
External Morphology of the Tubercles on the Ears of the Brazilian Free-tailed Bat, *Tadarida brasiliensis*

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Abstract: The Brazilian Free-tailed bat, *Tadarida brasiliensis*, has small tubercles along the dorsal leading edge of the ears. Ear tubercles may serve an aerodynamic function similar to the hydrodynamic function of tubercles on the pectoral flippers of humpback whales. Descriptive morphology of 52 adult bats was examined and the average number of tubercles was nine for both ears, ranging from five to twelve on each ear. Distances between tubercles and mean volumes are variable. Possible physiological functions for tubercles include thermoregulation and thermosensory capability, in addition to increased maneuverability during foraging bouts and enhanced control during cave entry and exit.

Introduction

Small tubercles along the outer anterior edges of the Brazilian Free-tailed bat, *Tadarida brasiliensis*, ears have been referenced in the literature (Wilkins 1989; Caire et al. 2024); however, their external morphology has not been described in detail nor have all the possible functions they serve been examined. We describe the external morphology of the ear tubercles, including the number of tubercles, successive distances apart, tubercle volume, and a scanning electron microscopic (SEM) view of the tubercles. Based on the external anatomy and other studies presented in the literature we suggest possible functions of the tubercles.

Methods and Results

Fifty-two (23 males, 29 females) adult *T. brasiliensis* preserved in 70% ethanol and deposited in the University of Central Oklahoma Museum of Natural History were used for the external morphological descriptions. The general location of the tubercles located across the leading edge of the bat ears is shown in Figure 1.

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Figure 1. General location of tubercles along the leading edge of *Tadarida brasiliensis* ear.



Left and right ears of each bat were photographed at 10x magnification with a Moticam 1000 1.3MP Live Resolution Microscope Camera mounted on an Omano Microscope. The number (minimum, maximum, mode, mean) of tubercles on the left and right ears of each specimen were counted through examination of the photographs. For the 52 adult bats examined (sexes combined), the number of tubercles on an ear ranged from 5–12 with a mode of 9 on left ear and 8 on right ear (Table 1). The average was 9 tubercles for both ears.

Table 1. Minimum, maximum, mode, and mean number of tubercles on left and right ears of 52 *Tadarida brasiliensis*.

	Minimum	Maximum	Mode	Mean
Left Ear	5	12	9	9
Right Ear	5	11	8	9

Males had a mode and mean of 9 tubercles ranging from 6–12 on the left ear and a mode of 8 and a mean of 9 tubercles ranging from 7–11 on the right ear (Table 2). Females had a mode and mean of 8 tubercles ranging from 5–11 on the left ear and a mode of 8 and a mean of 9 tubercles ranging from 5–11 on the right ear (Table 2).

Table 2. Mode, mean and range of the number of tubercles counted on male (n=23) and female (n=29) *Tadarida brasiliensis* ears.

Gender		Mode	Mean	Range
Male	Left Ear	9	9	6–12
	Right Ear	8	9	7–11
Female	Left Ear	8	8	5–11
	Right Ear	8	9	5–11

All the ears on the bats examined had the first 5 tubercles on the left and right ears (Table 3). However, the number of ears having each of the successive tubercles along the ear varied. On the left ear of 51 bats, tubercle 6 was present; 48 possessed the 7th; 41 possessed the 8th; 28 possessed the 9th; 12 possessed the 10th; 3 possessed the 11th; and 1 bat had a 12th tubercle. On the right ear of 50 bats, tubercles 6 and 7 were present; 44 possessed the 8th; 26 possessed the 9th; 16 possessed the 10th; 4 possessed the 11th; and none of the bats had a 12th tubercle. The number of male and female bats having each tubercle on the left and right ears are in Table 4.

Table 3. Number of bat (males and females combined n = 52) ears having each tubercle.

Tubercle	1	2	3	4	5	6	7	8	9	10	11	12
Left ear	52	52	52	52	52	51	48	41	28	12	3	1
Right ear	52	52	52	52	52	50	50	44	26	16	4	0

Table 4. Number of male (n = 23) and female (n = 29) bats having each tubercle.

