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Macrotus waterhousii.

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Macrotus Gray, 1843

Macrotus Gray, 1843:21. Type species *Macrotus Waterhousii* Gray, 1843, by monotypy.

Otopterus Lydekker, 1891:673. A name substituted for Gray's *Macrotus* because it was interpreted as a homonym of *Macrotis* Reid, 1837, a marsupial. Most later workers and the present International Code of Zoological Nomenclature do not regard names that differ in one letter as homonyms.

CONTEXT AND CONTENT. Order Chiroptera, Family Phyllostomatidae, Subfamily Phyllostomatinae. The genus *Macrotus* now includes one species *Macrotus waterhousii* as treated below.

Macrotus waterhousii Gray, 1843

Macrotus Waterhousii Gray, 1843:21. Type locality "Hayti."

CONTEXT AND CONTENT. Context noted in generic summary above. Seven subspecies are recognized (Anderson and Nelson, 1965) as follows:

M. w. waterhousii Gray, 1843:21, see above (*heberfolium* Shamel a *synonym*).

M. w. californicus Baird, 1859a:116. Type locality Old Fort Yuma on the right bank of the Colorado River opposite the present town of Yuma, Arizona, and now in Imperial County, California.

M. w. mexicanus Saussure, 1860:486. Type locality Cuautla, near Yautepec, Morelos, Mexico, (*bocourtianus* Dobson a synonym).

M. w. minor Gundlach *in* Peters, 1865:382. Type locality western Cuba.

M. w. bulleri H. Allen, 1890:73. Type locality Bolaños, Jalisco, Mexico.

M. w. jamaicensis Rehn, 1904:432. Type locality Spanish Town, Jamaica.

M. w. compressus Rehn, 1904:434. Type locality Eleuthera Island in the Bahamas.

DIAGNOSIS. Because the genus includes only one species, the following diagnosis applies to genus and species: nose-leaf simple, erect, lanceolate, about 7 mm. high, ears more than 25 mm. from notch to tip, distally rounded, joined basally by ridge of skin, forearm from 45 to 58 mm. in length (including wrist), larger in southern subspecies, total length 85 to 108 mm., tail 25 to 41 mm. long and extending to or slightly beyond edge of relatively large interfemoral membrane, membranes thin, wings broad, pelage basally whitish and distally brownish, hind limbs longer than tail (tibia slightly shorter than femur and about 21 mm. long), calcaneum short and stout, rostrum moderately long, lower than braincase, auditory bullae large (length 3.3 to 4.1 mm., largest in subspecies *M. w. californicus*), medial upper incisors long and chisel-shaped, lateral upper incisors weaker, dentition i 2/2, c 1/1, p 2/3, m 3/3 (modified from Rehn, 1904:428).

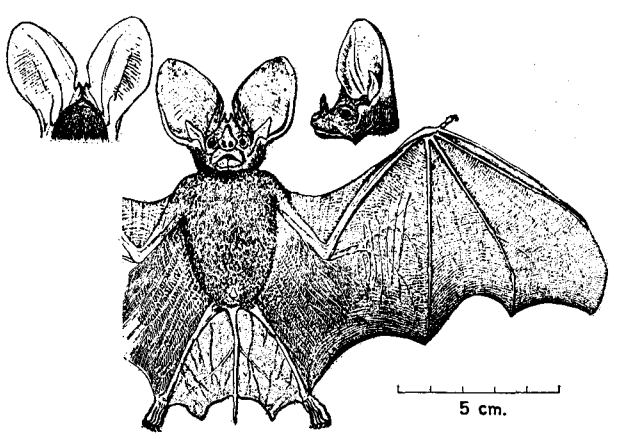

FIGURE 1. External views of *M. w. californicus* (adapted from Baird, 1859b, plate 1).

