

# Comparative Morphology of Dorsal Hair of New World Bats of the Family Molossidae

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## Abstract

The morphology of dorsal hair of 31 species of New World molossid bats was studied using both conventional light microscopy and scanning electron microscopy to determine if hair structure, which has proven useful in other mammalian groups, could be of assistance in resolving some interesting systematic relationships within this group of bats. Dorsal hairs of each species are described and figured.

## Resumen

La morfología del pelo dorsal de 31 especies de murciélagos molósidos del Nuevo Mundo se estudió usando tanto microscopio óptico de luz convencional como electrónico para determinar si la estructura del pelo, que ha mostrado su utilidad en otros grupos de mamíferos, puede ser de ayuda para resolver algunas de las relaciones sistemáticas dentro de este grupo de murciélagos. Se describe e ilustra el pelo dorsal de cada especie.

Most bats of the family Molossidae in the New World are restricted in distribution to the Neotropics. The systematics of these species is poorly understood in some instances, particularly at the generic and subgeneric levels. For example, opinions differ as to whether *Cynomops*, *Neoplatymops*, and *Cabreramops* are generically or only subgenerically distinct from *Molossops*. Similarly, there is some uncertainty as to whether *Nyctinomops* should be regarded as distinct at the generic level from *Tadarida*, and as to the status of the recently proposed genus-group name *Rhizomops* (Legendre, 1984).

The most comprehensive recent study of relationships among molossids is that of Freeman (1981), based primarily on cranial morphometrics. She recognized two groups of genera in "terms of primitive-derived traits" the *Mormopterus* group, which also includes *Molossops* and its relatives (*Cynomops*, *Neoplatymops*, and *Cabreramops* among American subgenera or genera), and the *Tadarida* group (including also the New World *Nyctinomops*).

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*Eumops*, *Promops*, and *Molossus*). Other authors, however, have regarded *Mormopterus* as closely related to *Tadarida* and have even placed it as a subgenus of the latter (Koopman, 1982, for example). Perhaps *Mormopterus* and *Tadarida* are near the basal divergence of the two groups as defined by Freeman; she regarded them as the "two most primitive genera (of Molossidae) to which all other genera can be related".

A number of authors have opined that hair structure is of rather limited taxonomic value in bats (Cole, 1924; Nason, 1948; Benedict, 1957; Miles, 1965). However, many investigators of other taxonomic groups have held the opposite opinion (Mathiak, 1938; Williams, 1938; Brown, 1942; Mayer, 1952), and have used hair structure to construct keys to various taxa. In so doing, they tended to use characteristics other than cuticular scale pattern, including such aspects of hair as longitudinal form, cortical cell shape, medullar structure, and pigmentation patterns. Moore and Braun (1983) developed a key to Tennessee bats in which they were able to discriminate among most of the 13 species (of seven genera) that occur in that state.

Benedict's (1957) study of hair structure in bats strongly suggested that hair morphology provides a suite of conservative systematic characters that may serve as good taxonomic criteria at the generic level. However, she found interspecific variation to be relatively insignificant and generally limited to differences in size and pigmentation of the filaments. Concerning free-tailed bats in particular, Benedict concluded "that generally the generic differences in hair structure in the Molossidae are small".

Variation in scale shape sometimes are associated with differences among species (Smith, 1933). Benedict (1957) proposed a more complex grouping of coronal forms than did Smith, based on scale type, degree of divergence of scales from the hair shaft, nature of the distal scale margin, and degree of hastateness (that is, degree to which part of the distal edge of a scale is shaped like the head of a spear).

Benedict's (1957) study of chiropteran hair structure involved 16 families and included more than 20 species of molossids, the majority being New World taxa. She noted (p. 300): "Within *Tadarida*, there appears to be as much variation in the hair form as there is among the remaining genera of the entire family", which is not surprising inasmuch as she included in *Tadarida* species representing at least four genera as defined by Freeman (1981). Mayer (1952) surveyed four molossid species and concluded that this family could be distinguished from others by the prominent, spinelike margins of scales. Nason (1948) included two molossids in her study, but found no correlation between hair structure and life history strategy. She concluded that there was little evidence of seasonal variation in hair color and structure in bats. Benedict (1957) found that the only sexual variation was "occasional differences in color intensity". She also found no distinction between guard hairs and underhair in molossids.

## Methods

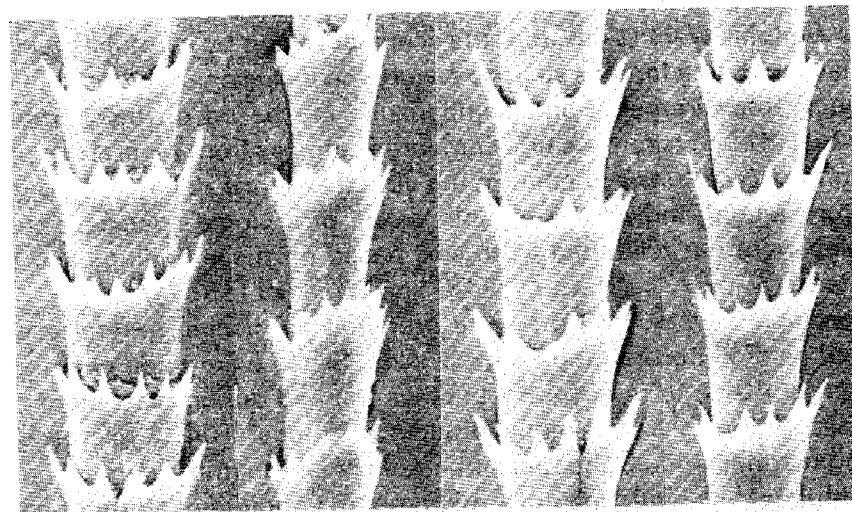
Thirty-one New World species from the family Molossidae were selected for study and samples of middorsal hairs were obtained from museum specimens. These samples were taken from the scapular region by carefully plucking a few hairs with fine forceps so as to ensure the inclusion of the base of each. Although measurements and comparisons are based on hairs from one individual of each taxon, we first compared samples from several specimens of *Tadarida brasiliensis* to confirm the virtual absence of differences in hair structure among individuals of both sexes of a single species. Thus our samples were not restricted as to sex, based on these findings and those reported previously by Nason (1948) and Benedict (1957).

