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Is bat hair morphology exceptional?

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Abstract. Surface hair scale patterns from 19 bat species (families Vespertilionidae and Molossidae) from Utah were studied using scanning electron microscopy (SEM). Hair width, scale length, pattern, and position in relation to the long axis were used to characterize morphology within species, and families within the order Chiroptera. Previous studies indicate variations within families. Hair morphology results make it evident that large variations and similarities within the families can be seen visually and codified for the order. In the family Vespertilionidae, variations in hair morphology necessitated better terminology, including two new terms for morphology patterns. In the family Molossidae, distinctions between species, and possibly within the family, may be evident using SEM imaging to characterize morphology characteristics, although only two species were studied in this family. More precise morphological measurements than used for this study may be necessary to construct useful keys for species within at least some families of bat.

Bat hair, Chiroptera, hair characteristics, identification chart, SEM, Utah

Introduction

Bats are one of the most unusual mammals. Features that make them unusual include the ability to fly up to 50 km/h (30 mph) through complete darkness. They are the only mammal capable of powered flight. Bats are heterothermic with body temperatures that may vary from up to 41 °C (106 °F) in flight to under 2 °C (36°F) during hibernation. Bats are able to inhabit all but the highest mountains and isolated oceanic islands. The order Chiroptera has 18 families, close to 200 genera and more than 1300 species among approximately 5,400 species of mammals (Wilson & Reeder 2005, Macdonald 2006, Gunnell & Simmons 2012). Bats, therefore, comprise approximately one-fourth of all species of mammals.

Pteropodiformes is a suborder of Chiroptera, and comprises six families (Gunnell & Simmons 2012). One of these six families, Pteropodidae, includes flying foxes (also known as megabats). Given their size, these flying foxes may be more closely related to primates than to the other sub-order, Vespertilioniformes, which includes many of the microbat families (Hutcheon 2006, Gunnell & Simmons 2012). Members of Vespertilioniformes range in size from the world's smallest mammal, the hognosed bat (1.08 g, 0.07 oz) to the hairless bats of Indo-Malaysia, which weigh 175 g (6 oz) (Macdonald 2006). Additionally, this suborder comprises 14 families and is ecologically diverse, particularly in the tropics (Gunnell & Simmons 2012).

Millions of years of adaptation have resulted in significant variation in hair morphology and genetics. The Vespertilionid bat family (Vespertilionidae) is one of the largest families, and includes 488 species, second only to Muridae (Old World rats and mice) (Macdonald 2006, Gunnell & Simmons 2012). The Free-Tailed bats (family Molossidae) comprise 112 species and are robust bats with a large proportion of the thick tail projecting beyond the tail membrane (Macdonald 2006, Gunnell & Simmons 2012). Diversity may also be reflected in morphological differences in hair from species to species and within species. Teerink (1991) reviewed studies of mammalian hair with a variety of light microscopy procedures that spanned the last 180 years. Electron microscopy, and image analysis procedures have also been used to study mammalian hair (Short 1978, Muto et al. 1981, Riggott & Wyatt 1981, Weedon & Strutton 1981, Hino et al. 1982, Maxwell et al. 1982, Raphael et al. 1982, Hess & Allen 1985, Hess et al. 1990, Meyer et al. 1997a, Swift & Smith 2001, Ball et al. 2002, Černova 2002, Smith & Swift 2002, Poletti et al. 2003). A variety of procedures have also been used, more specifically, to study bat hair (Nason 1948, Benedict 1957, Gaisler et al. 1967a, b, 1968a, b, Gaisler 1971, Amman et al. 2002, Pierallini 2004).

Differences in scale patterns and structure of mammalian hair vary significantly from species to species (Teerink 1991, Jones et al. 1994, Quadros & Monteiro 2006), and provide an indication of species identity that is very useful for taxonomic and forensic applications (Barsegiants & Kozlov 1994, Meyer et al. 1997b, Van den Broeck et al. 2001, Tobin 2005). Nason (1948) concluded that bat hair morphology differs significantly within a species and significant variation was also observed within the *Antrozous pallidus* species (unpubl. data).

The higher-level of classification of Chiroptera is unresolved due to conflicting results of phylogenetic studies that strongly suggest many traditionally recognized groups are not monophyletic (Wilson & Reeder 2005). Nevertheless, the large number of species in the two clades reveal significant morphological and genetic diversity of Chiroptera. Scanning electron microscopy (SEM) images of bat hair provides another taxonomic tool. Additionally, although numerous studies have been conducted to characterize bat hair morphology, few have solely focused on scanning electron microscopy (SEM).