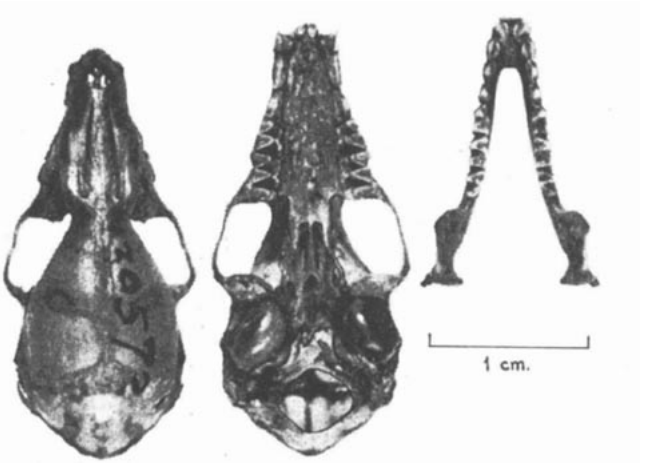

FIGURE 2. Photographs of skulls and lower jaw of (left to right): A.M.N.H. No. 139572, *M. w. californicus*; A.M.N.H. No. 22800, *M. w. minor*, skull in ventral view and jaw in dorsal view. Slightly retouched from Anderson and Nelson, 1965.

GENERAL CHARACTERS. Longer descriptions may be found in Rehn (1904) and Grinnell (1918).

Photographs of skulls of different subspecies and graphs of measurements appear in Anderson and Nelson (1965), for black and white photographs and anatomical drawings see Vaughan (1959).

DISTRIBUTION. The range of the species and of its subspecies are mapped in figure 4. Fossil or subfossil occurrences in west Texas (Cockerell, 1930) and in Puerto Rico (Choate and Birney, 1968) lie beyond the present range as documented by Anderson and Nelson (1965), and suggest a reduction in former range. Marginal records of the species in the southwestern United States were given by Hall

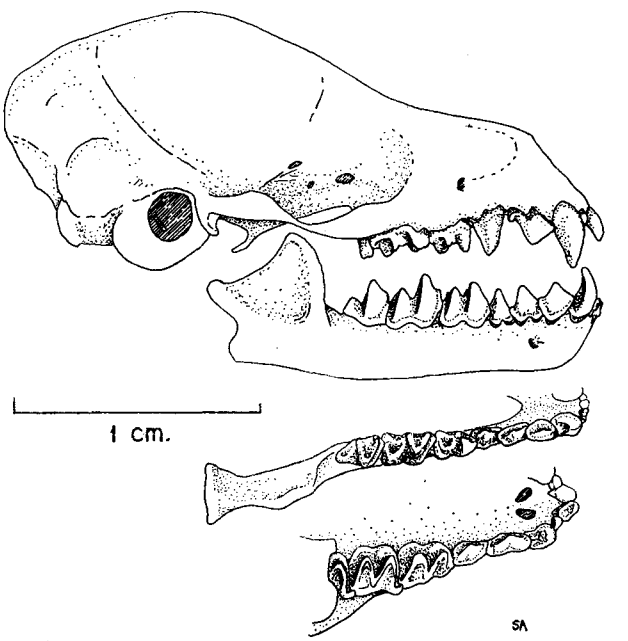

FIGURE 3. Lateral view of skull and jaw and occlusal views of lower and upper dentition. All drawn from A.M.N.H. No. 178755, *M. w. mexicanus*.

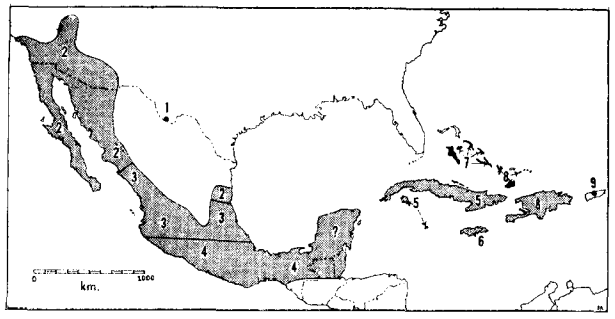

FIGURE 4. Map showing the geographic range of *Macrotus waterhousii* and its subspecies: 1. Site of fossil find in western Texas; 2. *M. w. californicus*; 3. *M. w. bulleri*; 4. *M. w. mexicanus*; 5. *M. w. minor*; 6. *M. w. jamaicensis*; 7. *M. w. compressus*; 8. *M. w. waterhousii*; 9. fossil find in Puerto Rico; the ? on the Yucatan Peninsula indicates the need for futher documentation of the presence of the species there. Adapted from Anderson and Nelson, 1965.

and Kelson (1959). Altitudinal range is from sea level to at least 1400 meters (in Guerrero, Mexico). Ecological range is tropical and sub-tropical.