Permanent whole mounts were prepared by placing several acetone-cleaned hairs in Permout on a glass slide. Slides were dried overnight (in an oven at 40°C) to remove any bubbles trapped during placement of the coverslip. Samples were examined under a Spencer 1042A microscope at varying magnifications, and measurements of length (mm) were taken from six complete hairs with an ocular micrometer. Longitudinal form of the hair and distribution of pigment in the cuticle and cortex also were recorded, using the terminology of Benedict (1957). Reference slides have been deposited in The Museum, Texas Tech University.

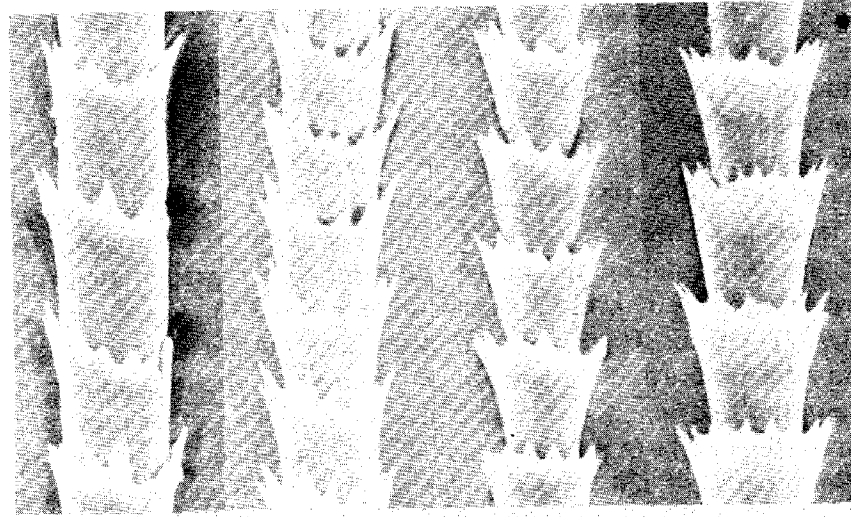
For scanning electron microscopy, several hairs were cleaned in acetone and mounted on double-sided tape on metal stubs. These were coated with gold to a depth of 550 Å in a Technics Hummer V Sputter coater and viewed in Hitachi S-570 scanning electron microscope (working distance 12 mm, 10 KV). Each specimen was studied extensively and photographed at a magnification of 3500 (figs. 1-5). Measurements of cuticular scale width and length were taken from these micrographs. For comparative purposes, only the midsection (the area that is least variable and most representative) of each hair was used (Benedict, 1957; Gaisler and Barus, 1978). According to Benedict (1957), "consensus holds that only the scales in the mid-region of a hair shaft are the mature and uniform types". Our own extensive scanning upheld the view that midsections are much less variable than other parts of hairs. Moreover, the middle of the hair is less likely to have been damaged naturally or in the process of acquiring samples for analysis. Scale index was calculated by dividing the greatest diameter of the hair into the greatest, exposed, proximo-distal length of a scale, and represents the average of many scale measurements in the midsection of the hair where diameter was recorded.

We carefully calculated hair width or diameter by measuring microphotographs. We note that our measurements are considerably smaller than those few published by Benedict (1957), and we do not know why. We are confident, however, that our measurements represent a rather close approximation of the actual width of individual hairs, and that mean measurements are meaningful representations thereof.

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Figure 1. Microphotographs at midsection of dorsal hairs of eight species of molossids: A, *Molossops abrasus*; B, *M. greenhalli*; C, *M. neglectus*; D, *M. paranus*; E, *M. planirostris*; F, *M. temminckii*; G, *Cabreramops aequatorianus*; H, *Neoplatymops mattogrossensis*. Scale same throughout.

