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Mesophylla macconnelli.

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Mesophylla Thomas, 1901

Mesophylla Thomas, 1901:1943. Type locality "Kanuku Mountains, British Guiana."

CONTENT AND CONTEXT. Order Chiroptera, Family Phyllostomidae, Subfamily Stenodermatinae. Tribe Stenodermatini. *Mesophylla* is recognized here as having full generic status (Gardner, 1977; Greenbaum et al., 1975; Jones and Carter, 1979; Starrett and Casebeer, 1968; Thomas, 1901), not as a subgenus of *Ectophylla* (Goodwin and Greenhall, 1962) or as a member of the genus *Vampyressa* (Owen, 1987). The genus is monospecific.

Mesophylla macconnelli Thomas, 1901

Little Yellow-faced Bat

Mesophylla macconnelli Thomas, 1901:145. See above. First use of current name.

Ectophylla macconnelli Goodwin and Greenhall, 1962:2. Holotype. Type locality "Talpara, Trinidad."

Mesophylla macconnelli Starrett and Casebeer, 1968:14. (*E. macconnelli* Goodwin and Greenhall, a synonym.)

Vampyressa macconnelli Owen, 1987:46. (*M. macconnelli* Thomas, a synonym.)

CONTENT AND CONTEXT. Context same as for genus. Two subspecies of *Mesophylla macconnelli* are described; their distributional status remains unclear (Anderson et al., 1982; Koopman, 1978; Webster and Jones, 1980).

M. m. macconnelli Thomas, 1901:145, see above.
M. m. flavescens Goodwin and Greenhall, 1962:2, see above.

DIAGNOSIS. *Mesophylla macconnelli* is distinguished from *Ectophylla* and *Vampyrops* in tooth proportions, especially the m2 (which is rounded and basin-shaped), and the presence of m3. It also differs from *Ectophylla* by its slightly larger size and the presence of a minute secondary leaflet behind the muzzle. It differs from *Vampyrops* in having a smaller, triangular-shaped m1. The skull of *M. macconnelli* shows more similarity to *Vampyressa pusilla* than to *E. alba* (Starrett and Casebeer, 1968; Thomas, 1901).

GENERAL CHARACTERS. The little yellow-faced bat, *M. macconnelli*, is a small stenodermatine with a simple, non-crenulated, medium-size noseleaf (Fig. 1). The tragus is pointed with two projecting lobules on its external border and a thickened projection in front of the tragus. There is a supplementary lobule on the antitragus. The ears and noseleaf are light buff in color and the flight membrane is mummy brown. The dorsal fur is thick and darkens from an anterior dull brownish-white to wood brown, posteriorly; the underparts are uniformly buffy-gray. Each patagium extends to the distal end of the metatarsus where it is supported by a short, recurved calcar. Scattered hairs extend over the basal half of the forearms and femora and the wing membranes between them (Thomas, 1901). *M. m. flavescens* is distinguished from *M. m. macconnelli* by its larger size; pale grayish-buff pelage and a bright-yellow noseleaf, ears, and second and third metacarpals. *M. m. flavescens* is larger and grayer in color, with a larger skull, longer rostrum, larger teeth (especially the m2 and pm2), flatter braincase, and a greater ratio in the length of skull to braincase (Goodwin and Greenhall, 1962).

The skull of *M. macconnelli* is relatively small and fragile (Fig. 2). The dental formula is i 2/2, c 1/1, p 2/2, m 2/3, total 30. The molars are "very peculiar," with the anterior one being much smaller and more triangular than the posterior one; m2 is longer than m1, oval in section, pointed anteriorly, lacks interior basal cusps, and is broadly basin-shaped (Thomas, 1901:144). *M. macconnelli* also has a small third molar in the lower jaw. The upper canines of *M. m. flavescens* lack a small posterior cusp near the tip, which is usually present in *M. m. macconnelli* (Goodwin and Greenhall, 1962).

Ranges (in mm) of representative external and cranial measurements are: length of head and body, 45–49; length of ear from notch, 9.5–13.5; length of forearm, 29.5–34.0; greatest length of skull, 16.8–19.0; zygomatic breadth, 9.2–11.0; interorbital breadth, 4.0–4.9; palatal breadth, 6.6–7.9; mastoid breadth, 8.4–9.1; breadth of braincase, 6.8–8.3; depth of braincase, 8.4–8.5; length of maxillary tooth row, 5.5–6.6; and body mass 6.5 g (Cunha Vierra, 1942; Goodwin and Greenhall, 1962, 1964; Lima, 1926; Sanborn, 1951; Starrett and Casebeer, 1968; Swanepoel and Genoways, 1979; Thomas, 1901; Williams and Genoways, 1980).

