MAMMALIAN SPECIES No. 279, pp. 1-4, 4 figs.

Uroderma bilobatum. By Robert J. Baker and Cora L. Clark

Published 27 February 1987 by The American Society of Mammalogists

Uroderma bilobatum Peters, 1866

Peters' Tent-making Bat

Uroderma bilobatum Peters, 1866:394. Type locality Sao Paulo, Brazil.

Uroderma convexum Lyon, 1902:83. Type locality Colon, Panama.

CONTEXT AND CONTEXT. Order Chiroptera, family Pyllostomidae, subfamily Stenodermatinae. The genus *Uroderma* has two species (Davis, 1968), *Uroderma bilobatum* and *U. magnirostrum*. Six subspecies of *bilobatum* are recognized (Baker and McDaniel, 1972; Davis, 1968) as follows:

- U. b. bilobatum Peters, 1866:394. See above.
- U. b. trinitatum Davis, 1968:690. Type locality Caroni County, Trinidad.
- U. b. thomasi Andersen, 1908:390. Type locality Bellavista, Departmento de Beni, Bolivia.
- U. b. convexum Lyon, 1902:83. See above.
- U. b. molaris Davis, 1968:696. Type locality Palenque, Chiapas, Mexico.
- U. b. davisi, Baker and McDaniel, 1972:1. Type locality La Paz, El Salvador.

DIAGNOSIS. Urodema bilobatum has bilobed upper medial incisors; a narrow white line on middle of upper back; a distinct white line above and below each eye (Fig. 1a); no external tail; hairless posterior border of uropatagium; dorsal profile of skull from crown to tip of snout usually markedly depressed in frontal region (Fig. 2); mesethmoid much less expanded laterally; and facial stripes more pronounced (Davis, 1968) in comparison with U. magnirostrum

GENERAL CHARACTERS. Geographic variation in *Uroderma bilobatum* was reviewed by Davis (1968) who recognized five subspecies based on cranial and pelage color variation. A sixth subspecies subsequently was described (Baker and McDaniel, 1972) based on chromosomal characters.

The skull (Fig. 2) and dentition of *U. bilobatum* was described by Miller (1907). The dental formula is i 2/2, c 1/1, p 2/2, m 3/3, total 32. The published records of cranial and forearm measurements were reviewed by Swanepoel and Genoways (1979). Selected average external and cranial measurements (Swanepoel and Genoways, 1979) for eight specimens (four males and four females) from Trinidad and Nicaragua are (in mm, extremes in parentheses): length of forearm, 41.7 (39.6 to 43.1), greatest length of skull, 23.5 (22.6 to 24.7), condylobasal length, 21.0 (19.9 to 21.6), zygomatic breadth, 12.9 (12.5 to 13.4), postorbital constriction, 5.4 (4.6 to 5.7), breadth of braincase, 9.6 (9.3 to 9.9), length of maxillary toothrow, 8.1 (7.8 to 8.6), breadth across upper molars, 9.4 (8.9 to 9.9).

The nose leaf is simple but well developed; the ears are rimmed with pale yellowish pigment; the eyes are large (Fig. 1a); a calcar is present; and the dactylopatagium minus is broad, slightly pigmented and permanently open (Miller, 1907).

DISTRIBUTION. Uroderma bilobatum (Figs. 3, 4) is known from the lowlands of tropical America from Oaxaca and Veracruz, Mexico, south to Peru, Bolivia, and southeastern Brazil (Davis, 1968). Most records are from below 600 m elevation, but specimens have been taken in Central America as high as 1,500 m, and the altitudinal record for South America is 1,800 m at Guayabamba, Peru (Davis, 1968).

FORM AND FUNCTION. Secondary sexual dimorphism was noted (Baker et al., 1972) in samples of U. b. davisi (2 of 25 characters: zygomatic breadth and breadth across canines) and U. b. molaris (8 of 25 characters: skull length, condylobasal length,

mandible length, occipitonasal length, depth of brain case, palatal length, zygorostral length, and breadth across canines). In all instances, males were larger than females.