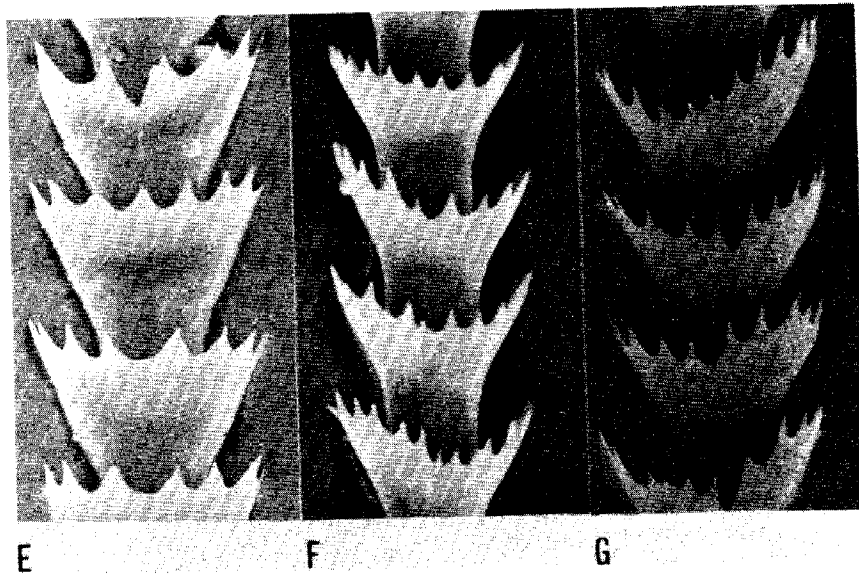
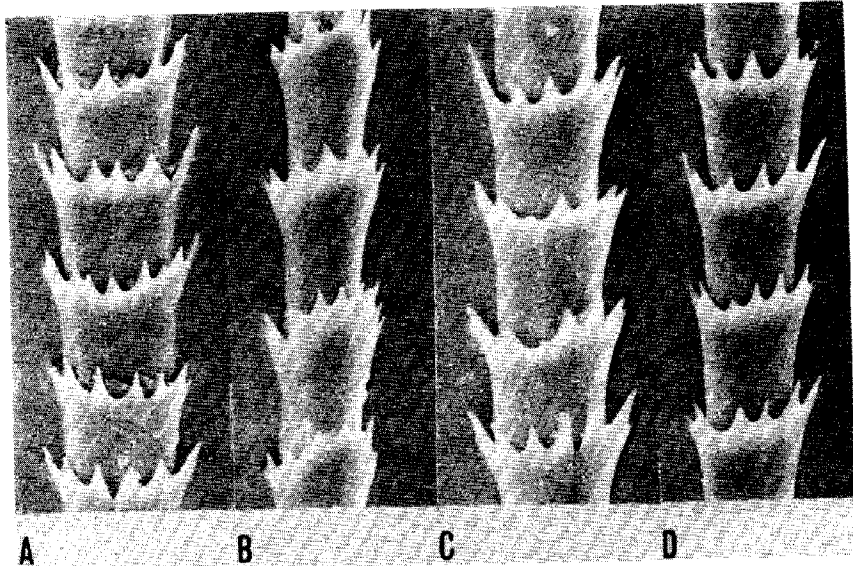
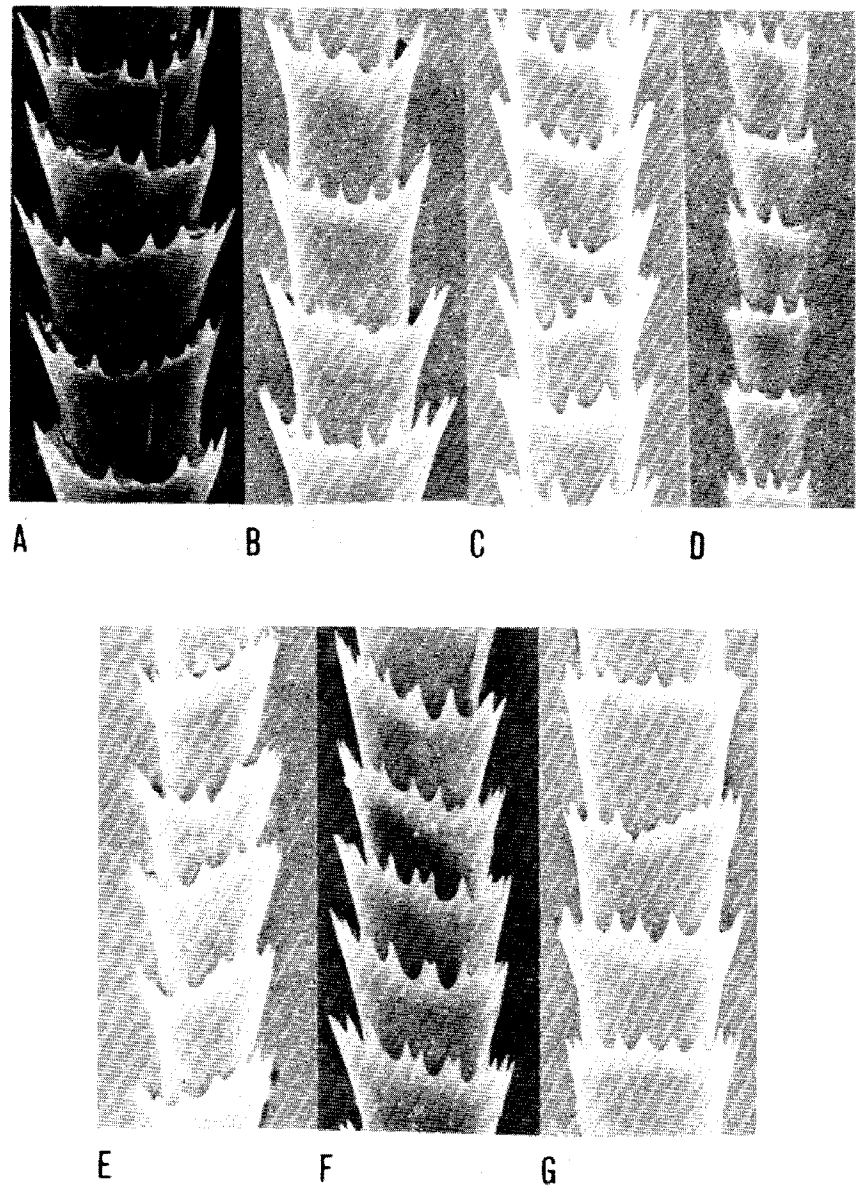


Figure 2. Microphotographs at midsection of dorsal hairs of seven species of molossid: A, *Mormopterus kalinowskii*; B, *M. phrudus*; C, *Tadarida brasiliensis*; D, *Nyctinomops aurispinosus*; E, *N. femorosaccus*; F, *N. laticaudatus*; G, *N. macrotis*. Scale same throughout.

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**Figure 3. Microphotographs of midsection of dorsal hairs of seven species of *Eumops*: A, *E. auripendulus*; B, *E. bonariensis*; C, *E. glaucinus*; D, *E. hansae*; E, *E. perotis*; F, *E. trumbulli*; G, *E. underwoodi*. Scale same throughout.**

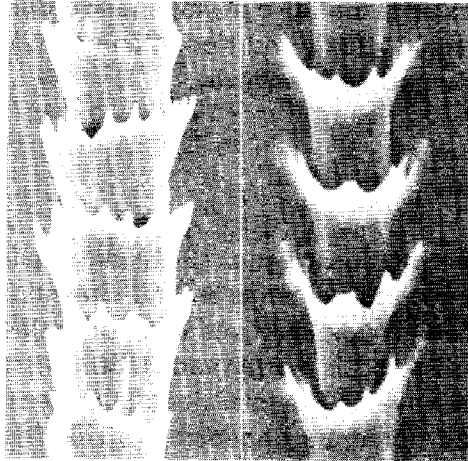
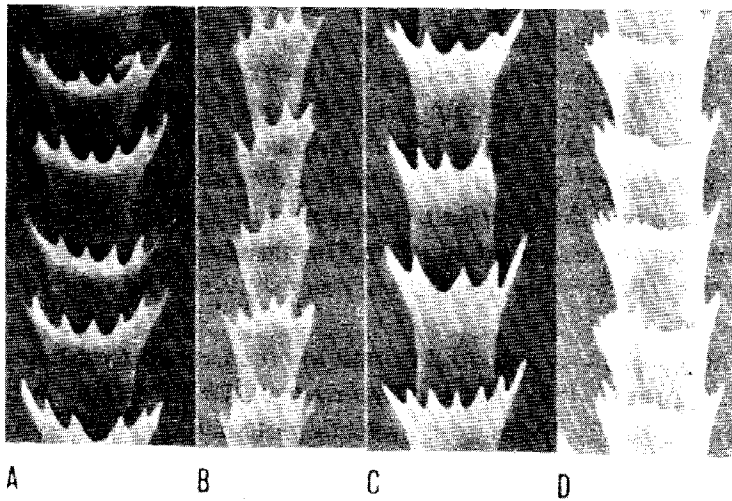
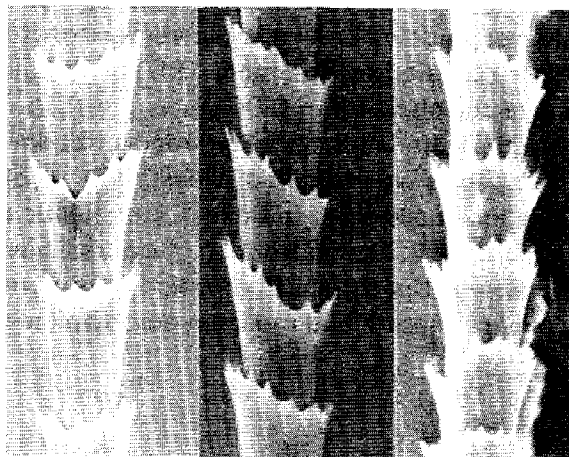