FOSSIL RECORD. The specimens from caves in several Caribbean Islands are no older than late Pleistocene and perhaps only sub-Recent, the age in years has not been established. These bats were not substantially different from those now in the same or nearby areas. In Jamaica (Williams, 1952) *Macrotus* seems to have replaced *Tonatia* and to have arrived before *Artibeus*.

FORM. Dorsal and ventral hairs are much alike (Benedict, 1957: 410), 10 mm. long, 25.5 to 28.9 microns (μ) in diameter, thinner in basal third, and without medulla. Melanin granules are generally dispersed in distal three-quarters of hair. The intensity of pigmentation varies geographically, the palest subspecies is *M. w. californicus*, indistinct banding may be present in distal quarter of coarsest hairs. Scales are relatively long (23.8 to 28.9 μ *vs.* 25.5 to 28.9 μ width), divaricate distally, coronal, alternately entire and hastate. The deciduous dentition (Nelson, 1966) is heterodont, di 2/2, dc 1/1, dp 2/2, the incisors and canines are strongly recurved, upper di 1 is bilobed, di 2 and dc are simple stylets, dp 1 is laterally flattened and recurved, dc and dp 2 are largest, the lower deciduous incisors are variable but usually trilobed, dc and dp 1 are recurved stylets as in upper jaw, dp 2 is laterally flattened. The gross anatomy of the vertebrae and limb bones and of the locomotor muscles was described and functionally interpreted by Vaughan (1959) and the pectoral and pelvic girdles were compared with those of many other bats by Walton and Walton (1968); vertebral column relatively short, broad, and deep; 12 thoracic, 6 lumbar, 5 sacral, and 7 caudal vertebrae; prominent manubrial keel on sternum; rib cage (as in most bats) relatively large, broader than deep, ribs 1 to 6 vertebrosternal, 7 to 9 vertebrocostal, 10 and 11 vertebral; scapula shorter, broader, and less specialized than in *Eumops* and *Myotis*; phalangeal formula 2–1–3–3–3, distalmost phalanx on d 4 and 5 cartilaginous; pelvis lightly built and narrow, sacroiliac joint not ankylosed, ilium rotated far, so that gluteal fossa faces dorsomediad, femur slender, breadth of shaft about 3.6 per cent of length of femur, trochanters small and knoblike, tibia and fibula slender, pes retains primitive mammalian phalangeal formula of 2–3–3–3–3, foot slightly extended and supinated when relaxed, calcar about 10 mm. long, cartilaginous. Other organ systems have not been studied much.

FUNCTION. Temperature regulation (Reeder and Cowles, 1951), ammonia tolerance (Mitchell, 1963), and echolocation (Novick, 1963, and Grummon and Novick, 1963) have been studied. No phyllostomatid hibernates. Bats of the genus *Macrotus* regulate their internal temperature, maintaining it higher than ambient temperature, for example 18.0°C when ambient drops to 5.7°C. Usual body temperature is 37°C, sustained temperatures below 26°C are lethal (Bradshaw 1962). Probably movement from one part of a cave to another is sometimes a behavioral means of regulating temperature. In the limited air of occupied chambers, ammonia from excreted material may reach higher concentrations than humans can tolerate, but these bats not only tolerate 3000 ppm of ammonia for up to 9 hours but respond adaptively to its presence by reducing cardiac and respiratory rates (to 60 per cent of usual rate), by increasing nonprotein nitrogen in the blood, by retaining constant urea and ammonia in the urine, and by maintaining a constant temperature. Echolocation, as in microchiropterans generally, involves laryngeally produced, nasally emitted, high frequency, pulsed sounds that are reflected, heard, and interpreted in such a way that the animal can avoid obstacles or locate food. Specifically, for *Macrotus*, obstacle avoidance is optimally effective for wires down to 0.27 mm. in diameter, and better than chance down to 0.19 mm. in diameter, in which case the wave length of the highest harmonic frequency, the fourth, is more than 10 times the wire diameter. Ultrasonic pulses are both frequency modulated and harmonic in pattern, usually two but up to four harmonics occur. There is a frequency drop, usually less than one octave, in each pulse (35 to 40 kc dropping to 26 to 30, in the second harmonic 78 kc dropping to 54 kc, and 102 kc dropping to 81 kc in the third harmonic, which appeared when the fundamental frequency dropped below 34 kc). The duration of pulses seemed fairly regular in each of four bats studied (ranges in milliseconds were 2.5 to 3.5, 3.1 to 3.7, 1.7 to 3.9, and 2.0 to 3.6). Although their eyes are relatively large (for a microchiropteran) vision is unimportant in obstacle avoidance. Experimental change in the nose leaf produced no regular interference with obstacle avoidance.

