10442; (24 adults) CML 10347, 10348, 10386, 10388, 10389, 10390, 10438, 10439, 10446, 10447, 10517, 10519, 10531, 10539, 10559, 10562, 10623, 10627, 10628, 10636, 10639, 10640, 10641, 10642, *Sturnira oporaphilum* (1 subadult) CML 10650; (3 adults) CML 10648, 10651, 10652.

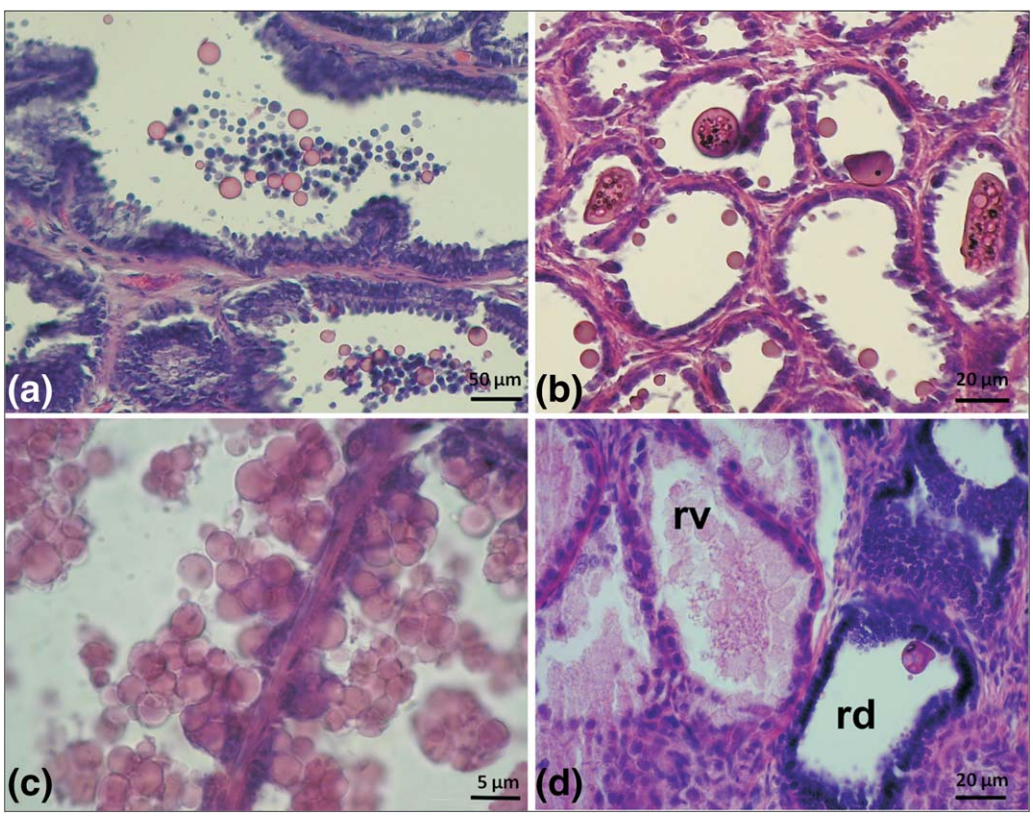


**FIGURE 3** *Sturnira lilium*: prostatic secretions. (a, b) Morphology of the two prostatic secretions in the dorsal region. (c) Prostatic secretions in the ventral region. (d) Two types of secretions, doral and ventral regions. rd dorsal region; rv ventral region. Hematoxylin and eosin staining