The stomach and gut anatomy of U. bilobatum shares a suite of features characteristic of stenodermatines in general (Forman et al., 1979). The stomach of Uroderma is intermediate in form between Sturnira and Artibeus. The caecum is long and has a narrow apex (Forman et al., 1979). The anatomy of the gastric muscosa in Uroderma is different from that of Vampyressa, Vampyrops, Chiroderma, and Sturnira in that in Uroderma rugae are distributed diagonally only within the mid-region of the stomach, whereas in the other stenodermatine genera examined, these rugae are restricted to the caecum (Forman et al., 1979). Sperm morphology of U. bilobatum is similar to that of Artibeus jamaicensis (Forman and Genoways, 1979). The sperm head of U. bilobatum has an unusually short acrosome that covers an extremely small portion of the nucleus. The flattened base of the head with its pointed corners is unique among the stenodermatines examined (Forman and Genoways, 1979).

Internal and external brain anatomy of *U. bilobatum* is characteristic of stenodermatine species (McDaniel, 1976). The brain has a deep cerebrum with large pseudotemporal lobes that project ventrally but not to the extent observed in *Artibeus*. The sulci anterior to the pseudocentral sulci and the pseudocentral sulci are well developed. The inferior colliculi are not exposed dorsally and the vermiform body of the cerebellum forms a medial crest. At the

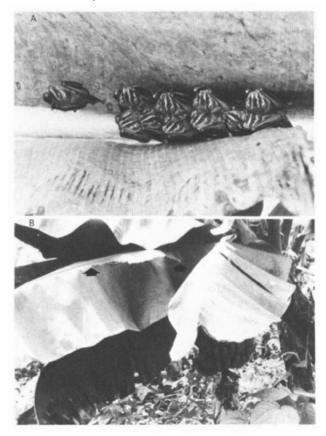


Fig. 1. Tent constructed by *Uroderma bilobatum* from a banana leaf; (a) tent occupied by 11 individuals, (b) line (between arrows) where bats have chewed veins in the leaf to make a more protective tent. Photographs taken at Cana, Panama by R. J. Baker.

2 MAMMALIAN SPECIES 279

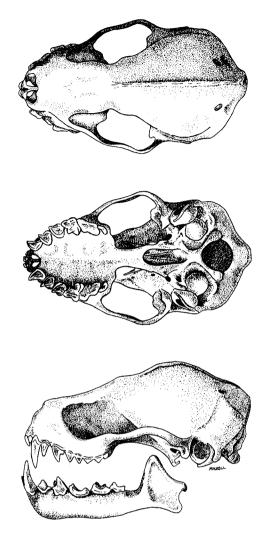


Fig. 2. Skull of *Uroderma bilobatum* (TTU 12628, male). Bar equals 10 mm. Drawing by Michael W. Nickell.

lateral edges of the vermiform body there are secondary foliations (McDaniel, 1976).

The uterus is simplex and is like other Stenodermatinae examined in being tubular in form (Hood and Smith, 1983). The oviducts contact and enter the uterine body near the midline of the fundus. *U. bilobatum* shares two unique anatomical features (orientation of oviductal entry into uterus and position of the ovarian ligament) with other Stenodermatinae (Hood and Smith, 1982).

The morphology of the wings of *U. bilobatum* are similar to that of species of *Chiroderma* and *Artibeus* (Smith and Starrett, 1979). No single feature of the wing elements in this species distinguishes it from other members of the subfamily.

FOSSIL RECORD. The only fossils of *U. bilobatum* on record are subRecent remains from Cueva de Quebrada Honda, Venezuela (Linares, 1968).

ONTOGENY AND REPRODUCTION. Wilson (1979) reviewed the literature on reproduction in *U. bilobatum*. Based on collections from Panama, Fleming et al. (1972) concluded that *U. bilobatum* has a reproductive cycle of bimodal polyestry, with young born in February and June. A single young is produced during each pregnancy. The spermatogenic cycle appears correlated with seasonal changes in female receptivity. Testes size is largest just preceding those times when females are sexually active (February–March and September–October). Extrapolating from these data, the gestation period probably would be 4 or 5 months. Females appear to have two young per year as individuals that were both lactating

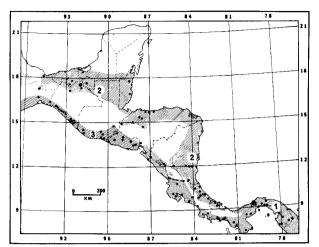


FIG. 3. Map showing distribution of *Uroderma bilobatum* in Middle America. (1) *U. b. convexum*, (2) *U. b. molaris*, (3) *U. b. davisi*. (Map modified from Davis, 1968).

and pregnant have been taken. There is some evidence that females have a postpartum estrus (Fleming et al., 1972).

