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Mormoops megalophylla.

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Mormoops Leach

Mormoops Leach, 1821*a*:76. Type species *Mormoops blainvillii* Leach.
Aëllo Leach, 1821*b*:70. Type species *Aëllo cuvieri* Leach.

CONTEXT AND CONTENT. Order Chiroptera, Suborder Microchiroptera, Family Mormoopidae, Subfamily Chilonycterinae, Genus *Mormoops*. The genus *Mormoops* contains two species, *Mormoops blainvillii* and *M. megalophylla* (Smith, 1972) which can be distinguished by size and geographic distribution. *M. blainvillii* is the smaller member of the genus (length of forearm <41 mm) and is restricted to Cuba, Jamaica, Hispaniola, and Puerto Rico. *M. megalophylla* is the larger member of the genus (length of forearm >50 mm) and is distributed on the mainland of North and South America and on a few closely adjacent islands.

Mormoops megalophylla Peters, 1864

Ghost-faced Bat

Mormoops megalophylla Peters, 1864:381. Type locality "[Parrás, Coahuila-Smith, 1972] Mexico."
Mormoops intermedia Miller, 1900:160. Type locality "cave at Hatto, north coast of Curaçao, Dutch West Indies [Netherlands Antilles]."
Mormoops tumidiceps Miller, 1902:403. Type locality "Point Gourde Caves, Trinidad."

CONTEXT AND CONTENT. Context in generic account above. Four subspecies are recognized (Smith, 1972):

M. m. megalophylla Peters, 1864:381, see above (*rufescens* Davis and Carter and *senicula* Rehn are synonyms).
M. m. intermedia Miller, 1900:160, see above.
M. m. tumidiceps Miller, 1902:403, see above.
M. m. carteri Smith, 1972:119. Type locality "Gruta Rumichaca, 2 mi E La Paz, 8,700 ft, Carchí Province, Ecuador."

DIAGNOSIS. The larger size of *M. megalophylla* is the primary feature distinguishing it from *M. blainvillii* (Fig. 1*a*). The length of the forearm of *M. blainvillii* usually is <41 mm, whereas that of *M. megalophylla* is >50 mm. The rostrum of *M. megalophylla* is extremely upturned and broad; the braincase is squared and flattened dorsally, or pyramidal and lacking noticeable flattening, the forehead arises abruptly from the rostrum; the basioccipital and basisphenoid are broad and trough-like between the auditory bullae, and have a prominent longitudinal, medial septum. By contrast, the rostrum of *M. blainvillii* is upturned and narrow, the braincase is globular with the frontal region inflated; the basioccipital and basisphenoid are narrow, with a wide depression lacking a longitudinal, medial septum. The ears of *M. megalophylla* are rounded and connected by two high bands that fuse on top of the rostrum, whereas the ears of *M. blainvillii* are rounded with an inconspicuous dorsal portion that is short and pointed. The tragus of *M. megalophylla* is complex with a prominent secondary fold; *blainvillii* has a lanceolate flap above the secondary fold. The labionasal plate of *M. megalophylla* is complex, each nostril is surrounded by a separate pad, the margin above and between nostrils contains several wart-like tubercules, and a long, prominent ridge separates the nostrils (Smith, 1972; Fig. 1*b*).

GENERAL CHARACTERS. The dorsal pelage of *M. megalophylla* is long and lax with four zones of coloration on each hair (Smith, 1972). Means of external measurements (in mm, with range in parentheses) for 18 males and 13 females of *M. m. megalophylla* from Jalisco, Mexico, were: total length, 88.9 (85.0–97.0), 90.9 (87.0–95.0); length of tail vertebrae, 24.9 (22.0–28.0), 25.1 (23.0–27.0); length of hind foot, 13.0 (12.0–14.0), 13.0 (all 13.0); length of ear from notch, 14.3 (13.0–15.0), 14.5 (14.0–15.0); for 4 males of *M. m. intermedia* from Curaçao, Netherlands Antilles: total length, 78.0 (74.0–83.0); length of tail vertebrae, 19.5 (18.0–21.0); length of hind foot, 10.5 (9.0–12.0); for 18 males and 3 females of *M.*

FIG. 1. Ghost-faced bat, *Mormoops megalophylla*: lateral view of bat in flight (above); face (below). Photographs copyright by Merlin D. Tuttle, used by permission.