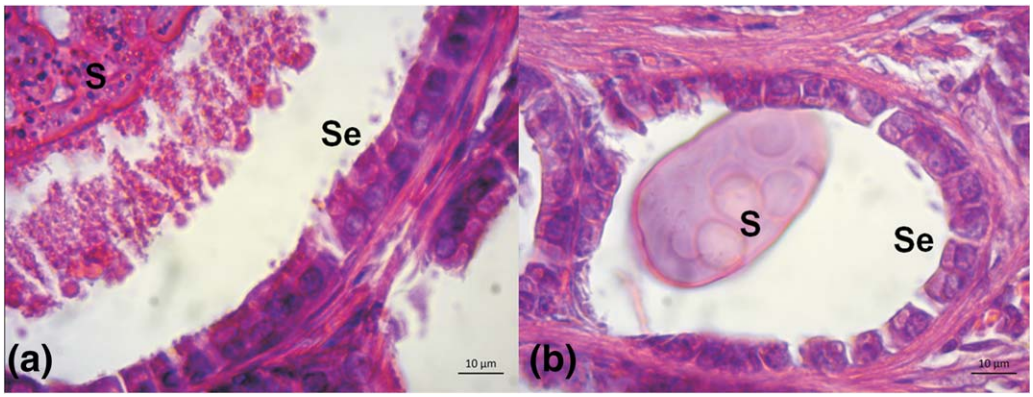


**FIGURE 4** *Sturnira erythromos*: secretory epithelium of the glands of the dorsal region of the prostate and the two types of secretions. A simple columnar secretory epithelium, B simple cubic secretory epithelium. S secretion; Se secretory epithelium. Hematoxylin and eosin staining

## 3 | RESULTS

Macroscopically two regions can be observed in the prostate: the dorsal and ventral regions, which are differentiated by color, observed before fixation, appearance, and texture. The dorsal region is more cephalic, has a pale and translucent appearance and in this area the deferens ducts converges with the prostatic urethra. The ventral region is more caudal, has a whitish color, a compact appearance and completely encloses the urethra.

The microscopic analysis confirms the existence of the two regions (Figure 2). The dorsal region has tubuloalveolar glands of different shapes and sizes supported by a reticular parenchyma. In some areas of the gland lumen, secretions appear to be fine granular, in other parts they looks like large accumulations of a gel-like substance with bubbles (Figure 3a,b) and we also observed concretions like corpora amylacea. The secretory epithelium is simple and varies from cubic to low columnar in different regions; the nuclei of these cells are located basally, and at the cell apex there is a lighter area (Figure 4). In this dorsal region, the stroma is more abundant than in the ventral region, has more smooth muscle and the ejaculatory ducts can be found laterally (Figure 2). Ejaculatory ducts are coated by a simple columnar epithelium and lamina of elastic fibers. The muscular layer is observed only in the first portion of the ducts. In some adult males the presence of sperm was observed in several parts of the reproductive tract: ejaculatory ducts, in lumen of many of the prostate glands that surround the ejaculatory ducts, and even in the urethra lumen in the prostate caudal zone (Figure 5).


**FIGURE 5** *Sturnira erythromos*: sperm in the lumen of some parts of the dorsal prostate. Insert, close-up of sperm in the prostate Ed ejaculatory ducts, RD dorsal region; RV ventral region; U urethra. Hematoxylin and eosin staining

In the ventral region, the alveolar glands are close to each other and little connective tissue containing some smooth muscular cells was observed. The secretory cells of the glandular epithelium form a single-layer of small cells. In each gland lumen, there are secretion granules of different sizes (Figure 3c,d), staining positive with PAS while secretions of the dorsal region gland have a mixture of PAS positive and negative granules.

In addition to the dorsal and ventral regions, the prostate also has a cephalo-caudal polarization. The glands of the dorsal region are more clearly observed in the cephalic zone, while towards the caudal zone the glands of the ventral region predominate.

The prostatic urethra changes its microscopic anatomical appearance from the entrance at the cephalic region to the exit at the caudal region of the prostate. It has three distinctive regions: cranial, medial and caudal. In the cranial region is surrounded by connective tissue only. In the medial region, the wall of the urethra is folded and has its own lamina propria constituted by a single-layer of fibrous connective tissue and two layers of smooth muscle fibres: an internal longitudinal one, and an outermost with circular arrangement. This is where both deferent ducts connect with the urethra. Is not until the caudal prostatic zone that glands appear included in the urethra's lamina propria and the epithelium has lost the folds. These glands, called urethral glands or glands of Littré are smalls, alveolar and surrounded by connective tissue.