Figure 4. Microphotographs of midsection of dorsal hairs of *Promops centralis* (A) and *P. nasutus* (B). Scale same throughout.



A B C D



E F G

Figure 5. Microphotographs of midsection of dorsal hairs of seven species of *Molossus*: A, *M. aztecus*; B, *M. bondae*; C, *M. coibensis*; D, *M. molossus*; E, *M. pretiosus*; F, *M. rufus*; G, *M. sinaloae*. Scale same throughout.

In the accounts beyond, genera are listed in tentative phylogenetic order, principally following Freeman (1981), Hall (1981), and Koopman (1982). Species within polytypic genera are arranged alphabetically.

## Results

All molossids examined, unlike most chiropterans (Nason, 1948), have hair with coronal cuticular scales that is, a single scale extends around the entire hair shaft. Unlike many other mammalian groups, only one layer of scales appears to be present. The nature of the distal scale margin varies somewhat within the family although most species have an irregular dentate pattern, often with deep, V-shaped incisions as noted by Benedict (1957). The hastateness of the distal margin also is variable. The divergence of scales from the filament varies among bats and may be classified (after Hausman, 1930) in a relative sense, as oppressed (closely adhering to the filament), divergent (diverging from the filament), or divaricate (diverging considerably from the filament); all molossids we have examined have dorsal hairs that fall, more or less, into one of the last two categories. A medulla is absent in all species examined (Nason, 1948; Mayer, 1952; Benedict, 1957), the cortex comprising the entire central core of the shaft. Cortical fusi were not observed, but the degree and distribution of pigment granules in the cortex is distinctly variable and in some cases diagnostic. The predominant pattern is one of horizontal bands. The longitudinal form of hairs shows some variation among species studied.

A number of authors have described a trough in cross sections of hairs of other mammalian groups (Homan and Genoways, 1978; Vogel and Kopchen, 1978; Keogh, 1985). There is no indication of such concavities in molossid hairs.

A simple regression of scale index against total hair length showed a significant negative correlation ( $P = 0.042$ ). This implies that as hairs lengthen the scales become shorter and wider. A simple regression of forearm size (for the 25 species also studied by Freeman, 1981) and hair length showed a significant positive correlation ( $P < 0.001$ ).

Details of shape, cuticular scale characteristics, and pigment distribution of dorsal hairs are given for the 31 species we examined. Measurements of length and width of hairs and scale index are given in table 1. A tabulation of certain scale characters is listed in table 2. The midsection of a dorsal hair from each species also is figured (figs. 1-5). Specimens from which hairs were examined are identified as to locality of capture and museum acronym (see acknowledgments).



**Table 1**

LENGTH (MM), DIAMETER OR WIDTH ( $\mu\text{M}$ ), AND SCALE INDICES (SCALE LENGTH/SCALE WIDTH AT MIDSECTION OF MIDDORSAL HAIRS) OF REPRESENTATIVE NEW WORLD MOLOSSID BATS. N, NUMBER OF HAIRS OR SCALES MEASURED; SD, STANDARD DEVIATION