DISTRIBUTION. *Mesophylla macconnelli* is known from Bolivia, Brazil, Colombia, Ecuador, Guyana, French Guyana, Panama, Peru, Surinam, Trinidad, and Venezuela (Fig. 3). Specimens from Trinidad are *M. m. flavescens* (Goodwin and Greenhall, 1962). Peruvian lowland specimens (elevations <1,000) are referable to *M. m. macconnelli* and those taken at higher elevations (1,270–1,570 m) to *M. m. flavescens* (Koopman, 1978). All specimens from Bolivia are considered to be the nominate form (Anderson et al., 1982; Webster and Jones, 1980).

FORM AND FUNCTION. There is no significant relationship between forearm length, head-plus-body length, and cube root of body mass in *M. macconnelli* (Ralls et al., 1982). These authors concluded that unless these variables were highly correlated they could be used as independent variables when making intraspecific comparisons.

The palatal ridges of *M. macconnelli* are strikingly different from other phyllostomids to which they have been compared (e.g., *Uroderma, Artibeus, Sturnira, Rhinophylla, Carollia*). The ridges on the palatal bone of *M. macconnelli* are remarkably porous with many minute vacuities (Thomas, 1901). Between these ridges the palatal surface is smooth posteriorly; the anterior surface between the canines and incisors is irregular and rugose. The posterior margin of the anterior palatal areas covers the large palatine foramina forming a false ridge. The functional significance of palatal ridges is unknown, although they are probably important in food mastication and pellet formation. The presence of 15–16 transverse, denticu-

FIG. 1. Adult female *Mesophylla macconnelli flavescens* from the Aripo Savannas Scientific Reserve, Trinidad.

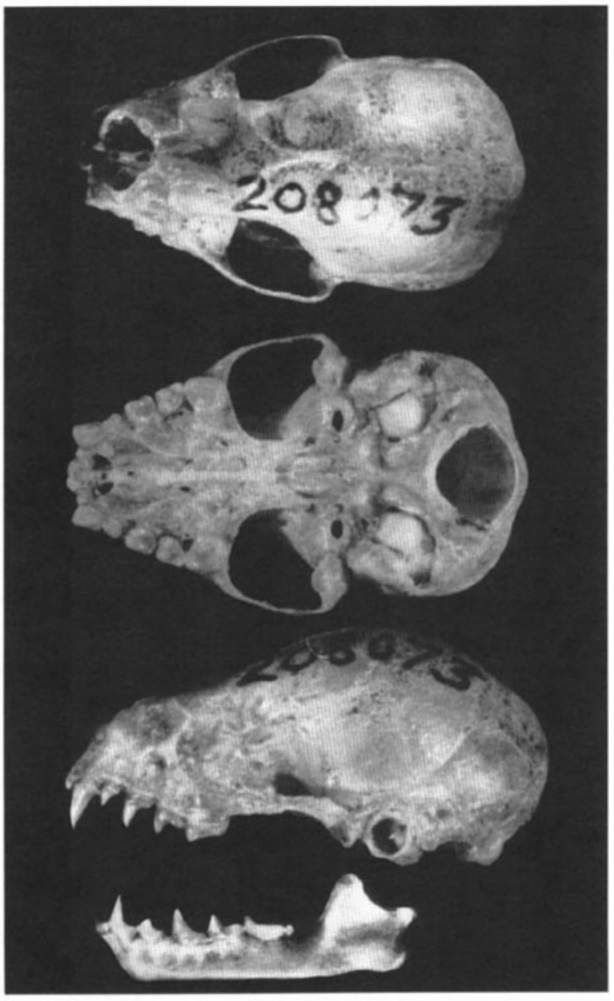

FIG. 2. Dorsal, ventral, and lateral views of the cranium and lateral view of the mandible of *Mesophylla macconnelli macconnelli* from Peru (male, American Museum of Natural History 208073). Greatest length of skull is 17.7 mm.