Since SEM makes it possible to visualize morphological differences in hair, the diversity in hair scale patterns can be quantitatively evaluated. The purpose of these studies was to use SEM images of hair of selected species of Utah bats from the families Vespertilionidas and Molossidae to study variation in scale patterns and to determine whether SEM images can be used to differentiate species.

Materials and Methods

Bat hair samples were secured from nineteen specimens curated in the Monte L. Bean Life Sciences Museum, at Brigham Young University. To achieve uniform results samples were cut at, or near, the shoulder (Hess et al. 1985). Previous studies showed that hair morphology from tanned and untanned specimens are identical (Hess et al. 1985, unpubl. data).

Following previously described procedures (Hess & Allen 1985, Hess et al. 1985), hair samples were submerged in distilled water with a drop of Teepol detergent. The samples were then sonicated for three minutes to remove dirt and debris. Samples were then rinsed in distilled water and air dried.

Specimens were positioned on aluminum stubs mounted with carbon film. Notches were filed into stubs to assist with specimen orientation on stubs. However, specimens were so small that orientation and separation of bat hair was, so we mounted hair without respect to orientation. We sputter-coated samples with gold and recorded images with an FEI XL 30 ESEM FEG (FEI Company, Hillsboro, Ore., USA) as described by Castillo et al. (2005). We measured hair width and scale height using Image J software (available online: http://rsb.info.nih.gov/ij/).

We classified hair morphology according to (or 'consistent with') patterns given by Nason (1948), Benedict (1957) and Teerink (1991). Nason (1948) explained that unlike other mammals, bats do not have typical guard hair and underfur.

Table 1. Hair morphometrics (based on 30 measurements) in 19 species of American bats. HW – hair width [μm], SH – scale height [μm]

species	scale position	scale pattern	HW min	HW max	SH
Vespertilionidae					
Myotis californicus	coronal	class 1, equal hastate, simple	4.4	10.0	14.11
Parastrellus hesperus	coronal	class 2, equal hastate, unequal hastate	7.6	9.5	12.10
Perimyotis subflavus	coronal	class 1, unequal hastate	6.9	8.8	11.76
Myotis yumanensis	coronal	class 2, simple, unequal hastate	6.3	9.2	13.43
Euderma maculatum	coronal	class 1, equal hastate, unequal hastate, simple	8.4	10.4	12.06
Lasionycteris noctivagans	coronal	class 2, unequal hastate, simple	6.7	8.6	12.29
Myotis ciliolabrum	coronal	class 1, class 2, equal hastate, simple	5.0	8.9	14.87
Myotis thysanodes	coronal	class 1, class 2, equal hastate, unequal hastate, simple	7.1	9.2	12.40
Lasiurus cinereus	coronal	class 2, unequal hastate, simple	5.7	8.4	10.78
Myotis volans	coronal	class 2, simple, lobate	7.1	10.0	18.38
Antrozous pallidus	coronal	class 1, class 2, unequal hastate, simple	6.3	10.7	16.25
Myotis lucifugus	coronal	class 1, unequal hastate, repand, emarginate	6.1	7.7	10.53
Idionycteris phyllotis	coronal	class 1, unequal hastate, simple	6.3	8.9	11.27
Corynorhinus townsendii	coronal	class 1, unequal hastate, simple, repand	7.9	9.3	8.38
Myotis evotis	coronal	class 1, class 2, simple	6.1	9.2	13.09
Lasiurus blossevillii	coronal	class 2, simple, elongate	7.1	8.4	15.16
Eptesicus fuscus	coronal	class 2, equal hastate, emarginate	6.0	8.8	11.33
Molossidae					
Tadarida brasiliensis	coronal	dentate	6.1	14	14.33
Nyctinomops macrotis	coronal	dentate, denticulate	8.5	15	10.16

As such, distinction between guard hair and underfur is not included in the analysis. Descriptive scale patterns follow Benedict (1957) who created the most comprehensive coronal classification method. Due to greater accuracy and detail of SEM, we added two additional descriptive scale patterns to Benedict's classification: class 1 and class 2. Class 1 is similar to Benedict's coronal entire pattern except it exhibits a Barber-pole-like twist. Class 2 exhibits an interlocking coronal 'bone' pattern similar to Benedict's coronal simple pattern except it is stretched out more fully. For each of the orders and species listed, SEM was used to visualize morphological characteristics of scale patterns. Additionally, comparative descriptions (based on analysis of ≥ 30 hairs) as well as the mean of hair width (maximum and minimum) and scale height were included.

Results

Comparative descriptions and quantitative hair information are summarized in Table 1. Statistical box plot values based on analysis of SEM images of 30 hairs, are included in Tables 2–4. Box plots of the underfur minimum and maximum widths, and scale height are included in Figs. 1–3. Hair images (Figs. 4–22) captured by SEM demonstrate variations in bat hair morphology for species we analyzed.