| Species                              | Length (mm) |      |       | Width ( $\mu\text{m}$ ) |       |       | Scale index |
|--------------------------------------|-------------|------|-------|-------------------------|-------|-------|-------------|
|                                      | N           | Mean | SD    | N                       | Mean  | SD    |             |
| <i>Molossops abrasus</i>             | 6           | 3.39 | 0.246 | 30                      | 10.89 | 0.578 | 1.78        |
| <i>Molossops greenhalli</i>          | 6           | 4.06 | 0.135 | 30                      | 9.13  | 0.673 | 1.03        |
| <i>Molossops neglectus</i>           | 6           | 3.31 | 0.260 | 23                      | 10.41 | 1.382 | 1.09        |
| <i>Molossops paranus</i>             | 6           | 3.03 | 0.198 | 29                      | 9.70  | 0.617 | 1.01        |
| <i>Molossops planirostris</i>        | 6           | 3.90 | 0.226 | 27                      | 9.64  | 0.601 | 1.09        |
| <i>Molossops temminckii</i>          | 6           | 4.84 | 0.482 | 23                      | 7.87  | 1.920 | 1.09        |
| <i>Cabreramops aequatoriannus</i>    | 6           | 3.00 | 0.603 | 28                      | 9.80  | 0.620 | 1.04        |
| <i>Neoplattymops mattogrossensis</i> | 6           | 3.04 | 0.212 | 28                      | 11.67 | 1.075 | 0.95        |
| <i>Mormopterus kalinowski</i>        | 6           | 4.26 | 0.092 | 14                      | 14.87 | 1.375 | 1.02        |
| <i>Mormopterus phrudus</i>           | 6           | 3.96 | 0.293 | 28                      | 11.29 | 2.482 | 1.02        |
| <i>Tadarida brasiliensis</i>         | 6           | 4.30 | 0.340 | 15                      | 16.66 | 1.587 | 0.99        |
| <i>Nyctinomops aurispinosus</i>      | 6           | 2.85 | 0.254 | 14                      | 15.39 | 0.969 | 0.94        |
| <i>Nyctinomops femorosaccus</i>      | 6           | 5.55 | 0.668 | 16                      | 15.57 | 1.921 | 0.80        |
| <i>Nyctinomops laticaudatus</i>      | 6           | 5.53 | 0.550 | 10                      | 15.39 | 0.832 | 0.95        |
| <i>Nyctinomops macrotis</i>          | 6           | 7.17 | 1.050 | 24                      | 16.37 | 0.694 | 0.73        |
| <i>Eumops auripendulus</i>           | 6           | 7.76 | 0.837 | 25                      | 13.38 | 1.391 | 0.79        |
| <i>Eumops bonariensis</i>            | 6           | 5.94 | 0.229 | 15                      | 11.20 | 1.901 | 1.00        |
| <i>Eumops glaucinus</i>              | 6           | 6.49 | 0.505 | 27                      | 9.67  | 1.439 | 1.02        |
| <i>Eumops hansae</i>                 | 6           | 3.25 | 0.412 | 20                      | 9.13  | 0.681 | 1.02        |
| <i>Eumops perotis</i>                | 6           | 7.76 | 0.421 | 27                      | 9.88  | 1.035 | 1.82        |
| <i>Eumops trumbulli</i>              | 6           | 6.76 | 0.302 | 34                      | 12.69 | 0.672 | 1.82        |
| <i>Eumops underwoodii</i>            | 6           | 7.64 | 0.527 | 24                      | 12.15 | 1.052 | 0.91        |
| <i>Promops centralis</i>             | 6           | 6.17 | 0.227 | 14                      | 12.71 | 0.768 | 0.77        |
| <i>Promops nasutus</i>               | 6           | 5.12 | 0.198 | 31                      | 9.60  | 1.275 | 1.06        |
| <i>Molossus aztecus</i>              | 6           | 3.70 | 0.240 | 34                      | 12.26 | 0.982 | 0.74        |
| <i>Molossus bondae</i>               | 6           | 2.73 | 0.150 | 26                      | 8.35  | 0.726 | 1.07        |
| <i>Molossus coibensis</i>            | 6           | 3.96 | 0.452 | 27                      | 10.82 | 1.382 | 1.03        |
| <i>Molossus molossus</i>             | 6           | 4.33 | 0.201 | 36                      | 9.86  | 1.473 | 0.82        |
| <i>Molossus pretiosus</i>            | 6           | 3.82 | 0.250 | 24                      | 9.48  | 0.775 | 1.13        |
| <i>Molossus rufus</i>                | 6           | 4.45 | 0.180 | 25                      | 9.57  | 0.889 | 1.12        |
| <i>Molossus sinaloae</i>             | 6           | 3.72 | 0.267 | 20                      | 11.36 | 1.353 | 0.74        |

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**Table 2**

SUMMARY OF SCALE CHARACTERISTICS ON MIDDORSAL HAIRS OF 31 SPECIES OF NEW WORLD MOLOSSID BATS

| <i>Species</i>                      | <i>Scale margin</i> | <i>Divergence from shaft</i> | <i>Degree of hastateness</i> |
|-------------------------------------|---------------------|------------------------------|------------------------------|
| <i>Molossops abrasus</i>            | Irregular dentate   | Divergent                    | Repand                       |
| <i>Molossops greenhalli</i>         | Dentate             | Divergent                    | Equal hastate                |
| <i>Molossops neglectus</i>          | Irregular dentate   | Divergent                    | Repand                       |
| <i>Molossops parvus</i>             | Irregular dentate   | Divergent                    | Repand                       |
| <i>Molossops planirostris</i>       | Irregular dentate   | Divergent                    | Equal hastate                |
| <i>Molossops temminckii</i>         | Irregular dentate   | Divergent                    | Equal hastate                |
| <i>Cabreramops aequatorianus</i>    | Irregular dentate   | Divergent                    | Repand                       |
| <i>Neoplatymops mattogrossensis</i> | Dentate             | Divergent                    | Entire                       |
| <i>Mormopterus kalinowski</i>       | Irregular dentate   | Divaricate                   | Repand                       |
| <i>Mormopterus phrudus</i>          | Irregular dentate   | Divaricate                   | Repand                       |
| <i>Tadarida brasiliensis</i>        | Irregular dentate   | Divaricate                   | Equal hastate                |
| <i>Nyctinomops aurispinosus</i>     | Irregular dentate   | Divaricate                   | Equal hastate                |
| <i>Nyctinomops femorossacus</i>     | Irregular dentate   | Divaricate                   | Equal hastate                |
| <i>Nyctinomops laticaudatus</i>     | Irregular dentate   | Divaricate                   | Equal hastate                |
| <i>Nyctinomops macrotis</i>         | Irregular dentate   | Divaricate                   | Equal hastate                |
| <i>Eumops auripendulus</i>          | Irregular dentate   | Divergent                    | Equal hastate                |
| <i>Eumops bonariensis</i>           | Irregular dentate   | Divaricate                   | Equal hastate                |
| <i>Eumops glaucinus</i>             | Irregular dentate   | Divergent                    | Equal hastate                |
| <i>Eumops hansae</i>                | Irregular dentate   | Divergent                    | Equal hastate                |
| <i>Eumops perotis</i>               | Irregular dentate   | Divergent                    | Equal hastate                |
| <i>Eumops trumbulli</i>             | Irregular dentate   | Divergent                    | Equal hastate                |
| <i>Eumops underwoodii</i>           | Irregular dentate   | Divergent                    | Equal hastate                |
| <i>Promops centralis</i>            | Narrow lobate       | Divergent                    | Repand                       |
| <i>Promops nasutus</i>              | Narrow dentate      | Divergent                    | Equal hastate                |
| <i>Molossus aztecus</i>             | Irregular dentate   | Divaricate                   | Equal hastate                |
| <i>Molossus bondae</i>              | Irregular dentate   | Divergent                    | Equal hastate                |
| <i>Molossus coibensis</i>           | Irregular dentate   | Divaricate                   | Equal hastate                |
| <i>Molossus molossus</i>            | Irregular dentate   | Divergent                    | Equal hastate                |
| <i>Molossus pretiosus</i>           | Irregular dentate   | Divergent                    | Equal hastate                |
| <i>Molossus rufus</i>               | Irregular dentate   | Divergent                    | Equal hastate                |
| <i>Molossus sinaloae</i>            | Irregular dentate   | Divergent                    | Equal hastate                |

## Genus *Molossops*

*Molossops abrasus* (USNM 114928-Sapucay, Paraguay, Fig. 1A). Base has slight bend; widest point of shaft approximately at middle of hair. Cuticular pigmentation light in proximal half and moderate in distal half of hair. Pigmentation in cortex diffuse in the middle third (possibly due to yellowish coloration). Horizontal banding distinct in distal third.

