

# THE EVOLUTION OF PERFUME-BLENDING AND WING SACS IN EMBALLONURID BATS

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## 1. INTRODUCTION

Although bats comprise the second largest mammalian group and despite the fact that bats have diverse organs for the display of chemical signals (Bloss, 2003), studies on olfaction in bats are scarce. Some members of the family Emballonuridae are remarkable among bats in having highly complex, sexual dimorphic organs for the storage and display of scents. Emballonurid bats include the Old World sheath-tailed and tomb bats and the New World sac-winged bats (Voigt in press). Among the New World members, only males of the genus *Saccopteryx*, *Balantiopteryx*, *Peropteryx*, and *Cormura* have a sac in each of their front wing membrane (= antebrachium) and these sacs usually contain odoriferous liquids (Starck, 1958; Quay, 1970; Bradbury and Emmons, 1974; Voigt and von Helversen, 1998; Scully et al., 1999). Position and size of the wing sacs vary between the males of different species; females have only rudiments of this organ and do not use it in a behavioural context.

## 2. WING SAC MORPHOLOGY IN EMBALLONURID BATS

Here, I describe the wing sac morphology of five species of Emballonuridae, namely *Saccopteryx bilineata*, *Saccopteryx leptura*, *Balantiopteryx plicata*, *Peropteryx macrotis*, and *Cormura brevirostris*, and discuss possible phylogenetic relationships and origins.

Male *Saccopteryx bilineata* weigh about 7.5 g and have relatively large wing sacs of 8 to 10 mm length that protrude the antebrachium ventrally (Figure 1). The opening is formed as two lips: a lateral lip adjacent to the forearm and a medial lip at the thoracal side. In adult males, the sac interior lacks pigments and the membrane is thicker than the adjacent antebrachial membrane. In males that are less than a year old, the interior of the

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sac is usually brown and the epithelium is as thick as the wing membrane. The interior of the sac is structured by a large fold of the medial lips and 8 to 14 smaller folds at both sides of the sac. Two muscle ligaments attach to the sac opening: ligament 1 extends from the ventral lip to the thorax and functions as an opener of the sac and ligament 2 extends from the distal tip of the sac to the wrist and functions as a closure of the sac. The scent of male *S. bilineata* has been described as sweetish, with a touch of bitter almond. Despite the presence of scents, neither Starck (1958) nor Scully et al. (1999) could detect any glandular tissue in the sac interior. Starck postulated that the scents of the wing sacs are either produced by the cornified epithelial layers or that they serve as holding or storage organs for some external scents.

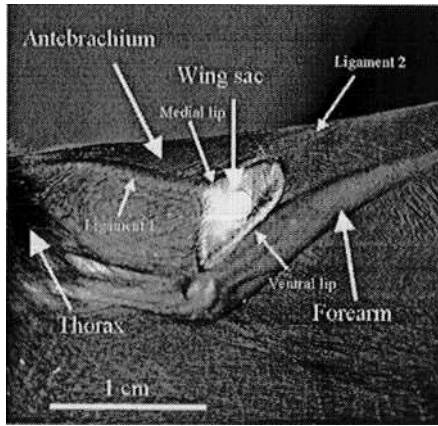
Wing sacs of male *Saccopteryx leptura* are almost identical to those of *S. bilineata*. Male *S. leptura* weigh about 5 to 6 g and have relatively smaller wing sacs than males of *S. bilineata* (Figure 2A) (length of sac opening: 5 to 7 mm). Within the genus *Saccopteryx*, the overall structure of the wing sacs seems to be similar. As in the previous species, the wing sac lays parallel to the forearm, the inner epithelium lacks pigments, one major fold and several minor folds divide it into smaller cavities, and two ligaments are present.

Male *Balantiopteryx plicata* (Figure 2B) differ in the wing sac morphology from the genus *Saccopteryx* in several aspects: the wing sacs are not attached to the forearm, the opening and also the cavity is relatively small, ligaments are not present, and the epithelium of the wing sac is almost as thin as the wing membrane. In addition, the interior of the wing sac is not structured by folds. The opening of the wing sacs is about 3 to 5 mm long. Wing sacs of male *B. plicata* caught in July in Northern Costa Rica did not contain any odoriferous liquids (pers. observation). Males weighed 4 to 6 g.