Discussion

Bat hair of species we studied cannot be sub-classified into distinct guard hair and underfur (Nason 1948, Benedict 1957, Pierallini 2004). The species in the family Vespertilionidae were much more

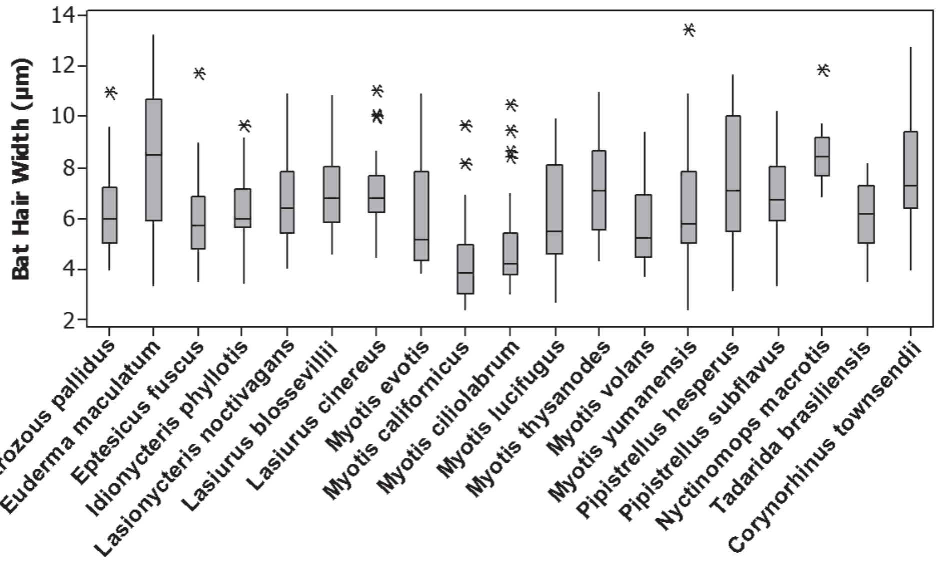

Fig. 1. Box plot of hair minimum widths (in µm) in 19 species of American bats.

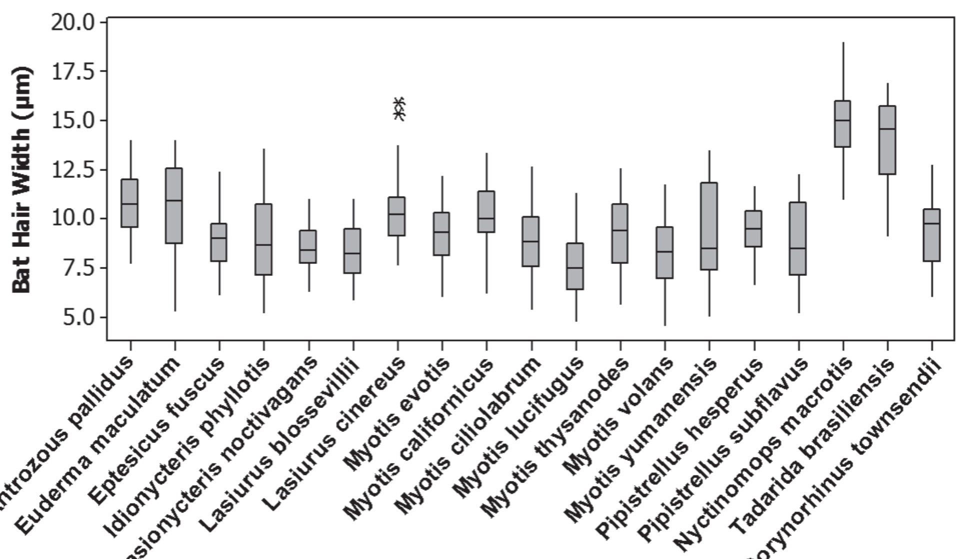

Fig. 2. Box plot of hair maximum widths (in µm) in 19 species of American bats.