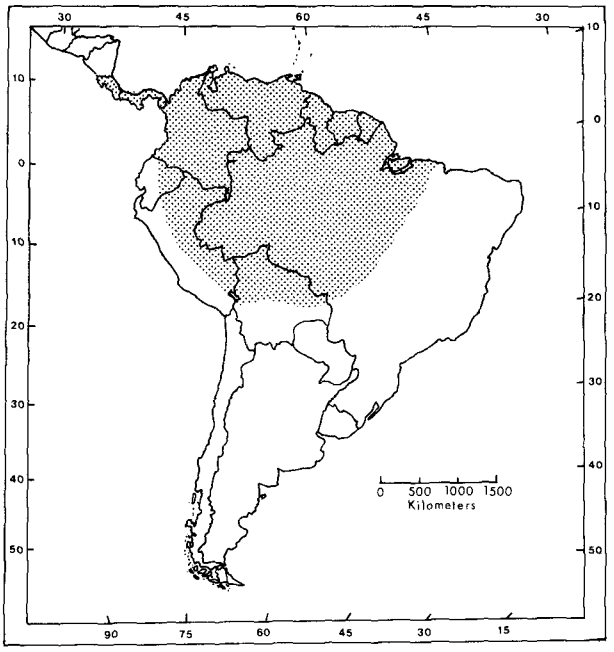

FIG. 3. Map of Central and South America showing the distribution of *Mesophylla macconnelli* Thomas (1901).

lated, and undivided ridges, each with regular minute trianglar projections are directed toward the anterior margin (Harrison and Horne, 1971).

The gross morphology of the brain in *M. macconnelli* is similar to that of *A. phaeotis*. The cerebral hemispheres are deep and relatively smooth. The major sulci are well developed and the prepseudocentral gyrus protrudes dorsally. The pseudotemporal lobes are angular and protrude ventrally. The inferior colliculi are exposed dorsally and the cerebellum is simple and crested (McDaniel, 1976). The brain mass and encephalization index for *M. macconnelli* are 345 and 238 mg, respectively (Stephan, 1977; Pirlot and Pottier, 1977; Pirlot and Stephan, 1970; Stephan and Pirlot, 1970; Stephan et al., 1981).

The main olfactory bulb (MOB) is 2.2 mm long and 1.4 mm wide (Frahm and Bhatnagar, 1980). The accessory olfactory bulb (AOB) is round and is located anterior to the MOB. The vomeronasal nerve enters the AOB posteriorly. The AOB has well-circumscribed glomeruli, numerous mitral cells, and many internal granuli cells. The pars distalis of the lateral olfactory tract is formed rostrally. The AOB has a volume of 0.1124% and is moderately developed as compared to other phyllostomids. The ratio of the MOB to the AOB = 0.98, approaches the average for Chiroptera (Frahm, 1981). The structure of the AOB of bats does not appear to differ in significant detail from other mammals. The occurrence of a well-formed vomeronasal system in *M. macconnelli* points to its primary functional role in feeding, as is the case for other fruit- and nectar-eating phyllostomids (Frahm and Bhatnagar, 1980).

The sperm head of *M. macconnelli* is small and relatively long and narrow (Forman and Genoways, 1979). The acrosome has a pointed, asymmetrical apex. The tip of the apex is on the same side of the head as the midpiece and is the most notable characteristic of the sperm. An extremely small portion of the short acrosome is located anterior to the apex of the nucleus. The posterior limit of the acrosome is slightly anterior to the mid-point of the nucleus. The acrosome is considerably shorter (often slightly more than half its length) but has the same breadth as the nucleus at its posterior limit. The base of the head is flattened with a slight concavity; it is narrower than its girth and it is asymmetrical, with the corner nearest the midpiece more pointed than the other. The nucleus is ovoid.

Measurements (μm) of the sperm from both sides (mean ± *SD* and range) are: length of head, 4.71 ± 0.14 (4.56–5.02), 4.68 ± 0.19 (4.28–4.93); length of acrosome, 2.73 ± 0.12 (2.51–2.88), 2.64 ± 0.13 (2.51–2.88); length of nucleus, 4.01 ± 0.15 (3.62–4.19), 3.99 ± 0.22 (3.81–4.37); and width of head, 3.13 ± 0.12 (2.98–3.34), 3.23 ± 0.10 (3.07–43.44). The neck is relatively long and the junction with the head is well off center and near the pointed border of the head. Except for *Centurio*, an extremely short midpiece distinguishes the sperm of *M. macconnelli* from other stenodermatines. The midpiece is short, broad anteriorly, and tapers abruptly posteriorly. The length of the midpiece is 7.61 ± 0.23 (7.25–7.92), 7.66 ± 0.27 (7.25–8.18) μm. The junction of the midpiece with the tail is indistinct (Forman and Genoways, 1979).