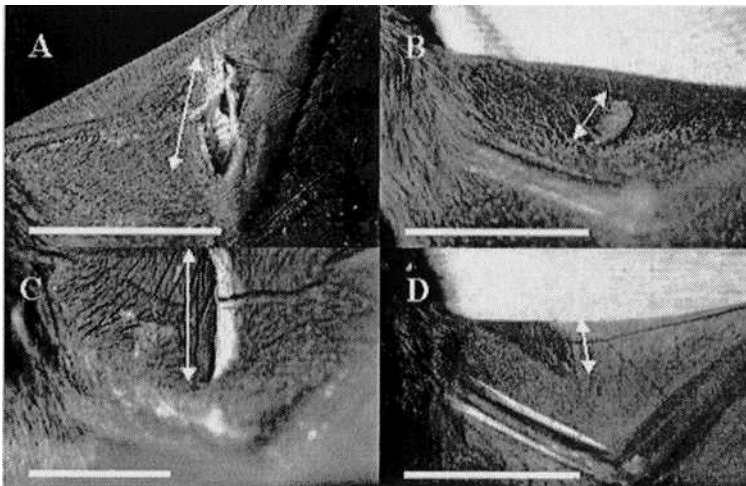
The wing sacs of the following two emballonurid species differ from those of the previous species in several basic features: the anterior tips of the wing sacs touch the front edges of the antebrium and they are flat without a cavity. The 7 to 11 g heavy males of *Cormura breviostris* have large wing sacs that extend almost over the whole antebrium from the anterior edge to almost the upper arm (approximately 10 mm length, Figure 2C). The inner epithelium is white and the scent has been described as pleasant and sweetish. The wing sacs of the 4 to 7 g heavy males of *Peropteryx macrotis* are similar to those of *C. breviostris* in respect to the distal tip of the wing sacs touching the edge of the antebrium (Figure 2D). However, the wing sacs of *Peropteryx* are much smaller than those of *Cormura* and reach only halfway through the antebrium. The inner epithelium of the wing sac is lighter than the wing membrane in *Peropteryx* but not as distinct white as in *Cormura*.

The phylogeny of the family Emballonuridae was studied using chromosomal banding (Hood and Baker, 1986), protein electrophoresis (Robbins and Sarich, 1988), and hyoid morphology (Griffiths and Smith, 1991). These phylogenetic analyses are currently based on a few selected taxa and therefore too coarse to permit a reconstruction of the evolution of wing sacs.

Based on wing sac morphology it is likely that *Saccopteryx* and *Balantiopteryx* shared a common ancestor with wing sacs forming a cavity as the synapomorphic trait. In contrast to these two taxa, *Cormura* and *Peropteryx* have flat wing sacs. The numerous folds found in the wing sacs of *Saccopteryx* are probably an autapomorphic trait for this genus. According to Griffiths and Smith (1991) *Saccopteryx* and *Cormura* are more closely related to each other than to *Balantiopteryx* and *Peropteryx*. This conclusion is not supported by wing sac morphology.



**Figure 1.** Dorsal view of a wing sac from a male *Saccopteryx bilineata*. The thorax of the bat is at the left side of the picture and the wing is fully extended.



**Figure 2.** Dorsal view of wing sacs of four emballonurid species: *Saccopteryx leptura* (A), *Balantiopteryx plicata* (B), *Cormura brevirostris* (C), and *Peropteryx macrotis* (D) (the thick white line indicates 1 cm and the thin line with the arrow heads the length and position of the sac opening). In all pictures, the position of the bats' thorax, wings, forearms, and sacs is similar to that of Figure 1. In contrast to *Balantiopteryx* and *Saccopteryx*, wing sacs of *Peropteryx* and *Cormura* touch the front edge of the antebrachium. *S. leptura* and *C. brevirostris* were caught at the biological stations “La Selva” (Costa Rica, province Heredia), *B. plicata* at “Palo Verde” (Costa Rica, province Guanacaste), and *Peropteryx macrotis* at “Tiputini Biodiversity Station” (Ecuador, province Orellano).