Table 2. Statistical data of minimum width (in μm) in 19 species American bats; Q1 – the lower quartile or the first range quartile, Q3 – the third quartile range (upper quartile)

species	Q1	median	Q3	SD
Vespertilionidae				
Myotis californicus	3.06	3.85	4.97	1.70
Parastrellus hesperus	5.51	7.07	10.05	2.57
Perimyotis subflavus	5.94	6.74	8.04	1.67
Myotis yumanensis	5.02	5.80	7.81	2.30
Euderma maculatum	5.93	8.55	10.72	2.66
Lasionycteris noctivagans	5.46	6.42	7.81	1.61
Myotis ciliolabrum	3.81	4.20	5.46	1.95
Myotis thysanodes	5.56	7.07	8.65	1.94
Lasiurus cinereus	4.49	5.26	6.92	1.53
Myotis volans	6.27	6.83	7.70	1.52
Antrozous pallidus	5.01	5.96	7.22	1.65
Myotis lucifugus	4.64	5.48	8.10	2.07
Idionycteris phyllotis	5.61	5.96	7.16	1.38
Corynorhinus townsendii	6.41	7.32	9.43	2.17
Myotis evotis	4.33	5.18	7.81	2.09
Lasiurus blossevillii	5.85	6.83	8.01	1.57
Eptesicus fuscus	4.83	5.68	6.90	1.88
Molossidae				
Tadarida brasiliensis	5.05	6.22	7.28	1.40
Nyctinomops macrotis	7.71	8.42	9.20	1.06

variable in hair morphology, both within species and among species, than the species in the family Molossidae. The variation in hair morphology between and among species in Vespertilionidae is also much greater than the variation in the morphology of underfur and guard hair of species of other mammals studied (unpublished data). For example, the hair for *Myotis thysanodes* (Fig. 11) contained five hair patterns for six separate hairs, each within a similar size diameter. Significant variation in hair morphology from *Myotis ciliolabrum* (Fig. 10) was also observed. Similar variation is also present for all the other species studied, especially for the Family Vespertilionidae, including *Myotis thysanodes* (Fig. 11), *Lasiurus cinereus* (Fig. 13), *Idionycteris phyllotis* (Fig. 16) and *Corynorhinus townsendii* (Fig. 17). In addition, Table 1 shows that hair from the family Molossidae is consistently larger than hair from the family Vespertilionidae.

Although only two of 77 species in 12 genera (Macdonald 2006) were studied from the family Molossidae, the distinctness of the morphology of the hair in these two species makes it evident that these two species can easily be distinguished from each other and from all of the species studied in the Vespertilionidae. In the family Molossidae, hair scale patterns of the two species studied were different due to the denticulate pattern (smaller teeth) found on *Nyctinomops macrotis*. However, additional study of all species of this family is necessary before conclusions can be made regarding the diagnostic value of scale morphology. Although SEM images of cross sections of bat hair were not investigated as part of the present study, earlier studies (Hess et al. 1985, Hess et al. 1990) make it evident that for some species hair cross section data can be an additional characteristic for classification.

Table 3. Statistical data of maximum width (in µm)) in 19 species of American bats; Q1 – the lower quartile or the first range quartile, Q3 – the third quartile range (upper quartile)

species	Q1	median	Q3	SD
Vespertilionidae				
Myotis californicus	9.32	10.06	11.40	1.46
Parastrellus hesperus	8.59	9.48	10.42	1.28
Perimyotis subflavus	7.11	8.51	10.83	2.07
Myotis yumanensis	7.43	8.48	11.81	2.50
Euderma maculatum	8.76	10.94	12.59	2.18
Lasionycteris noctivagans	7.71	8.35	9.41	1.21
Myotis ciliolabrum	7.59	8.82	10.10	1.77
Myotis thysanodes	7.71	9.38	10.72	1.92
Lasiurus cinereus	6.89	8.32	9.55	1.81
Myotis volans	9.07	10.16	11.08	1.97
Antrozous pallidus	9.59	10.77	12.01	1.55
Myotis lucifugus	6.35	7.48	8.77	1.67
Idionycteris phyllotis	7.07	8.68	10.72	2.11
Corynorhinus townsendii	7.78	9.75	10.45	1.89
Myotis evotis	8.12	9.27	10.28	1.47
Lasiurus blossevillii	7.23	8.18	9.50	1.40
Eptesicus fuscus	7.85	9.01	9.72	1.52
Molossidae				
Tadarida brasiliensis	12.28	14.53	15.76	2.02
Nyctinomops macrotis	13.66	15.01	15.98	1.76