ONTOGENY. A distinctive pattern of early embryology, termed "delayed development" was discovered in this species (Bradshaw, 1962); ovulation, insemination, and fertilization occur in early fall (mostly September in Arizona), embryonic development is slow until March, 5 months pass before the primitive streak stage is reached, ovulation is from the right ovary only and implantation usually is in right horn of the uterus, gestation lasts 8 months, birth occurs in May, June, or early July, weaning occurs after about 1 month of nursing, then the permanent dentition emerges. Females breed in their first autumn but later in the season than older females, males do not breed in their first year. Spermatogenesis begins in July and August while males live separately from females. Young usually are born singly, rarely as twins (summary by Barlow and Tamsitt, 1968; Hardy, 1949, also recorded a female with two embryos). This is true of phyllostomatids generally, 4 sets of twins were observed in 3100 females of 18 species, Barlow and Tamsitt postulate that single young born at different times of the year are an adaptation to tropical conditions including a nearly continuous food supply. However, the reproductive data in the literature and in the author's files on a few dozen specimens from various parts of the range of *Macrotus* all fit the seasonal reproductive pattern described for Arizona, except for four specimens from Cuba recorded by the collector H. E. Anthony as containing "large" embryos in March.

ECOLOGY. Most bats have few predators. *Macrotus waterhousii* has ectoparasites but these have never been thoroughly surveyed. Association with other species of bats in roosts is common, for example *Desmodus* and *Chilonycteris* in Guerrero (Lukens and Davis, 1957) and *Antrozous*, *Plecotus*, and *Myotis* in California (Vaughan, 1959:34). In the Fortuna Mine in Arizona (Bradshaw, 1961), the population of both sexes increased in March and April, in summer females segregate in a maternity colony and males disperse in smaller groups, from August to October the sexes reassociate, in winter only males are consistently present, and in November large numbers appeared. Perhaps this suggests some sort of migratory movement. Bradshaw banded 890 bats and their maximum life expectancy was estimated to be more than 10 years. The longest known time from marking to recovery of a banded individual was 40 months (Paradiso and Greenhall, 1967), but the minimal age was uncertain because the bat was dead when found. Bats generally are longer lived than most small mammals. Colonies of dozens or hundreds are common in some areas and up to 500 (Huey, 1925) have been observed in May in California. The species is common in most parts of its range and is the "most common bat in the semi-desert lowlands of Morelos" (Davis and Russell, 1952). They "seem to be totally insectivorous" in California (Vaughan, 1959:35) and food includes orthoptera, noctuid moths, scarab and carab beetles, sphinx moths, and cicadas. Most food probably is taken from the ground or vegetation. This assumption is based on the low maneuverable flight of the bat, the limited diurnal flight of some insects eaten, the capture of one bat in a mouse trap on the ground (Grinnell, 1918:257), and the discovery of another bat impaled on a thorn (Stager, 1943), presumably accidentally while in flight or upon landing on the thorny shrub. In Sonora (Burt, 1938) and Jamaica (Dobson, 1878) they are said to be partly frugivorous.

BEHAVIOR. General observations reported from Jamaica as early as 1851 by Gosse have since been verified and amplified by other observers. Locomotion and posture were studied by Vaughan (1959) and reproduction by Bradshaw (1962). Observations on other aspects of behavior have been less thorough and are scattered in the literature.