### 3. THE BLENDING OF PERFUME IN THE GREATER SAC-WINGED BAT

Although several emballonurid species possess wing sacs with an odoriferous content, only *Saccopteryx bilineata* has been studied in relation to the origin of the scent. Earlier histological studies revealed that wing sacs of *Saccopteryx* do not contain any glandular tissue (Starck, 1958; Scully et al., 1999). Instead of releasing scent secretions from epithelial cells directly into the sac, male *S. bilineata* transfer fluids from other body regions into them. Thus, wing sacs could also be called holding sacs or perfume containers (Starck, 1958; Scully et al., 1999; Voigt et al., in press).

Each day, male sac-winged bats perform a complex perfume-blending behaviour that lasts on average 31 minutes (max. 1 h). The behavioural sequence is divided into two distinct phases. Firstly, males take up urine orally and lick the sac interior extensively and afterwards males transfer secretions of the genital and gular region into the wing sacs.

During the mating season, phase 1 starts on average at 1552 hours and lasts 6.8 min. During this time, males bend towards the genital region on average 6 times for the oral uptake of urine. After each bending movements males lick the interior of the wing sacs extensively. At the end of phase 1, males rest for a few minutes.

Phase 2 lasts on average 21.5 min and ends at 1623 hours (Voigt, 2002). During phase 2, males bend towards the genital region and press their chin against the penis (Figure 3A). Males persist in this position for a fraction of a second and then bend upwards again to their normal roosting posture. With this movement, males take up a white droplet from the genital region. This droplet is smeared into one of the wing sacs with a sideward movement of the head (Figure 3B). Afterwards, males rest for a few seconds and then transfer a second droplet from the gular gland into the wing sac (Voigt, 2002). Ejaculate was not found in the wing sacs. Therefore, the droplet from the genital region probably originates from a preputial gland or some accessory gland. The behavioural sequence is repeated several times during phase 2 and during subsequent filling movements males switch between the right and left sac. On average, males transfer 11 droplets from the genital region into the wing sacs (Voigt, 2002).

Perfume-blending behaviour has not been observed in any other emballonurid species as yet. However, as (1) histological examinations indicate the absence of glandular tissue in the wing sac also in other species and as (2) odoriferous liquids are present at least in some of these species, it is very likely that other emballonurid bats perform a behaviour similar to that of *Saccopteryx bilineata*.

### 4. THE USE OF WING SACS FOR SCENT DISPLAYS IN THE GREATER SAC-WINGED BAT

The greater sac winged bat (*Saccopteryx bilineata*) has the most complex wing sacs among emballonurid bats (Starck, 1958; Scully et al., 1999) and is the species where we know most about its mating system and olfactory communication (Voigt et al., in press). *Saccopteryx bilineata* has a broad geographical distribution from northern Argentina to southern Mexico. Daytime roosts are located in well-lit portions of tree cavities, in buttress cavities of large rain forest trees and in abandoned buildings. *S. bilineata* roosts on vertical surfaces, supporting its body with the thumbs of the folded forearms. Individuals of a harem maintain minimum distances of 5 to 10 cm to each other. Violations against this spacing rule are punished by attacks with the folded forearm.