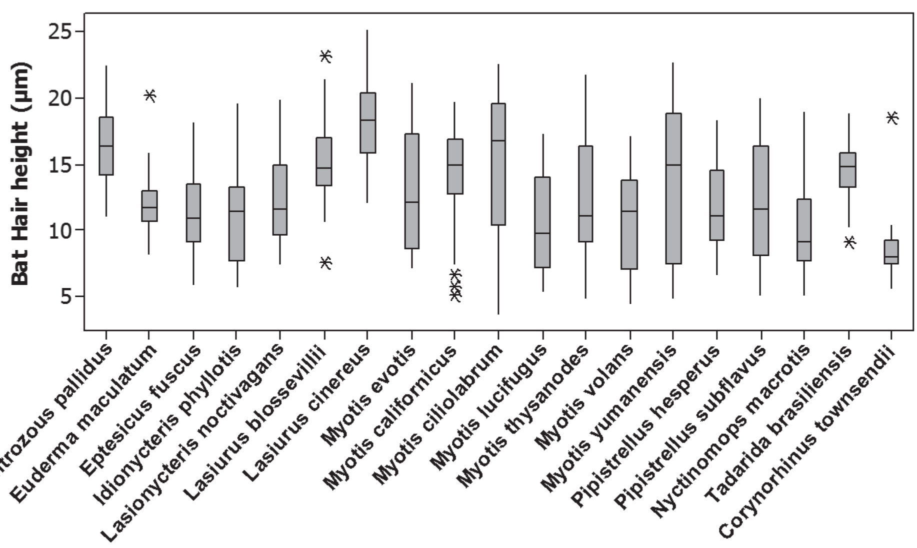

Fig. 3. Box plot of hair scale height (in µm) in 19 species of American bats.

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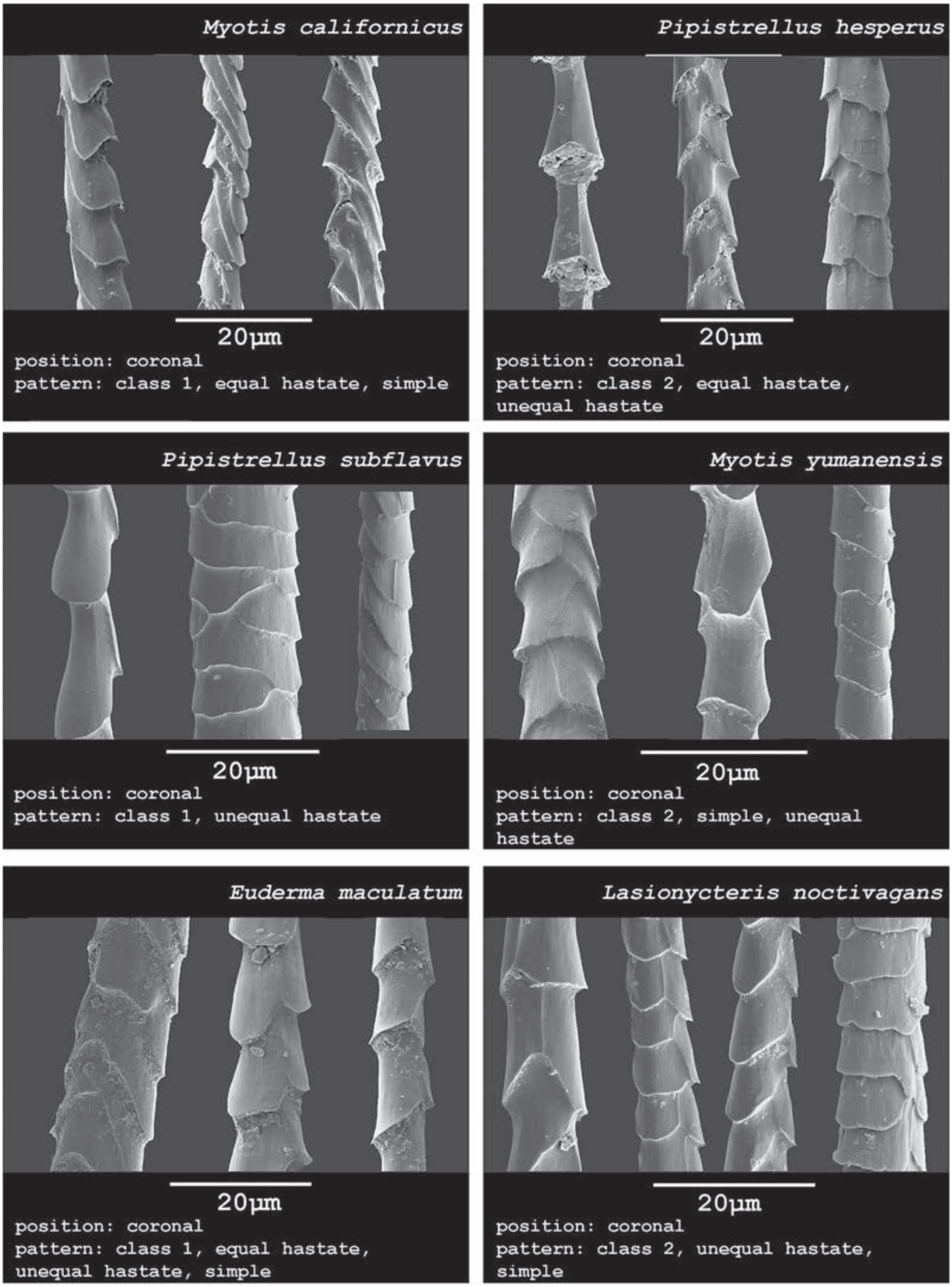
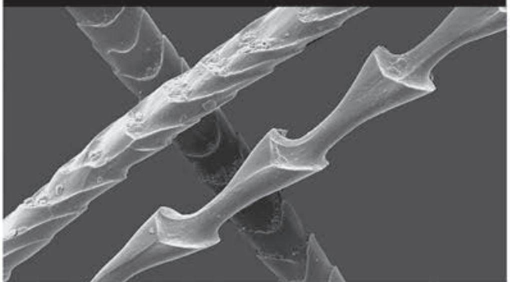
Figs. 4–9. Hair cuticle scales in American bats. 4 – *Myotis californicus*. 5 – *Parastrellus hesperus*. 6 – *Perimyotis subflavus*. 7 – *Myotis yumanensis*. 8 – *Euderma maculatum*. 9 – *Lasionycteris noctivagans*.