Unlike the prostate of adult males, the prostate of subadults has a more abundant interglandular stroma and smaller gland lumen. The gland is less developed and secretions are present but rare; both dorsal and ventral glandular areas are already differentiated but are not as visible as in adults (Figure 6).

In the three species studied, we observed a pair of Glands of Cowper (bulbourethral glands), at the base of the penis, immediately under

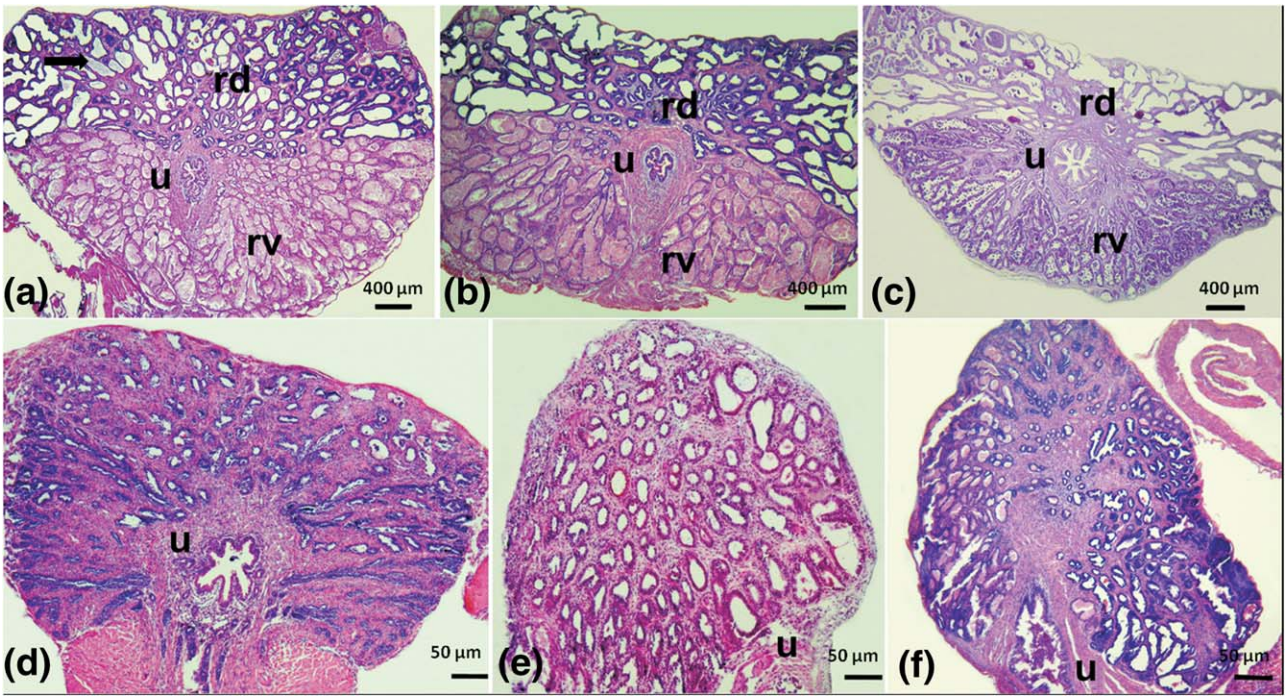


**FIGURE 6** Prostates of the three species of *Sturnira*. Adults and subadults of *S. erythromos*: A adult, D subadult; *S. lilium*: B adult, E subdult; *S. oporaphilum*: C adult, F subadult. rd dorsal region, rv ventral region, U urethra. Hematoxylin and eosin staining

the prostate near the urethra bulb (Figure 1). In adults, the glands are about half the size of the prostate (Table 1). Each gland is surrounded by a fibromuscular capsule constituted by an outer layer of striated muscle, and an inner layer of connective tissue. The capsule projects internally forming a grid of septa that divides the glandular parenchyma in lobes. The glands have the form of tubuloalveolar acini and are coated by a simple epithelium of cylindrical cells with basal nuclei and apical basophilic granular cytoplasm. Secretory granules are strong PAS positive, indicating that secretions are neutral mucoproteins (Figure 7). In the lumen of some acini, coarse grains were observed (Figure 8).