REPRODUCTION. *Mesophylla macconnelli* appears to be seasonally polyestrous, as has been reported for other stenodermatines (Wilson, 1973, 1979). Pregnant females have been reported from Colombia in January (Thomas, 1972); from Peru in May (Graham, 1987), July (Jones and Carter, 1979), and August (Koopman, 1978; Tuttle, 1970); from Bolivia in July (Webster and Jones, 1984); and from Trinidad in August (Carter et al., 1981). Pregnant females are known from Venezuela in January, February, and March; from Colombia in January; from Panama in March; and from Brazil in April and August. Lactating females are known from Ecuador in June (Webster and Jones, 1984); from Trinidad in August (Jones and Carter, 1979); from Peru in June, July, August, and October; and from Peru (Koepcke, 1984) and Surinam (Williams and Genoways, 1980) in September.

As in other phyllostomids, litter size in *M. macconnelli* is one. Juvenile bats were collected from Venezuela in June. Adult males with enlarged testes have been reported from Trinidad in July and August (Carter et al., 1981).

ECOLOGY AND BEHAVIOR. *Mesophylla macconnelli* has been observed or collected in lowland habitat, open clearings, and dense forested areas in Peru (Graham, 1987; Koopman, 1978); from lowland rainforests of Guyana (Genoways et al., 1981); in

humid forests in Bolivia (Cuervo-Diaz et al., 1986); near streams and other moist areas in evergreen forests of Venezuela (Handley, 1976); and in the dry llanos region of Venezuela (Ochoa and Ibanez, 1985). The general habitat from which specimens were captured in Venezuela (Handley, 1976) is tropical moist forest (after Holdridge, 1947) or tropical humid forest (Ewel and Madriz, 1968), ranging from 24 to 1,032 m, although 97% of all captured bats were taken at elevations below 152 m. *M. macconnelli* occurs in four of nine faunal provinces in South America, including the Amazon Basin, eastern slopes of the Andes, northern coasts and islands, and Middle America (Koopman, 1982).

Observations that *M. macconnelli* roosts "in leaves" (Sanborn, 1951:11), including *Anthurium jenmanni* (=*huegelli*; Goodwin and Greenhall, 1962) supports the findings that this bat makes tents (Koepcke, 1984). *M. macconnelli* most commonly makes tents by modifying palm leaves of *Geonoma* (Palmae) and succulent leaves of *Anthurium*, an epiphyte in the humid forests of Peru. Tents are constructed from the bifid leaves of *Geonoma* when bats sever the veins and plications at an acute angle on both lobes, terminating a few centimeters from the midrib. This causes a normally upward-growing frond to bend downward. One-half of the leaf folds on top of the other, forming an apical-shaped tent beneath which the bats roost. Bats normally hang onto the shaft of the leaf although claw marks evident on the leaf tissue indicate that bats also suspend themselves from other parts of the leaf. Small groups of 2–3 individuals alternate between nearby tents over a period of several months (Koepcke, 1984).

The use of the succulent arrowhead-shaped leaves of *Anthurium* sp. (which commonly grows along forest streams) for tent-making by *M. macconnelli* (Koepcke, 1984) is consistent with observations in Venezuela that this bat is most commonly captured near streams in humid forests (Handley, 1976). Tents appear to be formed in *Anthurium* when bats chew the basal veins of the leaf on either side of the midrib, causing the lobes to fold downward, forming an apical-shaped tent. Bats hang from the protruding ribs on the underside of the leaf. Groups ranging from 3 to 8 individuals, including lactating females and nursing young, have been observed in these tents (Goodwin and Greenhall, 1962; Koepcke, 1984). The habit of roosting beneath leaves, combined with a light-colored fur, may offer *M. macconnelli* protection from visually-oriented predators (Koepcke, 1984).

Nursing females use single shelters until young bats approach maturity; at other times females change shelters every few days (Koepcke, 1984). A shelter may be used by *M. macconnelli* for 4–5 months, after which the leaves and fronds begin to desiccate and disintegrate (Koepcke, 1984). Alternate use of several shelters appears to be a common behavior among some of the tent-making stenodermatines (Kunz, 1982; Timm, 1987). The diet of *M. macconnelli* consists mainly of fruit. Fecal samples analyzed from seven specimens taken in French Guyana indicated that most had eaten fruit although one had eaten pollen (Charles-Dominique, 1986).