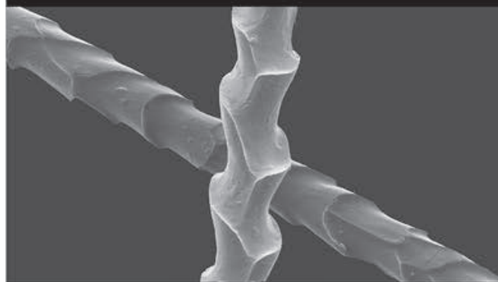

Myotis californicus
20µm
position: coronal
pattern: class 1, equal hastate, simple
Pipistrellus hesperus
20µm
position: coronal
pattern: class 2, equal hastate, unequal hastate
Pipistrellus subflavus
20µm
position: coronal
pattern: class 1, unequal hastate
Myotis yumanensis
20µm
position: coronal
pattern: class 2, simple, unequal hastate
Euderma maculatum
20µm
position: coronal
pattern: class 1, equal hastate, unequal hastate, simple
Lasionycteris noctivagans
20µm
position: coronal
pattern: class 2, unequal hastate, simple

Myotis ciliolabrum



20µm
position: coronal
pattern: class 1, class 2, equal hastate, simple

Myotis thysanodes

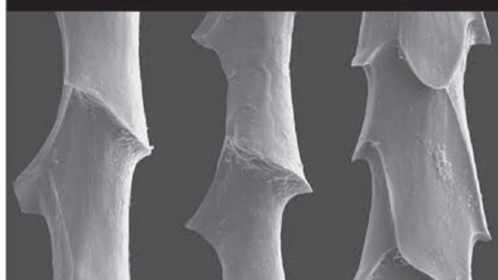


20µm
position: coronal
pattern: class 1, class 2, equal hastate, unequal hastate, simple

Myotis volans

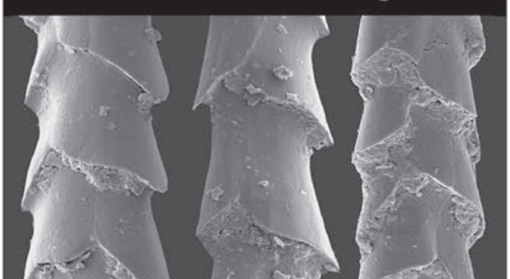
20µm
position: coronal
pattern: class 2, simple, lobate

Lasiurus cinereus



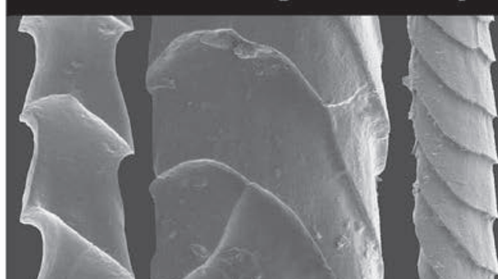
20µm
position: coronal
pattern: class 2, unequal hastate, simple

Antrozous pallidus



20µm
position: coronal
pattern: class 1, class 2, unequal hastate, simple

Myotis lucifugus



20µm
position: coronal
pattern: class 1, unequal hastate, repand, emarginate

Table 4. Statistical data of scale height (in µm) in 19 species of American bats; Q1 – the lower quartile or the first range quartile, Q3 – the third quartile range (upper quartile)