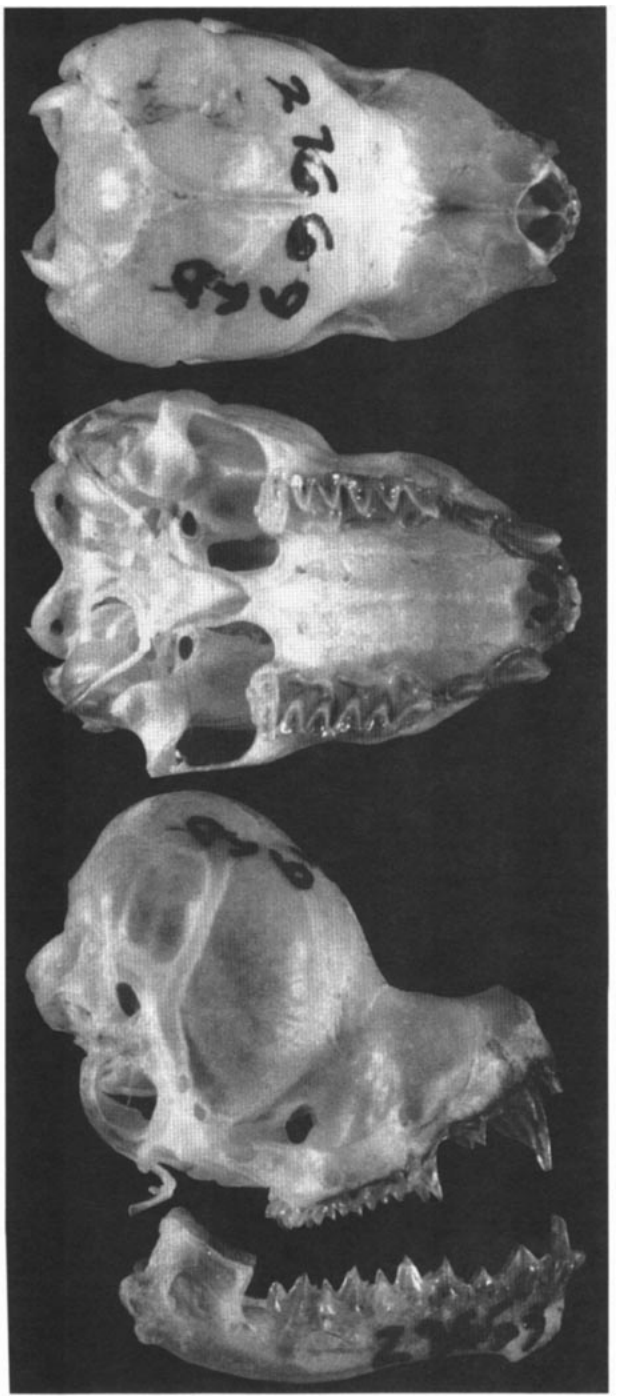

FIG. 2. Dorsal, ventral, and lateral views of skull and lateral view of mandible of *Mormoops megalophylla* from Queretaro, Mexico (male, Texas Cooperative Wildlife Collection, Texas A&M University, 27669). Greatest length of skull is 15.2 mm.

m. tumidiceps from Rio Salado, Venezuela: total length, 95.8 (88.0–104.0), 97.0 (92.0–100.0); length of tail vertebrae, 27.7 (24.0–31.0), 26.0 (24.0–29.0); length of hind foot, 11.9 (10.0–13.0), 11.7 (11.0–12.0); length of ear from notch, 14.8 (13.0–16.0), 14.7 (14.0–15.0); and for 16 males and 18 females of *M. m. carteri* from Gruta Rumichaca, Ecuador: total length, 98.1 (93.0–103.0), 98.6 (95.0–102.0); length of tail vertebrae, 28.3 (23.0–31.0), 27.5 (25.0–30.0); length of hind foot, 10.8 (10.0–13.0), 9.9 (9.0–11.0); length of ear from notch, 15.2 (14.0–16.0), 15.4 (15.0–16.0—Smith, 1972).