Benedict (1957) characterized the dorsal hairs of this species (under the name *Cynomops cerastes*) as: "Short, divergent, dentate coronal". She also noted that few scales had a noticeable V-shaped, marginal incision, a feature we found difficult to evaluate in hair we studied (see figures). Benedict reported length of hairs as 4.0 mm and the diameter as 17.0  $\mu\text{m}$ , the latter figure much larger than the average of 10.89  $\mu\text{m}$  found by us.

*Molossops greenhalli* (USNM 511544-El Casco, Nayarit, Fig. 1B). Shape as in *M. abrasus*. Both cuticle and cortical pigmentation moderate, resulting in clear horizontal banding along almost entire length of hair; at extreme tip, however, there is little or no pigment in cuticle. Together with *M. planirostris*, the teeth of the scale margin are somewhat more irregular in *M. greenhalli* than in other *Molossops* examined, and the scales of the two are less divergent than in other genera.

*Molossops neglectus* (USNM 364484-Oxapampa, Pasco, Perú, Fig. 1C). Shaft gradually tapers from widest point near base. No cuticular pigmentation in basal region, and pigmentation of cortex extremely light. Cuticular and cortical banding moderate along entire length, resulting in uniformly banded hair. This base-to-tip banding pattern distinguishes both this species and *M. greenhalli* from the remaining four taxa of *Molossops* we examined.

*Molossops paranus* (USNM 319086-Pacora, Panamá, Fig. 1D). Base moderately curved; width of hair shaft increases gradually in proximal third, reaching widest point in middle third; then tapers rapidly into first part of the distal third from which point width is maintained until gradually tapering at tip. Cuticular pigmentation moderate in proximal half and dense in distal half. No distinct bands evident in the proximal region; rather, there are variable alternating darker and paler spots. Cortical pigmentation heavy in distal half, rendering pattern indistinguishable. Dorsal hairs of *M. paranus* are comparatively short, averaging 3.03 mm as compared to a range of 3.31-4.84 for other species in the genus.

*Molossops planirostris* (USNM 393769-Serra do Rocandor, Matto Grosso, Brazil, Fig. 1E). Base moderately curved, with greatest width at midpoint of hair. Cuticle and cortex light and moderately pigmented, respectively, forming clear horizontal bands.

*Molossops temminckii* (USNM 507211-Villavicencia, Meta, Colombia, Fig. 1F). Proximal third of hair shaft narrow, widening in middle third and maintaining width until a gradual tapering at tip. Both cuticle and cortex only lightly pigmented in proximal half and moderately so in distal half.

The average hair length for this species is more or less in agreement with that reported by Benedict (1957), but measurements of maximum diameter differ considerably. We found an average width of 7.87  $\mu\text{m}$  (scale index 1.09) as compared to 17.0  $\mu\text{m}$  (scale index 0.4) in her data. *M. temminckii* has the longest (average 4.84 mm) and narrowest dorsal hairs of any species of *Molossops* we examined.

#### Genus *Cabreramops*

*Cabreramops aequatorianus* (USNM 513508-Río Chongon, Guayas, Ecuador, Fig. 1G). Form of hair not distinctive. Width of shaft gradually increases in proximal third, reaching widest part in middle third, then tapers gradually in distal portion. Both cuticle and cortex moderately pigmented along entire length of hair, producing a distinct horizontal banding pattern.

#### Genus *Neoplatymops*

*Neoplatymops mattogrossensis* (M. R. Willig 2295-Serrote Gamba, SSW Exu, Pernambuco, Brazil, Fig. 1H). Base moderately curved with no region of elongated scales before the mature scale pattern emerges; tapering at distal end of the hair abrupt. Cortex pigmented throughout but granules more diffuse in proximal third of hair; distal two-thirds clearly banded. Banding results from distribution of pigment in cuticle; not found in lateral extensions of scale but rather restricted to hair shaft.

#### Genus *Mormopterus*

*Mormopterus kalinowskii* (USNM 283175-Trujillo, La Libertad, Perú, Fig. 2A). Base of hair straight, with relatively rapid increase in shaft width in proximal third. Cuticular pigmentation moderate from base to tip; cortical pigmentation light to moderate throughout. Distinct horizontal banding pattern results from pigmentation in distal portion of each scale overlying cortical pigmentation.

*Mormopterus phrudus* (USNM 194450-Machu Pichu, Cuzco, Perú, Fig. 2B). Slight increase in width of shaft apparent in distal third of hair, with gentle tapering away from this point. Cuticular and cortical pigmentation heavy along entire length of hair, producing a distinct horizontal banding pattern.

The degree of divergence between the base and distal edge of individual scales is noticeably less in *M. phrudus* (average 5.73  $\mu\text{m}$ ) than in *M. kalinowskii* (8.67  $\mu\text{m}$ ). Scales otherwise as in *M. kalinowskii*. Benedict's (1957: 522) description of hair of "*M. peruanus*" evidently relates to *Tadarida brasiliensis* (at least the former is a synonym of *T. brasiliensis* according to De la Torre, 1956).

## Genus *Tadarida*

*Tadarida brasiliensis* (TTU 9177-Davis Mtns., Jeff Davis Co., Texas, USA, Fig. 2C). Base and shaft similar in diameter, with increase to widest point in distal third of hair. Cuticle lightly pigmented in basal two thirds, more densely so in distal third; pigment appears restricted to margins of scales. Cortex light to moderately pigmented; horizontal bands narrow and relatively far apart in the basal two thirds of hair, difficult to distinguish elsewhere because of cuticular pigmentation.

There is a greater lateral distance from the base of a scale to the edge of a scale (8.9  $\mu\text{m}$ ) in *T. brasiliensis* than in species of the genus *Nyctinomops* (range 7.0-8.3  $\mu\text{m}$ ), and the scales are thus more divergent. The scale index is 0.99 as opposed to 0.73 to 0.95 in species of *Nyctinomops*.

## Genus *Nyctinomops*

*Nyctinomops aurispinosus* (TTU 6260-Río Cuchahaqui, Sonora, México, Fig. 2D). Base slightly curved; shaft reaches widest point along small section in middle third of hair; distal two thirds with eight alternating broad and narrow areas (unique among molossids examined). Cuticular pigmentation light throughout. Cortical pigmentation dense in distal half of hair and showing distinct horizontal bands.