	Tubercle	1	2	3	4	5	6	7	8	9	10	11	12
Males	Left ear	23	23	23	23	23	23	22	18	16	8	2	1
	Right ear	23	23	23	23	23	23	23	20	12	7	2	0
Females	Left ear	29	29	29	29	29	28	26	23	12	4	1	0
	Right ear	29	29	29	29	29	27	27	24	14	9	2	0

The Moticam Camera Motic Images Plus 2.0 MS Software was used to measure the distance between successive tubercles on the left and right ears. Measurements rounded to the nearest one-hundredth micrometer (μm) were made starting from the lateral edge of the most medial tubercle to the medial edge of the next tubercle continuing along the ear distally until all distances between each successive pair of tubercles were recorded. The minimum, maximum, and mean distances between each tubercle on the left and right ears for the sexes combined are listed in Table 5 and for males and females separately in Table 6

Table 5. Number (n), minimum (min), maximum (max), and mean (\bar{x}) distances (μm) between successive tubercles on left and right ears of *Tadarida brasiliensis* (males and females combined).

Tubercles	Left Ear				Right Ear			
	n	min	max	\bar{x}	n	min	max	\bar{x}
1 → 2	52	117.6	1458.2	551.1	52	104.7	1137.1	576.8
2 → 3	52	297.7	1176.6	686.4	52	202.4	1367.3	616.3
3 → 4	52	88.7	1016.8	611.1	52	123.4	1434.4	603.9
4 → 5	52	108.9	1527.3	559.2	52	270.5	1051.1	527.8
5 → 6	51	91.5	995.0	438.0	50	83.2	821.7	441.9
6 → 7	48	96.5	775.2	373.6	50	74.4	776.2	331.8
7 → 8	41	88.7	575.0	292.9	44	80.1	493.6	256.6
8 → 9	28	90.6	432.2	271.7	26	80.1	554.5	187.7
9 → 10	12	74.4	422.5	204.6	16	115.8	307.0	190.9
10 → 11	3	137.9	231.2	170.4	4	123.4	213.0	176.7
11 → 12	1	403.9			0			

Table 6. Distances (μm) between successive left and right ear tubercles of male and female *Tadarida brasiliensis*. The mean distance between successive tubercles, (number) of distances measured, and [range] is presented for male and female left and right ears.

Tubercles	Male		Female	
	Left	Right	Left	Right
1-2	541 (23) [131-1350]	516 (23) [178-1140]	605 (29) [118-1460]	579 (29) [105-1090]
2-3	620 (23) [299-1120]	554 (23) [202-879]	739 (29) [298-1180]	665 (29) [364-1370]
3-4	629 (23) [88.7-1020]	627 (23) [332-997]	597 (29) [213-886]	586 (29) [123-1430]
4-5	513 (23) [161-869]	538 (23) [276-765]	596 (29) [109-1530]	520 (29) [271-1050]
5-6	418 (23) [91.5-995]	420 (23) [83.2-690]	455 (28) [178-840]	461 (27) [122-822]
6-7	352 (22) [108-748]	329 (23) [112-563]	392 (26) [96.5-775]	334 (27) [74.4-776]
7-8	316 (18) [91.5-575]	212 (20) [87.9-451]	275 (23) [88.7-496]	293 (24) [80.1-494]
8-9	264 (16) [112-432]	206 (12) [136-555]	282 (12) [90.6-432]	172 (14) [80.1-494]
9-10	193 (8) [74.4-423]	193 (7) [137-307]	227 (4) [120-305]	189 (9) [116-265]
10-11	187 (2) [142-231]	185 (2) [165-205]	138 (1)	168 (2) [123-213]
11-12	404 (1)			

Using the Motic Images Plus 2.0 MS Software, the height (μm^3) and radius (μm^3) taken at the base of each tubercle on the left and right ears were used to estimate tubercle volume ($1/3\pi r^2h$) Table 7 contains the mean (\bar{x}) of the estimated volumes (μm^3) of individual tubercles 1-12 on right and left ears (males and females combined). Males and females are separated in Table 8. Tubercles with the largest volumes were located at the medial edge of the ear closest to the head and the volumes of the subsequent tubercles decreased toward the distal edge of the ear.

Table 7. The number (n) of tubercles examined and the estimated mean volumes (\bar{x} in μm^3) of individual tubercles on left and right ears of *Tadarida brasiliensis* (males and females combined).