Means of forearm and cranial measurements (in mm) for 286 specimens of *M. m. megalophylla* from 14 localities in North

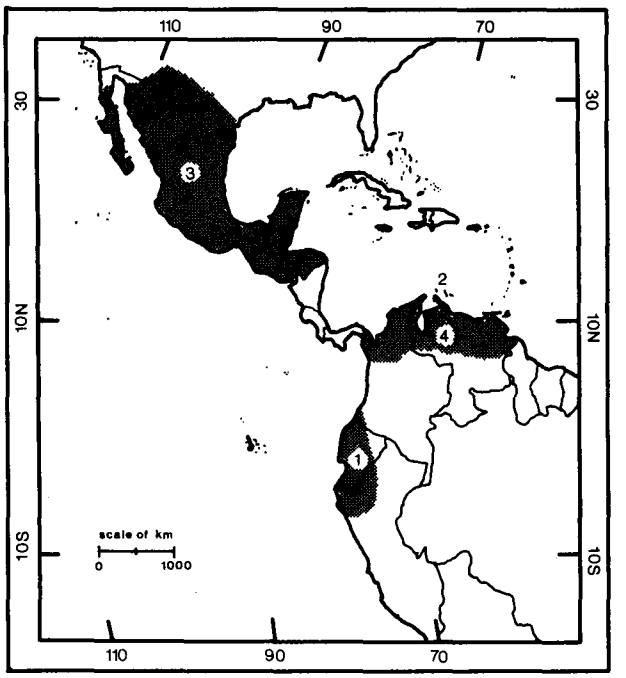

FIG. 3. Distribution of *Mormoops megalophylla* (Graham and Barkley, 1984; Smith, 1972): 1, *M. m. carteri*; 2, *M. m. intermedia*; 3, *M. m. megalophylla*; 4, *M. m. tumidiceps*.

America were: length of forearm, 54.5; zygomatic breadth, 9.5; rostral breadth, 7.4; length of maxillary toothrow, 7.9; condylobasal length, 14.1; depth of cranium, 9.7; for 21 specimens of *M. m. intermedia* from 3 localities in the Netherlands Antilles, length of forearm, 52.1; zygomatic breadth, 9.3; rostral breadth, 7.5; length of maxillary toothrow, 7.7; condylobasal length, 13.5; depth of cranium, 9.7; for 45 specimens of *M. m. tumidiceps* from four localities in northern South America, length of forearm, 56.1; zygomatic breadth, 9.6; rostral breadth, 7.6; length of maxillary toothrow, 7.9; condylobasal length, 14.1; depth of cranium, 10.1; and for 22 specimens of *M. m. carteri* from one locality in Ecuador, length of forearm, 58.8; zygomatic breadth, 10.1; rostral breadth, 7.9; length of maxillary toothrow, 8.3; condylobasal length, 14.7; and depth of cranium, 10.3 (Fig. 2; Smith, 1972).

There is little geographic variation among North American populations of *M. m. megalophylla* but more variation and slightly greater overall size in the extreme southern (Honduras) part of the range. Individuals of *M. megalophylla* from populations in South America averaged larger and had a less flattened braincase than those from Mexico and northern Middle America. Individuals from South America have pelage of a deep cinnamon red color with an iridescent, purplish frost over the back and rump, a pinkish or reddish pelage on the ventral surface, and a white or pinkish, fan-shaped cape over the shoulders, formed by relatively long stiff hairs. This cape and the rich cinnamon red coloration are absent in individuals from North America. Overall size of *M. megalophylla* increases gradually eastward along the Caribbean coast of South America. However, *M. m. intermedia* in the Netherlands Antilles is smaller and paler than *M. m. tumidiceps* on the adjacent mainland; the smallest and palest populations of *M. m. intermedia* are found on Curaçao and Bonaire. *M. m. carteri* from Ecuador has the largest external and cranial dimensions of the species (Smith, 1972).

DISTRIBUTION. *Mormoops megalophylla* inhabits humid, semi-arid, and arid regions below 3,000 m elevation from southwestern Texas and southern Arizona southward through Baja California and mainland Mexico into eastern Honduras and El Salvador (Fig. 3). There are no records of *M. megalophylla* from Nicaragua, Costa Rica, or Panama. Records resume in South America along the Caribbean Coast of Colombia and Venezuela, the Netherlands Antilles and Trinidad, and the Pacific coasts of Colombia, Ecuador (Smith, 1972), and northern Peru (Graham and Barkley, 1984).