Ectoparasites collected from *M. macconnelli* include two species of spinturnicid mites, *Peiglischrus iheringi* and *P. torrealbia* (Herrin and Tipton, 1975) and a streblid fly, *Neotrichobius ectophyllae* (Wetzel, 1976). Positive fungal cultures, representing two undescribed species, were isolated from the liver, spleen, and lungs from two of 29 specimens of *M. macconnelli* captured in Columbia (Mok et al., 1982).

GENETICS. *Mesophylla macconnelli* has a diploid number of 21 chromosomes for males and 22 chromosomes for females and a fundamental number of 22 (Baker and Hsu, 1970; Baker, 1979). All chromosomes are either acrocentric or nearly acrocentric (Hsu and Benirschke, 1971). The sex chromosome system is XX/XO and the XO condition for males may reflect the fact that the Y is present but is translocated to an autosome (Baker and Hsu, 1970). Baker and Hsu (1970) proposed that material from the Y chromosome was hidden in the males and that these genes may become inactivated during development. *M. macconnelli* shares this unusual sex chromosome condition and uniarmed autosomes with *Vampyressa pusilla* (Gardner, 1977). *Ectophylla*, which had been considered to be the authoritative genus for *macconnelli* (Goodwin and Greenhall, 1962), has a distinctly different karyotype (2n = 30, FN = 56) and an XX/XY sex-determining system (Greenbaum et al., 1975).

REMARKS. The taxonomic status of *Mesophylla macconnelli* has been an enigma. When Thomas (1901) first described this bat as *Mesophylla macconnelli*, he noted that it seemed to conform to the characteristics of *Ectophylla*. Upon further examination he found differences in the numbers and proportions of teeth that ultimately led him to assign it to a distinct genus. Thomas (1901: 144) noted that *Mesophylla* seemed to be a "modification of *Vampyrops* in the direction of *Ectophylla*." Goodwin and Greenhall (1962) acknowledged that there were differences between *E. alba* and *M. macconnelli* and, although both were so similar in all other morphological characters, they concluded that *Mesophylla* should be designated as a subgenus of *Ectophylla*. Others have considered *M. macconnelli* to be monotypic (Handley, 1966) and distinct from *Ectophylla* (Starrett and Casebeer, 1968).

Opposing views on the generic status of *macconnelli* launched a series of investigations in an effort to differentiate these and allied taxa. The sex chromosomes were considered to be uncommon for the family and not present in *Ectophylla* (Baker and Hsu, 1970). The palatal ridges of *M. macconnelli* differ strikingly from other phyllostomids (Harrison and Horne, 1971). Based on the arrangement of palatal ridges, *Ectophylla* was judged not to be related to *Mesophylla* (Peterson, 1971). Based on analyses of chromosomal data, *Mesophylla* was judged to be more closely related to *Vampyressa pusilla* than to other species of *Vampyressa* (Baker et al., 1973), which led to the suggestion that *Vampyressa* and *Mesophylla* formed an evolutionary line within the Stenodermatinae (Greenbaum et al., 1975). Smith's (1976) phylogenetic analysis showed *Mesophylla* and *Ectophylla* as sister taxa, placing *Vampyressa* in a separate clade with *Vampyrops* and *Vampyrodes*.

Reevaluation of chromosomal variation in *Vampyressa* (Gardner, 1977) led to the conclusion that primitive diploid numbers were the smaller and not the larger ones as postulated by Greenbaum et al. (1975). Alternatively, Gardner (1977) proposed that the model for chromosomal evolution in the Phyllostomidae would work better if the primitive diploid number was smaller, requiring fewer steps (inversions or fusions) to derive the larger diploid numbers.

Using continuous and discrete morphological data from 64 taxa of the Stenodermatinae, Owen (1987) derived ancestral relationships using Wagner tree and WISS (Weighted Invariant Step Strategy) analysis to isolate clades within this family. His analyses placed *Mesophylla* in a natural assemblage with *Vampyresa melissa*, *V. bidens*, and *Vampyrops-Vampyrodes*. From this he suggested that *Mesophylla* be placed in synonymy under *Vampyressa*, with the proper name being *Vampyressa macconnelli*. Using principal components and cluster analyses, Owen (1988) subsequently demonstrated that *Vampyressa* (=*Mesophylla*) *macconnelli* was most similar to *E. alba*.

The generic name *Mesophylla* is of Greek origin, derived from the word *mesos*, meaning middle, and *phyllon*, meaning leaf. The specific name *macconnelli* is in honor of the naturalist who supported the expedition when the type specimen was discovered (Palmer, 1904).

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