In Panama, parturition was correlated with the wet and dry seasons and time of fruiting of plants. In samples from Guatemala, El Salvador, Honduras, and Nicaragua taken during the same year, there seemed to be a geographic variation in the timing of the reproductive cycles (Baker, 1981). In samples studied by Baker (1981), females were in relatively early stages of pregnancy in May and early June indicating that samples from northern Central America are not synchronized with those from Panama (Fleming et al., 1972). However, samples of 122 females from the Pacific versant of Central America support the conclusions of Fleming et al. (1972) that local populations are synchronized seasonally (Baker, 1981). Young bats become independent from females at about 1 month of age (Fleming et al., 1972).

ECOLOGY. Uroderma bilobatum is a fruit-eating bat with a local distribution strongly influenced by availability of tall-standing tropical vegetation (Baker, 1981; Greenbaum, 1981).

Gardner (1977) concluded that *U. bilobatum* primarily is frugivorous, but also may feed on pollen, nectar, and insects associated with flowers and fruit. Most reports of food habits for the species simply note that this bat eats fruit (Goodwin, 1946; Tamsitt and Valdivieso, 1965; Villa-R., 1967). Bloedel (1955) reported *U. bilobatum* to eat the pericarp of small unidentified palm fruits in Panama, de Carvalho (1961) recorded fruits of three species of figs (*Ficus*) as food items of the species in Brazil, and Goodwin and Greenhall (1961) found remains of *Psidium guajava* in two *U. bilobatum* in Trinidad. An analysis of contents of 320 stomachs of *U. bilobatum* collected from Costa Rica and Panama indicated a diet (percent of volume) of 76% plant material (unidentified), 13% insects, and 11% unclassified material (Fleming et al., 1972).

Endoparasites recorded from *U. bilobatum* include *Trypanosoma cruzi* and a *Trypanosoma cruzi*-like protozoan (Ubelaker et al., 1977). Ectoparasites include *Alabidocarpus nicaraguae*, *Amblyomma* sp., *Basilia constricta*, *B. myotis*, *Chirohynchobia urodermae*, *Eutrombicula batatas*, *Macronyssoides* sp., *Neotrichobius delicatus*, *Ornithodoros hasei*, *Parasecia manueli*, *Paratrichobius dunni*, *P. longicrus*, *Periglischrus iheringi*, *Phyllostomonyssus conradyunkeri*, *Tichobius costalimai*, *T. joblingi*, *T. keenani*, and *T. urodermae* (Webb and Loomis, 1977).

 $Uroderma\ bilobatum$ occurs over a wide geographic range and a list of species that have been taken in mist nets with $U.\ bilobatum$ is extremely long and, at this time, virtually nondefinitive. The long list of associated species does indicate diversity in the ecology of $U.\ bilobatum$.

BEHAVIOR. Uroderma bilobatum rests singly or in groups ranging from 2 to 59 (Kunz, 1982). The most striking aspect of the biology of the species is the self-directed behavior of colonies to produce "tents" (Fig. 1a, b) by modifying leaves (Barbour, 1932; Kunz, 1982). Tents are constructed by weakening or severing the structural veins of leaves by biting or chewing. Foster and Timm

MAMMALIAN SPECIES 279

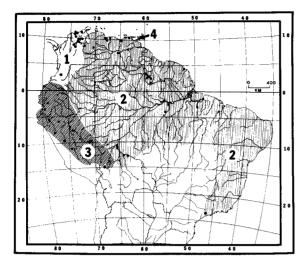


Fig. 4. Map showing the distribution of Uroderma bilobatum in South America. (1) U. b. convexum, (2) U. b. bilobatum, (3) U. b. thomasi, (4) U. b. trinatatum. (Map modified from Davis, 1968).