species	Q1	median	Q3	SD
Vespertilionidae				
Myotis californicus	12.78	14.99	17.53	3.95
Parastrellus hesperus	9.21	11.86	15.41	3.41
Perimyotis subflavus	8.06	11.55	16.36	4.17
Myotis yumanensis	7.50	16.06	19.62	6.02
Euderma maculatum	10.62	11.92	13.37	2.38
Lasionycteris noctivagans	9.70	11.53	15.06	3.04
Myotis ciliolabrum	10.42	16.73	19.68	5.75
Myotis thysanodes	9.15	11.55	16.69	4.26
Lasiurus cinereus	7.00	11.43	13.97	3.86
Myotis volans	15.88	18.32	21.11	3.45
Antrozous pallidus	14.17	16.34	18.55	2.99
Myotis lucifugus	7.23	11.23	14.19	3.79
Idionycteris phyllotis	7.73	11.48	13.28	3.68
Corynorhinus townsendii	7.49	8.00	9.42	2.31
Myotis evotis	8.77	12.95	17.46	4.40
Lasiurus blossevillii	13.44	14.63	17.36	3.37
Eptesicus fuscus	9.06	10.99	13.50	2.97
Molossidae				
Tadarida brasiliensis	13.25	14.80	16.10	2.30
Nyctinomops macrotis	7.72	9.07	12.80	3.35

Meyer (1995) hypothesized that variation in bat hair morphology may create a layer of turbulence around the animal, facilitating flight. This may explain the large amount of variation present in the family Vespertilionidae.

Bat hair morphology is difficult to measure and quantify and hair morphology for some species differs significantly throughout the length of the hair (Nason 1948, Teerink 1991). In this study we made an effort to define the morphological variation at the center of hairs to avoid axial confounding. Variation in scale height was also evident.

Based upon these limited studies it may be difficult to construct a useful key based solely on morphological hair data for Chiroptera, or even for families within the order. Some species characteristics may be distinct, such as in the Molossidae family reported in this study, but the variation reported between and within species of the family Vespertilionidae suggests that more precise morphological measurements than those used by Nason (1948), Benedict (1957), Terrink (1991), and our studies, may be necessary to accurately characterize the hair morphology between and within species. However, in the family Molossidae there are indications that between species distinctions, and possibly within family distinctions, may be possible using morphological characteristics evidenced by SEM, although, a more extensive morphological SEM study of this family is needed.

Since no specimens from the Megachiropterans were studied, and since the Megachiropterans may be more closely related to primates than to the Microchiropters (Macdonald 2006), it would

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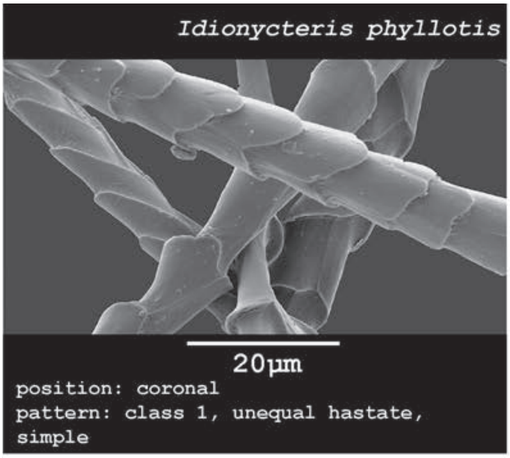
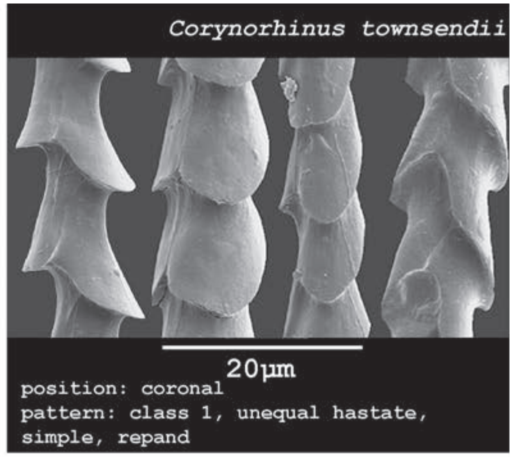
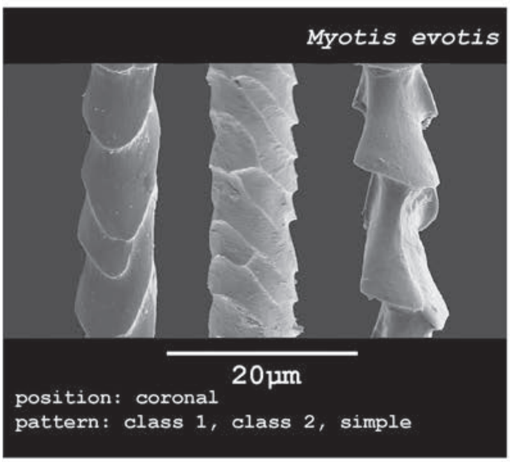
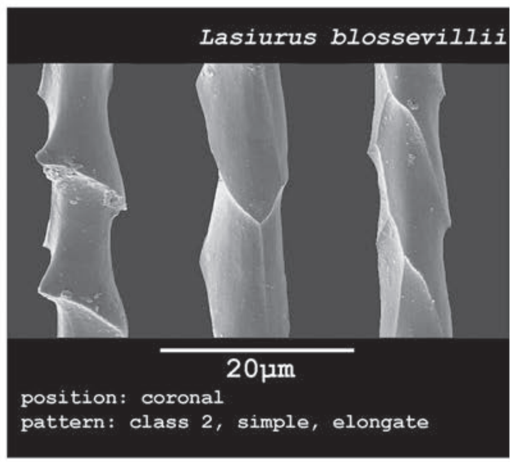
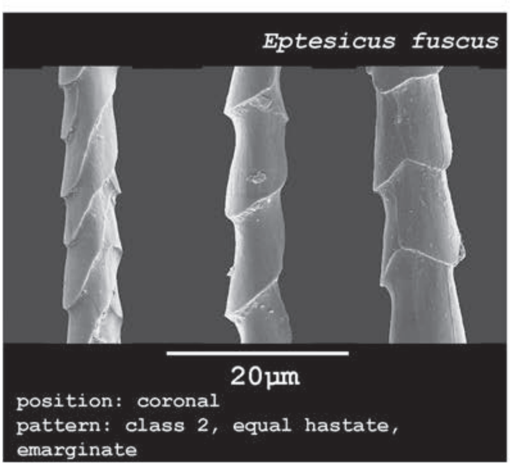
Figs. 10–15. Hair cuticle scales in American bats. 10 – *Myotis ciliolabrum*. 11 – *Myotis thysanodes*. 12 – *Myotis volans*. 13 – *Lasiurus cinereus*. 14 – *Antrozous pallidus*. 15 – *Myotis lucifugus*.