FOSSIL RECORD. The fossil record indicates this species once

had a broader range than at present. Ray et al. (1963) found remains in Pleistocene deposits in Florida (T. 20 S., R. 28 E., Sect. 15, Rock Springs, Orange County, Florida). The time was estimated to be the late Pleistocene (Pamlico or post Pamlico). *M. megalophylla* remains were discovered in Central Cuba in guano deposits of Masones Cave and Jaguey Cave. The fossils probably are late Pleistocene in age (Silva Taboada, 1974). Pleistocene fossils of this species also occur on the islands of Hispaniola, Jamaica, Andros (Bahamas), Aruba, Curaçao, Margarita, Tobago, and Trinidad (Eshelman and Morgan, 1985; Koopman, 1958; Morgan, 1989, 1991; Morgan and Woods, 1986).

FORM AND FUNCTION. The hairs are long and lax, with sennate terminal scales and hestate scales throughout the remainder of the hair. Zones of pigmentation occur from tip to base as follows: 1) palest and shortest; 2) darkest, and usually intermediate in length to zones 1 and 3; X) a zone possibly produced by a blending of zones 2 and 3 that varies greatly in length and usually is not evident in fresh pelages; 3) the longest zone, paler than zones 2 and 4 but darker than zone 1; 4) usually the same length and color as zone 2, but occasionally paler (Constantine, 1958). As the pelage ages the second zone gains a reddish tinge which makes the entire animal appear reddish (Smith, 1972). The pelage fades in adults, and patches of different hues occur on the body (Constantine, 1958). Molting occurs from June through September (Smith, 1972), beginning dorsally in patches on shoulders and sides and expanding over the back of the animal. Ventrally, the molt begins under the wings and on the chin and neck, spreading across the abdomen and joining the areas on the chin and neck (Constantine, 1958).

Mormoops megalophylla does not have a well-developed nose leaf like that found in the closely related family Phyllostomatidae, but instead has wart-like protuberances (Smith, 1972; Fig. 1*b*). The lips and chin have leaflike appendages, giving rise to one vernacular name used for this bat (leaf-chinned bat). The facial excrescences are composed of thick dermis, muscle fibers, and small scattered groups of sebaceous glandular cells. Sudoriferous glands are absent from the face. The skin surrounding the upper and lower jaws has heavy concentrations of sebaceous glands. The sublingual glands are composed of mucous cells and the submaxillary gland of serous cells (Dalquest and Werner, 1954). The tragus is the most complex found in mormoopid bats, having a large secondary fold of skin at right angles to the longitudinal axis, and a heavily swollen cranial edge (Smith, 1972).

The dental formula is i 2/2, c 1/1, p 2/3, m 3/3, total 34. The upper molars are unmodified dilambdodont, and the last upper premolars are slightly molariform (Smith, 1972). Cases of dentinogenesis imperfecta, a disease affecting formation of the dentin layers and the durability of the teeth, have been noted (Smith, 1972).

The distal articular surface of the humerus is offset from the centerline of the bone in this genus, with *M. megalophylla* having the least amount of offset (Vaughan and Bateman, 1970). This surface is large with a large spinous process (Smith, 1972; Vaughan and Bateman, 1970). The radius is strongly curved. The ulna does not articulate with the humerus and is small, represented by little more than an olecranon process. The elbow functions as a hinge joint with little lateral movement and the pisiform probably acts as a brace for the fifth digit during flight (Smith, 1972; Vaughan and Bateman, 1970).

Mormoops megalophylla can maintain a high constant body temperature over the range of ambient temperatures normally encountered in roost and foraging habitats (Bonaccorso et al., 1992). Ghost-faced bats are able to maintain normal body temperatures for 1.5–2 h in ambient temperatures of 10°C but suffer severe hypothermia when exposed to such temperatures for >2 h. Individuals of body mass ≥16.5 g are more efficient in maintaining body temperature in moderate ambient temperatures than are individuals below this body mass. Body temperature is efficiently maintained <40°C in ambient temperatures of ≥38°C, probably by evaporative water loss (Bonaccorso et al., 1992).

Body temperature of ghost-faced bats is 36.9 ± 1.1°C with a lower critical body temperature of 33.5°C. The basal metabolic rate (BMR) for males is 1.62 ± 0.10 ml O_2 g^{-1} h^{-1} and for females is 1.34 ± 0.17 ml O_2 g^{-1} h^{-1}. The rate of metabolism increases linearly as ambient temperature decreases from thermoneutrality. Minimum thermal conductance is 0.30 ± 0.05 ml O_2 g^{-1} h^{-1} °C^{-1} and is not a function of ambient temperature below thermoneutrality (Bonaccorso et al., 1992).