Hair scales in *N. aurispinosus* are somewhat less divergent than those in other members of the genus and the individual hairs are much shorter in *N. aurispinosus* than in other species and in the related *Tadarida brasiliensis* (Table 1).

*Nyctinomops femorosaccus* (TTU 10568-near Tecoripa, Sonora, México, Fig. 2E). Base slightly curved. Expansion of the hair shaft in the third quarter might be described as clublike but is less distinct than one would ascribe to such a description. Cortical and cuticular pigmentation distinct along entire length of hair, but banding clear only in distal third.

*Nyctinomops laticaudatus* (TTU 10026-Ojo de Agua del Río Atoyac, Veracruz, México, Fig. 2F). Base straight, first portion of distal third of hair widest, tapering gently and evenly in both directions from this point. Dense cuticular pigmentation found along length of hair, but with lighter zone at proximal end of distal third. Cortex lightly pigmented with no clear bands distinguishable. Cortex appears to be absent in distal third of hair. Distinct from other species of *Nyctinomops* in which distal part of cortex is relatively heavily pigmented.

*Nyctinomops macrotis* (TTU 9304-Sierra Vieja Mtns., Presidio Co., Texas, USA, Fig. 2G). Base of hair virtually straight, hair widest at base; tapering uniformly to tip. Cuticle pigmented from base to tip but only lightly so in proximal third. Cortical pigmentation only clearly banded in distal third.

## Genus *Eumops*

Although on average *Eumops* has broad hairs (average 11.67  $\mu\text{m}$ ), species of this genus are quite diverse in terms of hair size. Moreover, it is the most diverse of the molossid genera in terms of pigmentation pattern of hairs.

*Eumops auripendulus* (USNM 315786-Changuinola, Bocas del Toro, Panamá, Fig. 3A). Form of dorsal hair lacks distinction, but pattern of pigmentation diagnostic. Cuticular pigmentation in proximal half of hair contains three alternating light and moderate regions, whereas cuticle in distal portion is moderately pigmented. Pigment granules in cortex evenly dispersed throughout length of hair such that a banding pattern appears where cuticle pigmentation is moderate; pigmentation becomes to dense to distinguish banding patterns elsewhere.

*Eumops bonariensis* (TTU 14355-Mérida, Yucatán, México, Fig. 3B). As in other species of genus, form of hair simple, lacking distinctive characters. Moderate cuticular and cortical pigmentation yield a clear banding pattern beginning in the midsection of the hair; pigment reaches greatest density in middle of distal third of shaft.

*Eumops glaucinus* (USNM 391180-Silvestre, Minas Gerais, Brazil, Fig. 3C). Base slightly curved; widest part of shaft occurs as a "club" in middle of distal third of hair; from that point, hair tapers gradually to relatively broad tip. Cuticle pigmentation moderate in proximal quarter and light elsewhere, reaching minimum in distal quarter just beneath club. Cortical pigmentation uniform and moderate throughout. Horizontal banding evident in regions of light cuticular pigmentation.

This description contrasts with that of Nason (1948), both qualitatively and quantitatively:

Extreme base is colorless, followed by a pale brown pigmentation for 1/5th of the shaft length. The amount of pigment gradually increases so that 3/5th of the shaft has evenly distributed, medium brown pigments, the final fifth being more densely pigmented with brown.

According to Benedict (1957) the hairs of *E. glaucinus* are like those of *E. perotis*, being 7 to 9 mm long, 17.0 to 25.5  $\mu\text{m}$  in diameter, and with a scale index of 0.3 to 0.5. We found these same dimensions to average 6.49 mm, 9.67  $\mu\text{m}$ , and 1.02, respectively.

*Eumops hansae* (USNM 310278-Tacarcuna Village, Panamá, Fig. 3D). Slight curve to base; widest point of shaft occurs in middle third. Although cortex pigmented throughout length of the shaft, cuticular pigmentation occurs only in distal half of the hair.

Quantitatively, dorsal hairs of this species are unique in the genus because they have fewer teeth per scale than the other species. *E. hansae* also has the narrowest hairs of any species in the genus, averaging 9.3  $\mu\text{m}$  as compared to an average width of 12.09 (9.67-13.38)  $\mu\text{m}$  for other species

(Table 1), and the shortest hairs (3.25 mm) as compared to a range of 5.94 to 7.76 for other species.

*Eumops perotis* (TTU 6372-Río Alamos, Sonora, México, Fig. 3E). Base only slightly curved, form of hair not distinctive. Pigmentation of cuticle and cortex moderate from base to tip, resulting in distinct and uniform horizontal banding.

Although this description is consonant with previous studies in qualitative terms, there is little agreement in quantitative characteristics. The average length (7.76 mm) and width (9.88  $\mu\text{m}$ ) in our specimens are less than found by Mayer (1952). The length falls within the range reported by Benedict (1957) but the maximum diameter she recorded for *Eumops* (17.0-25.5  $\mu\text{m}$ ) is about twice as great, and scale index at the midpoint ranged from 0.3 to 0.5 in her study in contrast to a value of 1.82 reported here.

*Eumops trumbulli* (USNM 483972-Puerto Narino, Amazonas, Colombia, Fig. 3F). Base moderately curved; greatest width of shaft reached in midsection of hair, thereafter tapering uniformly to tip. Pigmentation moderate, becoming denser in distal quarter of hair, but not so dense as to obscure horizontal banding.

*Eumops underwoodii* (TTU 6128-Garcia's Represso, Pima Co., Arizona, USA, Fig. 3G). Hair with straight base, lacking any distinctive features. Both cuticle and cortex moderately pigmented, giving a clear banding pattern.

#### Genus *Promops*

This is the only genus in which we found major variation in the form of the teeth (dentate as opposed to narrowly lobate) and of the distal margin.

*Promops centralis* (TTU 18454-Mérida, Yucatán, México, Fig. 4A). Base only slightly curved. Proximal quarter of hair narrow, with a clear broadening in the second quarter, maintained until a gradual tapering to tip. Hair contrasts with that of *P. nasutus* in having a distinctive shape. Both cuticle and cortex moderately pigmented from base to tip, but horizontal banding slightly irregular until distal third.