In the three studied species the prostate and glands of Cowper were of the same size (Table 1). We have also not recorded differences in size of the glands in adult males in different seasons (winter from May to October and summer from November to April; Table 2). In both seasons the prostate and Glands of Cowper were active, with abundant secretions in the lumen of the glands.

The only difference recorded is related to the relative age of the specimens (adults and subadults) (Figure 9). The glands of subadults are smaller than those of adults (Table 1) and have no secretions indicating that they are not functionally active (Figure 6).

## 4 | DISCUSSION

There was no sign of a seminal vesicle in any of the three studied species. However, the presence of seminal vesicles, as well as their morphology and development, are variable in bats, especially in the family Phyllostomidae. Initially Krutzsch (1979), reported seminal vesicles for Phyllostomidae, but later showed that it occurs in only a few species (Krutzsch, 2000). Other authors (Martins et al., 2011; Puga et al., 2013, 2014) did not find the seminal vesicle, considering them to be absent in some but not all species of the Phyllostomidae.

As noted, the prostate of the three species has two distinct regions (dorsal and ventral), as described by Puga et al. (2013) in another species of Phyllostomidae (*Artibeus planirostris*) differing with the prostatic morphology of *Phyllostomus discolor* (Beguelini et al., 2012) and *Glossophaga soricina* (Martins et al., 2011; Martins et al., 2016), where three zones were recognized: dorsal, lateral, and ventral. Despite different zones, the prostate structure of Phyllostomidae is compact and has a greater similarity with that described for humans (Blacklock & Bouskill, 1977; McNeal, 1981; Mirowitz & Hammerman, 1992) than with others bat species studied to date. Just like the human prostate is an

**TABLE 1** Average sizes and standard deviation (width × high) of the prostates of adult and subadult and glands of Cowper of the species studied (mm)

| | Adult prostate | Subadult prostate | Gland of Cowper |
|---|---|---|---|
| *S. erythromos* | 4.1 ± 0.7 × 3.0 ± 0.8 | 2.1 ± 0.7 × 2.0 ± 0.7 | 1.8 × 1.5 |
| *S. lilium* | 3.8 ± 0.7 × 3.2 ± 0.9 | 2.4 ± 0.9 × 2.3 ± 0.5 | 2.0 × 2.0 |
| *S. oporaphilum* | 4.0 ± 1.0 × 3.0 ± 0.5 | 4.0 × 1.0 | 2.0 × 1.8 |

**TABLE 2** Seasonal variation in the size of the prostate of adult males (width × high; mm)

| | Prostate winter | Prostate summer |
|---|---|---|
| *S. erythromos* | 3.2 ± 0.8 × 3.8 ± 0.5 | 3.3 ± 0.7 × 3.7 ± 0.5 |
| *S. lilium* | 3 ± 0.9 × 3.1 ± 0.7 | 3.5 ± 0.5 × 3.4 ± 0.9 |
| *S. oporaphilum* | 3 ± 0.5 × 3.8 ± 1.0 | - |

externally homogeneus gland, it is contained within a single capsule and has no lobulations, but differs from the human prostate in the histological aspect, because in *Sturnira* only two well differentiated regions are observed, while in human four zones were described (Laczkó, Hudson, Freeman, Feneley, & Masters, 2005; Ross & Pawlina, 2007). In Vespertilionidae the prostate has a lobulated structure, similar to that found in rodents, and in Molossidae an intermediate degree of lobulation is observed, where the ventral region is compact and the dorsal is lobulated (Beguelini et al., 2012; Krutzsch et al., 2002).