ONTOGENY AND REPRODUCTION. Pregnant females carrying a single embryo have been collected from February (Campeche, Mexico) through June (Santa Cruz Co., Arizona—Barbour and Davis, 1969; Beatty, 1955; Jones et al., 1973; Nowak, 1991). Lactating females were observed from June through August (Nowak, 1991). Embryos removed from females collected in Mexico in March measured 18 mm, and in May measured 23 mm (Barbour and Davis, 1969).

ECOLOGY. Stomach and intestinal contents collected from four individuals of *M. megalophylla* suggest this species feeds exclusively on large-bodied moths (Easterla and Whitaker, 1972). *M. megalophylla* inhabits mixed boreal-tropical forests (the transitional zone between pine-oak forest and tropical deciduous forest between approximately 1,475 to 2,185 m elevation—Bateman and Vaughan, 1974; Webb and Baker, 1962), tropical rain forests (Sanchez-Herrera et al., 1986), and riparian areas with mature cottonwood, sycamore, and willow in oak-woodland habitat (Beatty, 1955). In Peru, the ghost-faced bat is found in arid coastal regions with rock outcrops containing caves or abandoned mine shafts suitable as roosting sites, in stands of *Acacia* and *Prosopis*, in orchards, and in large patches of *Acacia* forest in irrigated mountain areas (Graham and Barkley, 1984).

Chiropterans found in habitats with *M. megalophylla* vary by location within the range. Such associates reported from the southwestern USA are *Tadarida brasiliensis* (Jameson, 1959), *Tadarida mexicana, Myotis evotis, M. velifer, Eptesicus fuscus, Antrozous pallidus, Lasiurus borealis* (Beatty, 1955; Raun and Baker, 1958), *Euderma maculatum, Leptonycteris nivalis, Myotis californicus, Pipistrellus hesperus,* and *Plecotus townsendi* (Easterla, 1970). In Mexico, associates include *Pteronotus parnellii, Sturnira lilium, Uroderma bilobatum, Carollia brevicauda,* and *Tonatia brasiliensis* from Quintano Roo (Sanchez-Herrera et al., 1986); *Glossophaga commissarisi, Sturnira lilium, Artibeus aztecus, A. jamaicensis,* and *Eptesicus fuscus* from Durango (Webb and Baker, 1962); and *Pteronotus parnellii, P. personatus,* and *P. davyi,* which form an ecologically unified group (small, insectivorous bats which are colonial and cave-dwelling) with *M. megalophylla* in the state of Sinaloa (Bateman and Vaughan, 1974). Chiropteran associates from Peru and Venezuela are *Pteronotus davyi, Phyllostomus discolor, Nyctinomops macrotis, N. laticaudatus, Eumops glaucinus,* and *Leptonycteris curasoae* (Bonaccorso et al., 1992; Graham and Barkley, 1984). Of these associates *T. brasiliensis, M. velifer, P. parnellii, P. personatus, P. davyi,* and *L. curasoae* are known to share roosting caves with *M. megalophylla* (Bonaccorso et al., 1992; Graham and Barkley, 1984; Raun and Baker, 1958).

Internal parasites of *M. megalophylla* include *Plagiorchis* spp. (Trematoda) in the lower small intestine, and an unidentified species of nematode in the stomach and upper small intestine (Jameson, 1959). Ectoparasites include *Whartonia guerrerensis* and *Perissopalla lipoglena* (Acarina, Trombiculidae) on specimens from the Yucatán Peninsula (Loomis, 1969), *Periglischrus strandtmanni* on the wings, and *Trombicula* spp. on the wings and interfemoral membranes of bats collected from Frio Cave, Uvalde County, Texas (Jameson, 1959). *M. megalophylla* also is parasitized by two species of streblid flies, *Nycterophilia mormoopsis* and *Trichobius leionotus* (Whittaker and Easterla, 1975; Whitaker et al., 1987). Colonies of *M. megalophylla* in Mexico are known to suffer from epidemics of rabies that may be cyclic (Jimenez Guzman, 1982). Rabies may also be the cause of mass mortality in colonies inhabited by *M. megalophylla* (Villa-R., 1955; Villa-R. and Jimenez, 1960).