(1976) reported that the number of bites required to sever the veins of a frond ranged from 44 in simple bilobed leaves of Asterogyne, to 80 in the large leaves of Prichardia. Tents constructed from Prichardia pacifica, Cocos nucifera, Livistona chinensis, Sabal mauitiiformis, and Musa have been observed (Barbour, 1932; Foster and Timm, 1976). Details on the age at which bats make tents, the degree of cooperation between individuals, and whether this behavior is innate or learned are unknown (Kunz, 1982).

Little is known about the activity patterns of U. bilobatum. Erkert (1982) suggested that time of capture of Uroderma in nets indicates a bimodal activity pattern. When roosting in tents by day, individuals are alert and fly immediately upon being disturbed.

GENETICS. Uroderma bilobatum has at least three chromosomal races (Baker and Lopez, 1970) which have been studied by G- and C-banding. The 2n=38 and 2n=44 chromosomal races are derived from a telomere-centromere translocation, involving two acrocentrics, a telomere-centromere translocation involving a small biarmed element and an acrocentric and a centric fusion (Baker, 1979). The 2n=44 and the 2n=42 chromosome races are distinguished by a centric fusion and a pericentric inversion (Baker et al.,

The contact zone between the 2n=44 and the 2n=38 chromosomal races is located on the Pacific versant of Middle America in El Salvador, Honduras, and Nicaragua. This zone has been the object of intensive chromosomal (Baker, 1979, 1981; Baker et al., 1975) and electrophoretic (Greenbaum, 1981) studies. Backcross individuals have been found over a wide range (more than 400 km) but F₁'s are known over a much smaller distance (less than 50 km). Populations at the center of the zone are composed mostly if not entirely of hybrid individuals (Baker, 1981). Electrophoretically, the two chromosomal races are similar (genetic similarity for all populations was greater than 0.96; Greenbaum, 1981). The evolutionary implications of data from the Uroderma hybrid zone have been debated extensively (Barton, 1982; Hafner, 1982). Baker (1981) emphasized that the biology of Uroderma does not fit the parameters (low vagility, high prolificity, and highly inbred demes) most often described as characteristic of species that undergo extensive chromosomal evolution. He further concluded that the data from Uroderma indicate that the negative heterosis assumption in models of chromosomal evolution is often an overstatement. Barton (1982) disagreed with Baker (1981) and Greenbaum (1981) and concluded that the chromosomal contact zone in Uroderma shows all the characteristics expected from a hybrid zone maintained by moderate selection against heterozygotes or recombinant genotypes, whereas Hafner (1982) concluded that the zone does not depart significantly from that predicted by a model of simple diffusion of one parental form into another parental form. The posi-tions of Barton (1982) and Hafner (1982) are not compatible and at least one position is incorrect.

The G- and C-band karyotype of the 2n=44 cytotype of U.

bilobatum was compared to those of representatives of Artibeus, Sturnira, and Enchisthenes (Baker et al., 1979). Although the diploid number and fundamental number differ between the two groups (2n=44 in *Uroderma* but 30 to 31 in the other three genera). most of the euchromatic linkage groups could be identified among the genera. Also, C-band material was restricted to the centromeric region in all karyotypes studied.

3

ETYMOLOGY. The word Uroderma is from the Greek words uro, meaning tail, and derma, skin, referring to the presence of a uropatagium without tail vertebrae in this species. The species name bilobatum combines the prefix bi (Greek and Latin) meaning two, with lobat—(Greek and Latin) for lobed. This name describes the bilobed condition of the first upper incisors.

LITERATURE CITED

ANDERSEN, K. 1908. A monograph of the chiropteran genera Uroderma, Enchisthenes, and Artibeus. Proc. Zool. Soc. London. 1908:204-319.

BAKER, R. J. 1979. Karyology. Pp. 107-176, in Biology of bats of the New World family Phyllostomatidae. Part 3 (R. J. Baker, J. K. Jones, Jr., and D. C. Carter, eds.). Spec. Publ. Mus., Texas Tech Univ., 16:1-441.

. 1981. Chromosomal flow between chromosomally characterized taxa of a volant mammal, Uroderma bilobatum (Chiroptera: Phyllostomatidae). Evolution, 35:296-305.

BAKER, R. J., AND G. LOPEZ. 1970. Chromosomal variation in bats of the genus Uroderma (Phyllostomatidae). J. Mamm., 51:786-789

BAKER, R. J., AND V. R. McDANIEL. 1972. A new subspecies of Uroderma bilobatum (Chiroptera, Phyllostomatidae) from Middle America. Occas. Papers Mus., Texas Tech Univ., 7:1-4.