Tubercle	Left Ear		Right Ear	
	n	\bar{x}	n	\bar{x}
1	52	1.56E+07	51	1.80E+07
2	52	9.80E+06	51	1.10E+07
3	52	7.80E+06	51	8.20E+06
4	52	7.40E+06	51	6.60E+06
5	52	7.50E+06	51	7.10E+06
6	51	5.80E+06	49	7.80E+06
7	48	5.50E+06	49	7.30E+06
8	41	6.40E+06	42	6.10E+06
9	28	5.40E+06	26	6.20E+06
10	13	4.20E+06	16	8.10E+06
11	4	4.80E+06	4	9.30E+06
12	1	7.00E+06	0	

Table 8. The number (n) of tubercles examined and the estimated mean volume (\bar{x} in μm^3) of tubercles of male and female *Tadarida brasiliensis*.

Tubercle	Estimated mean volume				Estimated mean volume			
	Left Ear		Right Ear		Left Ear		Right Ear	
	n	\bar{x}	n	\bar{x}	n	\bar{x}	n	\bar{x}
1	23	1.21×10^7	23	1.18×10^7	29	1.72×10^7	29	2.24×10^7
2	23	8.29×10^6	23	7.01×10^6	29	1.10×10^7	29	1.42×10^7
3	23	7.25×10^6	23	6.27×10^6	29	8.20×10^6	29	9.69×10^6
4	23	5.86×10^6	23	5.54×10^6	29	8.66×10^6	29	7.28×10^6
5	23	6.48×10^6	23	5.79×10^6	29	8.37×10^6	29	8.06×10^6
6	23	5.66×10^6	23	5.36×10^6	28	5.98×10^6	27	9.78×10^6
7	22	5.88×10^6	23	5.77×10^6	26	5.21×10^6	27	8.42×10^6
8	19	6.57×10^6	20	6.02×10^6	22	6.11×10^6	24	6.34×10^6
9	18	5.49×10^6	13	5.13×10^6	12	5.26×10^6	14	6.88×10^6
10	8	4.32×10^6	8	6.27×10^6	4	4.25×10^6	9	9.14×10^6
11	3	4.91×10^6	3	1.02×10^7	1	4.32×10^6	2	6.02×10^6
12	1	7.00×10^6	0		0		0	0

A Zeiss DSM 960 scanning electron microscope (SEM) was used to provide a three-dimensional high-resolution visualization of the tubercles across the bat ear and the surface of a single tubercle. Figure 2 is a composite SEM photograph of the leading edge of the left bat ear showing the relative position and shape of the ear tubercles. The topography of a single tubercle is shown in SEM photographs in Fig. 3a, and the microtubercles on the tubercle and their arrangement are shown in Fig. 3b.

Figure 2. Scanning electron microscope composite photograph of a *Tadarida brasiliensis* right ear tubercles 1-9.

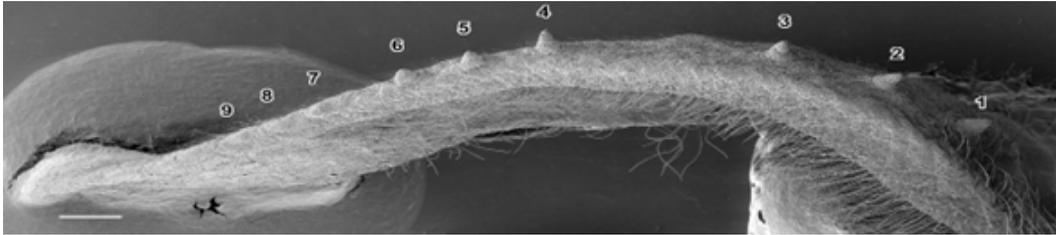
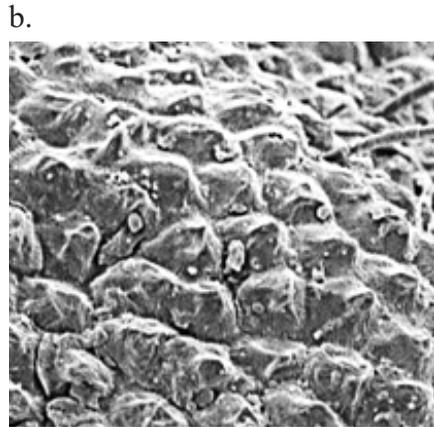
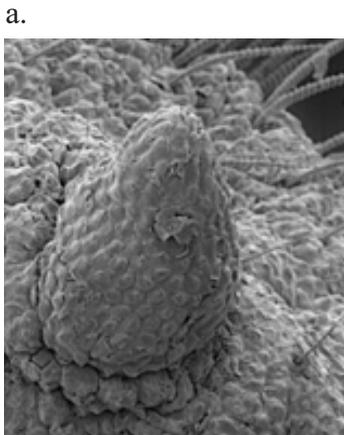