BEHAVIOR. The ghost-faced bat spends the day in caves or abandoned mine shafts and emerges soon after dark, flying in dense, fast-moving formations. Once out of the roost, individuals fly quickly to foraging sites along arroyos and canyons (Bateman and Vaughan, 1974). These bats are strong, fast flyers that travel at relatively high altitudes enroute to and from foraging sites (Bateman and Vaughan, 1974). Foraging sometimes occurs over standing water (Beatty, 1955; Graham and Barkley, 1984). Colonies may contain 500,000 individuals (Barbour and Davis, 1969) and are spatially isolated from colonies of other species of bats roosting in the same caves (Raun and Baker, 1958). Conspecific individuals maintain a distance of approximately 15 cm from each other (Raun and Baker, 1958). Individuals begin to return approximately 7 h after first leaving roosts (Bateman and Vaughan, 1974).

Males and non-reproducing females use caves separate from those

used by nursing females (Bonaccorso et al., 1992). In Falcon state, Venezuela, males form bachelor colonies in areas of caves having ambient temperatures of 30.6–30.8°C. Non-reproductive females use interior chambers with a temperature of 33.4–34.2°C, often roosting in nurseries of *Leptonycteris curasoae*. Nursing *M. megalophylla* roost in areas which minimize ventilation and maximize retention of heat obtained from their metabolism and from organic reactions occurring in the guano. These sites are usually the deepest and warmest (36°C) areas of occupied caves (Bonaccorso et al., 1992).

GENETICS. The karyotype of *Mormoops megalophylla* includes 11 pairs of metacentric chromosomes, 1 pair of submetacentrics, and 6 acrocentric pairs. The ghost-faced bat has an autosomal diploid number of 38 and a fundamental number of 62 (Baker and Hsu, 1970). Acrocentric chromosomes have nucleolar organizer regions in the centromeres (Sites et al., 1981).

REMARKS. Leach (1821*a*) established two new genera, *Aëllo* (type species *Aëllo cuvieri*) and *Mormoops* (type species *Mormoops blainvillii*) in 1821. Both genera were described as monotypic. After examining the type specimens, Dobson (1878) concluded that both names applied to the same species. The name *Aëllo* was rejected because its definition is incorrect; the type specimen has lost all traces of cutaneous processes, and the number of teeth was incorrectly given. The name *Mormoops* was accepted because it has the advantage of correct definition even though *Aëllo* has page priority. Rehn (1902) supported this opinion in his revision of the genus *Mormoops*.

The Rules of Zoological Nomenclature adopted by the Berlin Congress in 1901, but not published until after Rehn published his revision, gave official recognition to the Principle of First Reviser. Under this provision the first author to publish a revision has the authority to determine relative priority accorded to subjective synonyms published in the same work on the same date. Morrison-Scott (1955) believed the works of Dobson, Rehn, and others were of sufficient precision to secure effective priority of *Mormoops* over *Aëllo*. The Principle of First Reviser was replaced by the Principle of Page and Line Precedence by the Thirteenth International Congress of Zoology in 1948. Although this likely would have made *Aëllo* the official generic name, no author used *Aëllo* from 1948 to 1953, when the Principle of First Reviser was reinstated by the Fourteenth International Congress of Zoology (Morrison-Scott, 1955).

Dobson, Rehn, or the others mentioned by Morrison-Scott (1955) may not have met completely the provisions of First Reviser for this genus. The long uninterrupted use of *Mormoops* could be considered sufficient grounds to suppress the use of *Aëllo* (Morrison-Scott, 1955). Morrison-Scott (1955) petitioned the International Commission of Zoological Nomenclature to recognize Dobson as the first reviser of this genus, to place the name *Mormoops* on the Official List of Generic Names in Zoology, and to suppress the name *Aëllo* and the species name *Aëllo cuvieri* in favor of *Mormoops* and *Mormoops blainvillii*. *Aëllo* could only be suppressed by use of the Commission's Plenary Powers because this case involved subjective synonyms (Morrison-Scott, 1955). Opinion 462 of the International Commission of Zoological Nomenclature (International Commission of Zoological Nomenclature, 1957) officially recognized the generic name of *Mormoops* and the specific epithet *Mormoops blainvillii*. Hall (1981) ignored the Commission's opinion and the repeated use of the word *Mormoops* by modern authors and used *Aëllo* instead. Hall's use probably should not be followed. The vernacular names of leaf-chinned bat and old man bat have been used for this species. The generic name *Mormoops* is from the Greek *mormo* meaning a bugbear. The specific name *megalophylla* is from the Greek *megas* meaning great and *phyllon* meaning leaf (Jaeger, 1955).

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