BAKER, R. J., W. R. ATCHLEY, AND V. R. McDANIEL. 1972. Karyology and morphometrics of Peters' tent-making bat, Uroderma bilobatum Peters (Chiroptera, Phyllostomatidae). Syst. Zool., 21:414-429.

BAKER, R. J., R. A. BASS, AND M. A. JOHNSON. 1979. Evolutionary implications of chromosomal homology in four genera of stenodermine bats (Phyllostomatidae:Chiroptera). Evolution, 33: 220 - 226.

BAKER, R. J., W. J. BLEIER, AND W. R. ATCHLEY. 1975. A contact zone between karyotypically characterized taxa of Uroderma bilobatum (Mammalia: Chiroptera). Syst. Zool., 24: 133 - 142.

BAKER, R. J., M. W. HAIDUK, L. W. ROBBINS, A. CADENA, AND B. F. KOOP. 1982. Chromosomal studies of South American bats and their systematic implications. Pp. 303-327, in Mammalian biology in South America (M. A. Mares and H. H. Genoways, eds.). Spec. Publ. Pymatuning Lab. Ecol., 6:1-539.

BARBOUR, T. 1932. A peculiar roosting habit of bats. Quart. Rev.

Biol., 7:307-312.

BARTON, N. H. 1982. The structure of the hybrid zone in *Uro*derma bilobatum (Chiroptera:Phyllostomidae). Evolution, 36: 863-866.

BLOEDEL, P. 1955. Observations on the histories of Panama bats. J. Mamm., 36:232-235.

DAVIS, W. B. 1968. Review of the genus Uroderma (Chiroptera). J. Mamm., 49:676-698.

DE CARVALHO, C. T. 1961. Sobre os habitos alimentares de phillostomideos (Mammalia, Chiroptera). Rev. Biol. Trop., 9:53-

ERKERT, H. G. 1982. Ecological aspects of bat activity rhythms. Pp. 201-242, in Ecology of bats (T. H. Kunz, ed.). Plenum Press, New York, 425 pp.

FLEMING, T. H., E. T. HOOPER, AND D. E. WILSON. 1972. Three central American bat communities: structure, reproductive

cycles and movement patterns. Ecology, 53:555-569.
FORMAN, G. L., AND H. H. GENOWAYS. 1979. Sperm morphology. Pp. 177-204, in Biology of bats of the New World family Phyllostomatidae. Part 3 (R. J. Baker, J. K. Jones, Jr., and D. C. Carter, eds.). Spec. Publ. Mus., Texas Tech Univ., 16: 1-441

FORMAN, G. L., C. J. PHILLIPS, AND C. S. ROUK. 1979. Alimentary tract. Pp. 205-227, in Biology of bats of the New World family Phyllostomatidae. Part 3 (R. J. Baker, J. K. Jones, Jr., 4 MAMMALIAN SPECIES 279