Figure 3. Scanning electron microscope of (a) a single tubercle and (b) the surface of a tubercle showing arrangement of micro-tubercles across the tubercle surface.



Discussion

Fish and Battle (1995), Fish (2002), Fish et al. (2011) and Miklosovic et al. (2004) describe the leading-edge tubercles on humpback whale (*Megaptera novaeanglia*) flippers. The tubercles help delay the stall angle, decrease drag, and maintain lift of the flippers at high angles of attack, allowing for greater maneuverability. Thus, the humpback whale can make more extreme banking and turning maneuvers during its feeding bouts in comparison to other whale species (Jurasz and Jurasz 1979; Hain et al. 1982). Based

on the observed similarity between humpback whale flippers and the Brazilian Free-tailed bat tubercles, we propose that bat ear tubercles may serve an aerodynamic function similar to the hydrodynamic function of tubercles on the pectoral flippers of humpback whales.

The function of the leading-edge tubercles on *Tadarida* ears during exit flights from roosts, while foraging, and during steep returning dives to roosts might increase our understanding of *Tadarida* flight and morphological features. Petrin et al. (2018) used flow visualization studies of the wake behind a model *Tadarida brasiliensis* ear with and without tubercles to demon-

strate that tubercles influence lift and drag during flight and suggested they serve a similar function as tubercles on the leading edge of the pectoral flippers (Fig. 4a.) of the humpback whale. The tubercles seemingly allow bats to delay or stall more gradually at higher angles of attack (Petrin et al. 2018), as is the case with whales (Miklosovic et al. 2004; van Nierop et al. 2008).

Figure 4. Leading edge tubercles (a) on the pectoral flipper of the humpback whale *Megaptera novaeangliae* (Humpback *Stellwagen* by Whit Welles, under a CC-BY 3.0) and (b) the ear of the Brazilian Free-tailed Bat, *Tadarida brasiliensis*.

a.



b.



The fastest flight speed recorded for an animal in horizontal flight (up to 160 km/hr) was documented in *Tadarida brasiliensis* in 2016 (McCracken et al. 2016). The long, narrow wings of *Tadarida* are aerodynamically designed for high wing loading and high aspect ratios, but do not provide enough lift at slower speeds for the bat to take off directly from a surface and fly to foraging areas, sometimes as far as 50 km away (Best and Geluso 2003). To begin flight, they usually drop from a high roosting site and freefall

for several meters to build up speed before the wings generate enough lift to pull out of the drop. During these initial slower speeds, the ear tubercles probably help generate lift until the bat gains the speed necessary to produce sufficient lift via the wings. Ground and radar tracking have documented *T. brasiliensis* at altitudes up to 3,000 m and covering 100 km in one night (Williams et al. 1973). Long, narrow wings are obviously important for rapid long-distance travel, but the presence of ear tubercles may also contribute to their high flying, rapid flight adaptation. Martin (2017) reported that *T. brasiliensis* tubercles serve to reduce drag at low angles of attack and increase drag at high angles of attack. Also, airfoil models revealed bat ear tubercles delayed stall, making the ears the likely flow control structure during free fall (Petrin et al. 2018).

Another flight behavior that probably involves the ear tubercles are the tight counterclockwise circling turns (slower in speed in comparison to normal high-altitude flight) inside the cave opening prior to exiting. Although the reason for counterclockwise flight inside caves is not well understood, the loops have a sharp turn radius somewhat analogous to the tight feeding turns and loops made by humpback whales during bubble net feeding (Fish and Battle 1995, Fish 2002, Fish et al. 2011, Miklosovic et al. 2004). After the circling turns, the bats emerge from the roost and usually climb to higher altitudes around 3,000 m (Williams et al. 1973; McCracken et al. 2021).