Regarding the bulbourethral, or Glands of Cowper, they are always present in bats, but they appear to be highly variable in number and size. In Vespertilionidae, there are two pairs of small glands (Krutzsch, 2000) that differ from those found in *Sturnira erythromos*, *S. lilium*, and *S. oporaphilum* where there is a single large pair in adults.

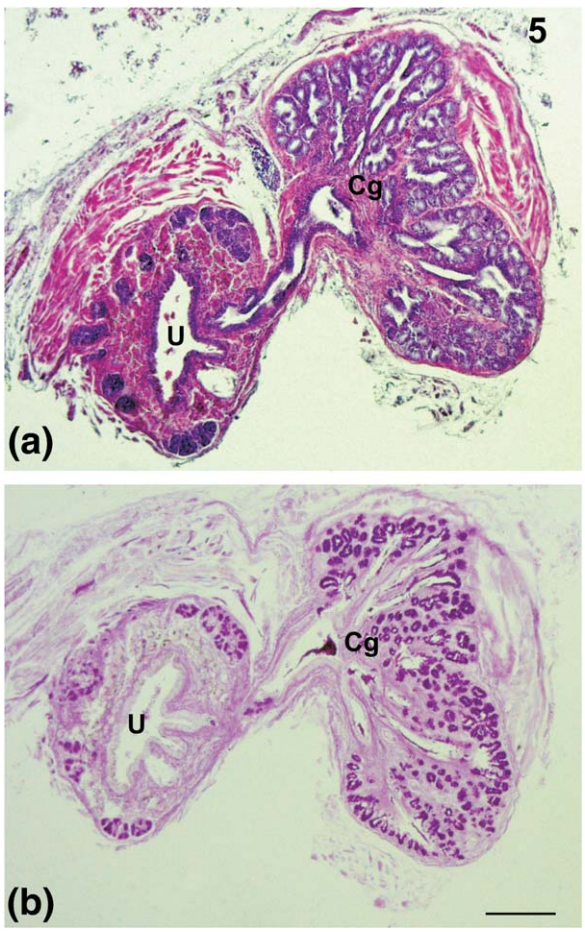


**FIGURE 7** *Sturnira oporaphilum*: glands of Cowper. Opening of the gland into the urethra. (a) Hematoxylin and eosin staining. (b) Periodic acid Schiff staining. Cg Glands of Cowper; u urethra

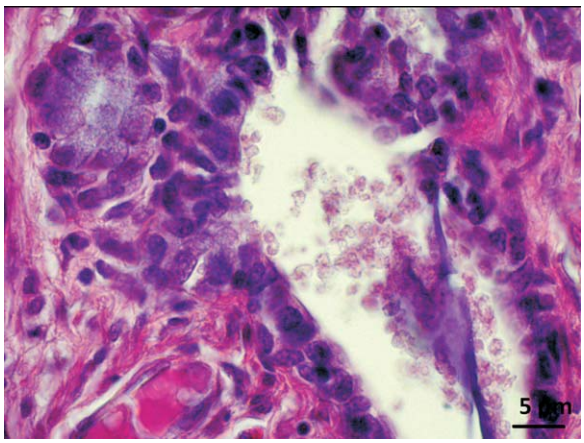


**FIGURE 8** *Sturnira oporaphilum*: secretions of glands of Cowper. Hematoxylin and eosin staining


**FIGURE 9** *Sturnira lilium*: ventral view of the prostate. Difference between size in adults (left) and subadults (right)

Autino and Barquez (1994) studied *S. erythromos* and *S. lilium* in northwestern Argentina determining their seasonal reproductive pattern as monoestrous but this study did not consider the RAG. However, Miotti (2013) studied the reproductive cycles of *S. lilium*, *S. erythromos* and *S. oporaphilum*, finding that all three species were bimodal polyestrous, and males were reproductively active throughout the year. Consistently, in this study we corroborate that the prostate in adults is also physiologically active throughout the year, which support the fact that males have an acyclic pattern of reproduction.

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