Although caves are the chief dwelling places this species also occupies mine tunnels and buildings, does not require complete darkness, is often found within 10 to 30 meters of the entrance of a tunnel or in partly lighted buildings. Roosts usually are in chambers with considerable ceiling surface and flying space. Temperature influences selection of roosts also, 45 ft. into one tunnel in California

it was 84°F when outside it was 110°F in the shade (Vaughan, 1959: 31). In Morelos, one was found hanging from the roof of an open porch (Davis and Russell, 1952). They hang by one or both feet and may scratch or groom with a free foot. The long and unusually rotated hind limbs are adaptations for this posture, and foot structure facilitates grip. They are sometimes in groups but rarely in contact with each other. Wings are held loosely folded. They cannot walk quadrupedally, but can take off directly from a flat horizontal surface. They do "walk" bipedally across ceiling. Flight is highly maneuverable, may be rapid but during foraging is usually slow and relatively silent, within a meter of the ground and often close to vegetation. They often hover, alight by an upward swoop and half-roll, launch by dropping a short distance before taking wing or by flying directly from the roost, and may ingest prey after alighting. They emerge 30 minutes or more after sunset, usually about 90 to 120 minutes after, temporary night roosts may be different from day roosts. There are two main feeding periods, the second about the hour 01:00, and each bat probably is on the wing less than 105 minutes each night. Wing loading is 0.23 lbs. per square foot, the aspect ratio (=span^2/area) is 6.8, these values and the relatively short, broad wings with high camber are adaptations for low-speed flight and high maneuverability. In three tests, individuals lifted weights of from 41 to 56 per cent of body weight from level surface into flight, a higher ratio than most bats tested (Davis and Cockrum, 1964). Nelson (1899) reported a maternity colony of more than 100 in an old, rather well-lighted, warehouse, in May, in the Tres Marias Islands. In Arizona, the caretaker of a mine reported that these bats were active all winter, descending to lower levels when weather was humid, they were found at more than 200 feet depth the day after a rain (Dice and Blossom, 1937). In mid-January in Nevada, Hatfield (1937) observed them in a building choosing rooms that he judged were protected from the cool night air, between the hours of 21:30 and 23:00. When alert their heads are held up and ears are horizontal, the large eyes reflect a yellowish shine from a flashlight beam. In observations between the hour 18:00 and 23:59 on 26 November in Sonora, two *Macrotus* were taken between 19:00 and 19:29 and one between 22:00 and 22:29 (Baker and Christianson, 1966).

GENETICS. The first major karyotypic variation of bats at the subspecific level was discovered in *Macrotus* (Nelson-Rees, *et al.*, 1968). Specimens from Morelos, Guerrero, and southern Sonora have 46 diploid chromosomes and a telocentric Y-chromosome (in males). Specimens from Arizona, California, and northern Sonora have 40 chromosomes, a telocentric Y-chromosome and a secondary constriction on the supposed X-chromosome. The California sample had an achromatic region near the centromere on one of the large pairs of telocentric chromosomes and a metacentric or submetacentric Y-chromosome. All of these variants are present in populations referred by Anderson and Nelson (1965) to the subspecies *M. w. californicus*. The karyology of other populations in southern Sonora and northern Sinaloa should be studied and correlated with other characters there.

REMARKS. The name *Macrotus europaeus* Leach, (?) 1816, was a *nomen nudum*, perhaps referring to *Plecotus auritus*. The name *Macrotus pygmaeus* Rehn, 1904, is a synonym of *Micronycteris megalotis mexicana*. *Micronycteris* is probably the genus most closely related to *Macrotus*, however, on the basis of karyology, Baker (1967) placed it with *Leptonycteris*, *Glossophaga*, *Phyllostomus*, and *Trachops*, rather than with *Micronycteris*. In the southwestern United States *M. waterhousii* has been called "the leaf-nosed bat" there being no other common phyllostomatid in most of the area.

Macrotus is from the Greek words *macros* and *otos* (genitive) for "long ear," neuter. Specific and subspecific names refer to localities, i.e. Jamaica, *jamaicensis*, Mexico, *mexicanus*, California, *californicus*; persons, i.e. the British zoologist G. R. Waterhouse (1810–1888), *waterhousii*, the French collector Bocourt, *bocourtianus*, the American collector Audley C. Buller, *bulleri*; or characteristics of the animals, i.e. *minor* from Latin for small, *compressus* from Latin for compressed, in reference to laterally flattened first lower premolar, and *heberfolium* from Latin *hebes* for blunt and *folium* for leaf, in reference to the allegedly blunt nose-leaf.

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