- and D. C. Carter, eds.). Spec. Publ. Mus., Texas Tech Univ., 16:1-441.
- FOSTER, M. S., AND R. M. TIMM. 1976. Tent-making by *Artibeus jamaicensis* (Chiroptera:Phyllostomatidae) with comments on plants used by bats for tents. Biotropica, 8:265-269.
- GARDNER, A. L. 1977. Feeding habits. Pp. 293-350, in Biology of bats of the New World family Phyllostomatidae. Part 2 (R. J. Baker, J. K. Jones, Jr., and D. C. Carter, eds.). Spec. Publ. Mus., Texas Tech Univ., 13:1-364.
- GOODWIN, G. G. 1946. Mammals of Costa Rica. Bull. Amer. Mus. Nat. Hist., 87:273-473.
- GOODWIN, G. G., AND A. M. GREENHALL. 1961. A review of the bats of Trinidad and Tobago. Descriptions, rabies infection and ecology. Bull. Amer. Mus. Nat. Hist., 122:187-302.
- GREENBAUM, I. F. 1981. Genetic interactions between hybridizing cytotypes of the tent-making bat (*Uroderma bilobatum*). Evolution, 35:306-321.
- HAFNER, J. C. 1982. Genetic interactions at a contact zone of Uroderma bilobatum (Chiroptera: Philostomidae). Evolution, 36:852-862.
- HOOD, C. S., AND J. D. SMITH. 1982. Cladistical analysis of female reproductive histomorphology in phyllostomatoid bats. Syst. Zool., 31:241-251.
- ——. 1983. Histomorphology of the female reproductive tract in phyllostomoid bats. Occas. Papers Mus., Texas Tech Univ., 86:1-38.
- Kunz, T. H. 1982. Roosting ecology. Pp. 1-55, in Ecology of bats (T. H. Kunz, ed.). Plenum Press, New York, 425 pp.
- LINARES, O. J. 1968. Quiropteros subfosiles encontrados en las cuevas venezolanas. Parte 1. Bol. Soc. Venezolana Espeleologia, 1:119-145.
- Lyon, M. W., Jr. 1902. Description of a new bat from Colombia. Proc. Biol. Soc. Washington, 15:83-84.
- McDaniel, V. R. 1976. Brain anatomy. Pp. 147-200, in Biology of bats of the New World family Phyllostomatidae. Part 1 (R. J. Baker, J. K. Jones, Jr., and D. C. Carter, eds.). Spec. Publ. Mus., Texas Tech Univ., 10:1-218.
- MILLER, G. S., Jr. 1907. The families and genera of bats. Bull. U.S. Natl. Mus., 57:1-282.
- PETERS, W. 1866. Machte eine Mittheilung uber neue oder un-

- genugend bekannte Flerthiere (Vampyrops, Uroderma, Chiroderma, Ametrida, Tylostoma, Vespertilio, Vesperugo) und Nager (Tylomys, Lasiomys). Monatsb. Kon. Preuss. Akad. Wiss. Berlin, 1866:392–397.
- SMITH, J. D., AND A. STARRETT. 1979. Morphometric analysis of chiropteran wings. Pp. 229-316, in Biology of bats of the New World family Phyllostomatidae. Part 3 (R. J. Baker, J. K. Jones, Jr., and D. C. Carter, eds.). Spec. Publ. Mus., Texas Tech Univ., 16:1-441.
- SWANEPOEL, P., AND H. H. GENOWAYS. 1979. Morphometrics. Pp. 13-106, in Biology of bats of the New World family Phyllostomatidae. Part 3 (R. J. Baker, J. K. Jones, Jr., and D. C. Carter, eds.). Spec. Publ. Mus., Texas Tech Univ., 16: 1-441.
- TAMSITT, J. R., AND D. VALDIVIESO. 1965. Reproduction of the big fruit-eating bat, Artibeus lituratus palmarum, in Colombia. Caribbean J. Sci., 5:157-166.
- UBELAKER, J. E., R. D. SPECIAN, AND D. W. DUSZYNSKI. 1977. Endoparasites. Pp. 7-56, in Biology of bats of the New World family Phyllostomatidae. Part 2 (R. J. Baker, J. K. Jones, Jr., and D. C. Carter, eds.). Spec. Publ. Mus., Texas Tech Univ., 13:1-364.
- VILLA-R., B. 1967. Los murcielagos de Mexico. Inst. Biol. Univ. Nac. Autonoma Mexico, 491 pp.
- WEBB, J. P., JR., AND R. B. LOOMIS. 1977. Ectoparasites. Pp. 57-119, in Biology of bats of the New World family Phyllostomatidae. Part 2 (R. J. Baker, J. K. Jones, Jr., and D. C. Carter, eds.). Spec. Publ. Mus., Texas Tech Univ., 13:1-364.
- WILSON, D. E. 1979. Reproductive patterns. Pp. 317-378, in Biology of bats of the New World family Phyllostomatidae. Part 3 (R. J. Baker, J. K. Jones, Jr., and D. C Carter, eds.). Spec. Publ. Mus., Texas Tech Univ., 16:1-441.
- Editors of this account were B. J. VERTS and J. KNOX JONES, JR. Managing editor was CARLETON J. PHILLIPS.
- R. J. Baker and C. L. Clark, Dept. Biological Sciences and The Museum, Texas Tech University, Lubbock 79409. Present address of Clark, Dept. of Biology, University of New Mexico, Albuquerque 87131.