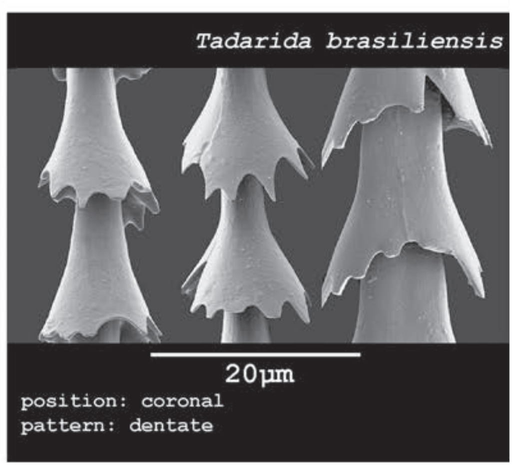

Idionycteris phyllotis
20µm
position: coronal
pattern: class 1, unequal hastate, simple


Corynorhinus townsendii
20µm
position: coronal
pattern: class 1, unequal hastate, simple, repand


Myotis evotis
20µm
position: coronal
pattern: class 1, class 2, simple


Lasiurus blossevillii
20µm
position: coronal
pattern: class 2, simple, elongate


Eptesicus fuscus
20µm
position: coronal
pattern: class 2, equal hastate, emarginate


Tadarida brasiliensis
20µm
position: coronal
pattern: dentate

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Figs. 16–21. Hair cuticle scales in American bats. 16 – *Idionycteris phyllotis*. 17 – *Corynorhinus townsendii*. 18 – *Myotis evotis*. 19 – *Lasiurus blossevillii*. 20 – *Eptesicus fuscus*. 21 – *Tadarida brasiliensis*.

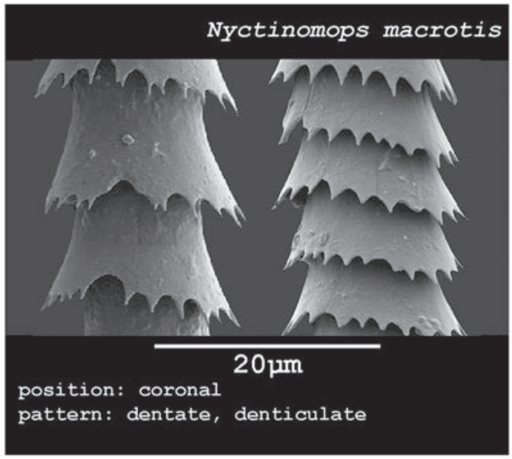

Fig. 22. Hair cuticle scales in *Nyctinomops macrotis*.

also be very interesting to study SEM images of species in the Megachiropteran single family of flying foxes (Pteropodidae) to see whether the hair characteristics are more like the Microchiropters or other mammals.

Acknowledgments

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