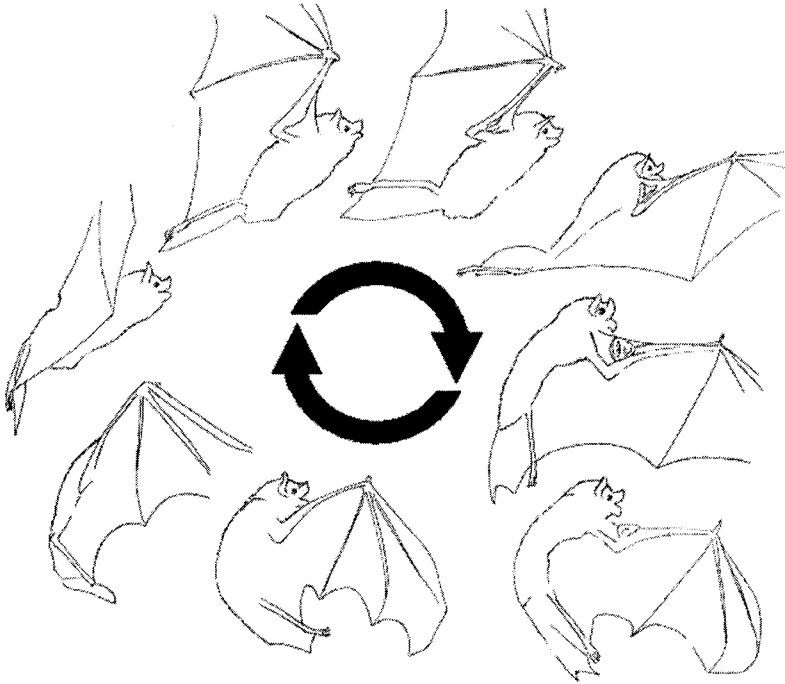


**Figure 3.** Male *Saccopteryx bilineata* transferring a droplet of secretion from the genital region into the right wing sac during phase 2. First, the male presses his chin against the penis (A) and then smears the droplet with a sideward movement of the head into the slightly opened right wing sac (B).

Colonies may count up to 60 individuals and are subdivided into smaller units, each including a single adult male and several females (Bradbury and Emmons, 1974; Bradbury and Vehrencamp, 1976, 1977). For reasons of simplicity, these social subunits are called harems in the remainder of this paper and the male defending the unit the harem holder. In the neighbourhood of harems, non-territorial males queue for the access to territories (Voigt and Streich, 2003).

Recent work of our group has focused on the mating system, especially on questions of reproductive tactics and mate choice (summarized in Voigt et al., in press). We have mainly worked with colonies that roost close to the biological station “La Selva” (Costa Rica, province Heredia) inside abandoned buildings. Using genetic methods, it was shown that harem males are not able to monopolize females within their territory: on average 70% of the offspring are not sired by the harem holder. This high percentage of extra-harem paternities indicates a high potential for free mate selection in the mating system of *S. bilineata*. Despite this high percentage of extra-harem paternities it pays for harem holders to defend a territory because they sire on average more offspring than non-territorial males (Heckel and von Helversen, 2002). In addition, reproductive success of harem males increases with increasing harem size (Heckel and von Helversen, 2003). Our behavioural observations indicate that harem holders use multiple signals for courtship and territory defence.

Whereas physical contests between males are rare, males predominantly use territorial songs and olfactory signals to mark territory boundaries (Voigt et al., in press). Gular gland secretions are used for marking of territory boundaries, especially in the morning or late afternoon. Males transfer the secretions of the sebaceous gular gland to the substrate at harem boundaries by rubbing their chin against the substrate. This is done by quick sideward movements of the head. In addition, wing sacs are also used for transferring scents across territory boundaries. Bradbury and Emmons (1974) called this behaviour salting because it resembles the shaking movement that is performed when people salt a large piece of food. Salting *Saccopteryx* males shake the folded forearm into the direction of the receiver with the wing sacs opened.



**Figure 4.** Wing stroke cycle of a scent-fanning male (each picture separated by 40 ms). During scent-fanning, both wings are pushed forward (instead of downward) and the tail membrane is pushed upwards towards the female (not shown in this picture sequence). Both movements probably direct the air towards the roosting female. During scent-fanning, males are at an almost constant distance to the roosting female (ca. 15 cm). Whereas normal wing beat cycles last only ca. 200 ms, cycles with scent-fanning last ca. 320 ms.