The ear tubercles likely aid bats aerodynamically during foraging flights for diverse prey including fast-flying moths, beetles, and slower-moving swarms (Easterla and Whitaker 1972; Whitaker 1996; McWilliams 2005). Considerable flight maneuverability which involves changes in lift and drag is required to capture the prey.

In many situations *Tadarida* return from foraging at high altitudes (Williams et al. 1973; Horn and Kunz 2008) and perform steep re-entry flights at close proximity to conspecifics (Wilkins 1989). They often drop perpendicular to the ground from altitude (Pudlo and Kloepper 2019) at speeds in excess of 128–158 km/h (Davis et al. 1962; Pudlo and Kloepper 2019) and make sharp

turns to enter the roost (Klopper and Kinniry 2018; Williams *et al.* 1973). The leading-edge tubercles are probably associated with positional control and orientation during these returns to the cave. This pattern of free-falling return flights has been described in bats at Carlsbad Caverns, New Mexico (Hill and Smith 1984). The bats approach the cave at an altitude of 300–400 m, fold their wings and plummet to about 2 m off the ground before reopening their wings and entering the cave (Hill and Smith 1984). The bats would need aerodynamic control of flight as they near the roost opening and coordinate a sharp turn to enter the roost while avoiding collision with conspecifics (Theriault *et al.* 2010; Klopper and Kinniry 2018; Wilkins 1989). Hubel *et al.* (2012) examined changes in kinematics and aerodynamics of *Tadarida* over a range of speeds, but future studies focused on the ear tubercles might help understand this complex flight behavior during re-entry or when flying close to conspecifics. Bats can adjust echolocation calls during these high-speed roost reentries (Pudlo and Klopper 2019).

These various flight maneuvers employed by *Tadarida* are energetically costly. *Tadarida* encounters a variety of thermal environments while transitioning from roost sites to high altitudes and during returns. To help maintain a stable body temperature, the bats regulate some of the heat generated during flight via thermal windows (Reichard *et al.* 2010; Reichard and Fellows 2010; Reichard *et al.* 2012). The ear tubercles increase the surface area of the bat and might also aid in thermoregulation. A histological examination of blood circulating to and from the tubercles might reveal possible heat retention and dissipation functions.

The microanatomy of microtubercles and the apparent hexagonal arrangement on the surface of the tubercles, visible in the electron microscopic images (Fig. 3), has not been investigated nor has the possible functional significance. In some vertebrates, skin cells appear to have a packing geometry that has been described as a flattened version of a 14-sided shape called a tetrakaidecahedron (Yokouchi *et al.* 2016) which allows cells to tightly interlock, providing a strong cohesive barrier. Thus, the apparent geo-

metrical arrangement of the microtubercles (Fig. 3) on the *Tadarida* tubercles might provide dense cell packing with minimal space between them which could provide structural stability, prevent water loss, and protect the bat from germicidal substances.

The microtubercles on the bat ears also have small hairs interspersed among them (Fig. 3) which might serve as sensory hairs. Similar structures referred to as Merkel cell-containing domes and hairs have been described on bat wings which allow bats to sense and detect airflow across the wing surface (Jones 2011; Marshall *et al.* 2015). These would aid in better maneuverability during flight, in capturing flying prey, and in navigating complex environments. A histological examination of the ear tubercles might help in understanding the function of the hairs and possible other functions.

A survey of natural history museum specimens and examination of closeup images of bats in the Family Molossidae revealed ear tubercles are present on some but not all species of molossid bats. Wilson and Mittermeier (2019) recognized 22 genera comprised of 126 species in Family Molossidae and of these, more than one species in each of the following genera had ear tubercles present: *Chaerephon*, *Eumops*, *Mops*, *Nyctinomops*, *Otomops*, and *Tadarida*. Ear tubercle functions may be similar among the species having them and comparisons of roosting, foraging, and flight behaviors of the species with and without the tubercles could be insightful.

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