The present description differs in a number of respects from that of Benedict (1957). We found the average hair length to be 6.17 mm and the width 12.7  $\mu\text{m}$ , whereas Benedict reported 9.0 mm and 18.7  $\mu\text{m}$ , respectively. Scale indices are 0.77 and 0.45 for this study and as recorded by Benedict, respectively. Furthermore she classified scale teeth as denticulate rather than narrowly lobate.

*Promops nasutus* (USNM 387798-85 km SSE El Dorado, Bolívar, Venezuela, Fig. 4B). Base of hair moderately curved. Form tapers evenly from base to tip with exception of a slight narrowing in proximal portion of middle segment. Pigment evenly dispersed in cuticle from base to tip, whereas cortical pigmentation light in basal half of hair and dense in distal half; in contrast to *P. centralis*, no banding is evident. Scale margins dentate

in contrast to those of *P. centralis*, which are narrowly lobate, and scales are noticeably more divergent.

### Genus *Molossus*

With the exception of *M. aztecus*, we found no distinct differences in hair form among species of *Molossus*, which are characterized by extremely dense cuticular pigmentation, particularly in the distal third of the shaft.

*Molossus aztecus* (TTU 29565-La Libertad, El Salvador, Fig. 5A). Base moderately curved. Hair reaches widest point in distal part of first third of shaft; slightly narrowed and flattened in middle third. Cuticle pigmented throughout. Cortical pigmentation light to moderate in basal half of hair. Horizontal banding distinct only in distal half.

This species has scales that are more divergent (thus divaricate) than the average for the genus,  $5.9 \mu\text{m}$  as compared to  $3.12 \mu\text{m}$  (range 2.4-3.5) in other species except *M. coibensis*. The average length is 3.7 mm, which agrees with Benedict (1957). Descriptions of pigment distribution are also in agreement. However, the width she reported is greater ( $17.0\text{-}18.7 \mu\text{m}$  for three species of the genus) as opposed to  $12.26 \mu\text{m}$  we recorded for *M. aztecus* (which has the broadest hairs among the species we examined, Table 1). Benedict classified scales of *Molossus* as "slightly divergent".

*Molossus bondae* (TTU 29548-Rama, Nicaragua, Fig. 5B). Base strongly curved. Cuticle densely pigmented from base to tip rendering cortex difficult to observe. There is some indication of horizontal banding.

The hairs of *M. bondae* are distinctly narrower than those in the other species of the genus,  $8.35 \mu\text{m}$  as compared to an average of  $10.56$  ( $9.48\text{-}10.26$ ) for the remainder of the group. They also are the shortest in the genus  $2.73 \text{ mm}$  as compared to an average of  $3.96$  ( $3.70\text{-}4.45$ ) for the other six species examined.

*Molossus coibensis* (TTU 29689-Chepo, Panamá, Fig. 5C). Base slightly curved. Cuticle pigmented throughout. Cortex lightly pigmented in proximal third and exhibiting horizontal banding, which becomes more distinct in middle third but undetectable in distal third because pigmentation of cuticle is quite dense. Scales more divergent than in other species of *Molossus* (except *M. aztecus*),  $4.7 \mu\text{m}$  as compared to an average of  $3.12 \mu\text{m}$ .

*Molossus molossus* (TTU 21052-Guadeloupe, West Indies, Fig. 5D). Base slightly curved. No distinct increase in width; even but relatively abrupt tapering to the tip. Basal third of hair lightly pigmented; middle third with heavier pigmentation in cuticle but cortex remaining light; distal third heavily pigmented.

*Molossus pretiosus* (TTU 29791-Los Cocos, Nicaragua, Fig. 5E). Base straight. Cuticular and cortical pigmentation in proximal third of hair light. Cuticular pigmentation medium in distal two-thirds of shaft, whereas cortical pigmentation becomes heavy and distinctly banded.



*Molossus rufus* (TTU 5388-San Rafael, Trinidad, West Indies, Fig. 5F). Base of hair straight with widest part in midregion. Cuticle densely pigmented from base to tip; cortical pigmentation pale and irregular in proximal half but indistinguishable in distal part because of the dense cuticle. We follow Dolan (1989) in referring to this species as *M. rufus* rather than *M. ater*.

*Molossus sinaloae* (TTU 14371-Mérida, Yucatán, México, Fig. 5G). Base gently curved, shaft widening slightly in middle and tapering gradually to tip. Basal region lacks pigmentation entirely; pigment located only in cortex and in distinct horizontal bands in remainder of proximal third of the hair; central third with diffuse and paler pigmentation in both cuticle and cortex, whereas distal portion of hair densely pigmented.

## Discussion

Opinions differ as to variability of hair structure in different regions of the body. In earlier studies in which light microscopy was used, little variation was found (Nason, 1948; Benedict, 1957), whereas more recent investigators, using scanning electron microscopes, have demonstrated wider variation (Short, 1978; Riggott and Wyatt, 1980; Hess *et al.*, 1985; Hickey and Fenton, 1987). There are a few cases in which distinctive shape is of value in differentiating between scales of different groups at the familial level, as is true of the Molossidae (Mayer, 1952). However, according to Hausman (1930), scales bear a greater relationship to diameter of hair shaft than to systematic position.

Although our study of morphology of dorsal hairs of molossids revealed some interesting features, the considerable differences in hair structure between the two species of *Promops* (Fig. 4), for example, it unfortunately did not result in any clear groupings as regards genera and subgenera of these bats. Hairs of *Cabreramops* and *Neoplatymops* do not differ much from those of *Molossops* (Fig. 1). Species of the latter fall into two distinct groups based on external, dental and karyological attributes, the subgenera *Molossops* (*neglectus*, *temminckii*) and *Cynomops* (*abrasus*, *greenhalli*, *paranus*, *planirostris*). Using hair morphology, however, no such grouping is apparent (Fig. 1).

*Mormopterus* hairs are narrower than those of *Tadarida* and its relative *Nyctinomops* (Fig. 2). In fact, hairs of the last two listed genera are the broadest of any examined (means ranging from 15.39 to 16.66  $\mu\text{m}$ ). The dorsal hair of *N. aurispinosus* is considerably shorter (2.85 mm) than those of other species (5.53-7.17 mm), the longest being in the large *N. macrotis*.

Among species of *Eumops* (Fig. 3), the short and narrow hair of *E. hansae* is noteworthy. In taxa of *Molossus* (Fig. 5) only hairs of *M. aztecus*, and to a lesser degree those of *M. coibensis*, are distinctive, being broader middorsally than hairs of other species.

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