Harem males use courtship songs and scent displays to attract females to their harem (Voigt et al., in press). The wing sacs of male *Saccopteryx* play a key role during aerial courtship displays. Mostly at dawn and dusk harem males hover in front of females when the latter return to their roosting site (Figure 4). These hovering flights can last up to 14 seconds. The normal hovering wing beat cycle is interrupted at approximately every 1.4 s to push the scent of the wing sacs towards the females (Voigt and von Helversen, 1998). During fanning movements, males push the stretched wings towards the recipient female instead of downwards. Thus, hovering males lose buoyancy during each fanning movement. To continue aerial scent-fanning, a male has to regain its original position in front of the female during subsequent wing beat cycles.

## 5. WING SAC MORPHOLOGY AND MATING SYSTEMS

Both the specific morphology of the wing sacs in the antebrachium (Starck, 1958; Scully et al., 1999) and the fragrances differ between species (pers. observation). Most likely the holding sacs are homologous organs with common characters, such as the location in the antebrachium, the cornified epithelium and the lack of secreting cells (Starck, 1958; Scully et al., 1999).

The specific morphology and location of olfactory organs may on the other hand present an adaptation to the particular needs of a species' social system. Males of *Balantiopteryx* and *Saccopteryx* for example have holding sacs with a cavity located either in the centre of the antebrachium or parallel to the forearm. Both taxa are polygynous (Bradbury and Emmons, 1974) and in both taxa males perform aerial displays; hovering flights in *Saccopteryx bilineata* and mating swarms in *Balantiopteryx plicata* during which several males and females fly around landmarks as a group (Bradbury and Vehrencamp, 1976). Possibly, the location of the antebrachial sac in *Saccopteryx* and *Balantiopteryx* facilitates the emission of fragrances during flight.

By contrast, *Peropteryx* and *Cormura* possess holding sacs that are flat and reach the front edge of the antebrachium. Aerial displays have not been observed in these taxa. Male *Peropteryx kappleri* (Bradbury and Vehrencamp, 1976) and *Cormura brevirostris* (Voigt, unpublished observation) guard single females at least occasionally by roosting on top of them. Thus far, behavioural observations indicate that emballonurid species with flat holding sacs roost in smaller groups with a presumably lower potential for polygyny.

## 6. THE EVOLUTION OF PERFUME-BLENDING AND WING SACS IN EMBALLONURID BATS

The wing sacs of emballonurid bats are unique within the order Chiroptera. In bats, scents are most often used for scent-marking of either territories or other individuals. Male bats for example frequently mark their potential mating partners by rubbing secretions of chest or gular glands onto them (*Molossus molossus* – Häussler, 1987). Such a marking behaviour is impossible at least in *Saccopteryx bilineata*, as individuals defend a minimum distance to their neighbour. Males are also smaller than females and therefore harem males cannot enforce the deposition of scent-marks on females. The only alternative for *Saccopteryx* males is to display scents from a distance.

Gular gland secretions, which are part of the sac perfume, are used by male *Saccopteryx* for the scent-marking of their territory. As these secretions are also involved during perfume-blending and hence during courtship display, it is likely that some compounds of the sac perfume indicate harem ownership. Possibly an ancestral form of *Saccopteryx* deposited gular gland secretions on its unstructured antebrachium. The antebrachium is easy to reach with the gular gland and it probably facilitated the emission of scents during normal flight or aerial displays. Sexual selection may have further modified the behaviour of ancestral males and thus also the specific morphology of the antebrachium. Several other advantages may have accelerated the evolution of wing sac morphologies: (1) wing sacs facilitate the transfer of scents during aerial displays while minimizing the weight associated with an actual gland (Scully et al., 1999), (2) closed

wing sacs minimize the evaporation of volatiles, and (3) via ligaments wing sacs enable a neuromuscular-controlled release of scent whose production may be under hormonal control.

Considering the fact that male *S. bilineata* spend up to an hour each day of their adult lives cleaning, moistening and refilling of their wing sacs, it appears that the wing sacs are an important sex-specific organ for communication in *S. bilineata* and possibly also in other Emballonuridae.

## 7. ACKNOWLEDGMENTS

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