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## Vampyrops lineatus. By Michael R. Willig and Robert R. Hollander

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## Vampyrops lineatus (É. Geoffroy St.-Hilaire, 1810)

Geoffroy's Rayed Bat

Phyllostoma lineatum É. Geoffroy St.-Hilaire, 1810:180. Type locality restricted to Asunción, Paraguay, by Cabrera (1958).
Vampyrops lineatus, Peters, 1865:356. First use of current name combination.

Vampyrops nigellus Gardner and Carter, 1972:1. Type locality Huanhuachayo, Ayacucho, Perú.

CONTEXT AND CONTENT. Order Chiroptera, suborder Microchiroptera, superfamily Phyllostomoidea, family Phyllostomidae, subfamily Stenodermatinae. The genus *Vampyrops* contains eight (Jones and Carter, 1976, 1979) or nine (Honacki et al., 1982; Koopman, 1982; Swanepoel and Genoways, 1979) species; they may be distinguished on the basis of characters discussed in the diagnosis that follows. *Vampyrops lineatus* contains two recognized subspecies (Koopman, 1978):

- V. l. lineatus (É. Geoffroy St.-Hilaire, 1810:180), see above (sacrillus Thomas is a synonym).
- V. l. nigellus Gardner and Carter, 1972:1, see above.

DIAGNOSIS. Vampyrops lineatus can be distinguished morphometrically from most other congeners by both external and cranial features. It is larger than V. helleri and V. brachycephalus in seven cranial characters (greatest length of skull, condylobasal length, zygomatic breadth, postorbital constriction, breadth of braincase, length of maxillary toothrow, and breadth across upper molars) used by Swanepoel and Genoways (1979). Conversely, V. lineatus is smaller than V. vittatus, V. infuscus, and V. aurarius for each of the same seven characters. There is slight overlap between the largest specimens of V. lineatus and the smallest specimens of V. dorsalis in postorbital constriction and forearm length; V. lineatus is smaller than V. dorsalis in all other characters used. Vampyrops umbratus is considered conspecific with V. dorsalis (Jones and Carter, 1976; Rouk and Carter, 1972; Sanborn, 1955; Swanepoel and Genoways, 1979). Measurements of V. recifinus overlap those of V. lineatus in four (zygomatic breadth, breadth of braincase, length of maxillary toothrow, and breadth across upper molars) of seven cranial characters; as such, these taxa have been proposed as being either conspecific (Honacki et al., 1982; Rouk and Carter, 1972), or subspecific (Jones and Carter, 1976). Nevertheless, V. lineatus can be distinguished from V. recifinus by the lobation of the lower incisors (bilobed incisors in V. lineatus and trilobed incisors in V. recifinus; Carter and Dolan, 1978).

**GENERAL CHARACTERS.** In external appearance, V. lineatus is like other species of Vampyrops in resembling Artibeus somewhat (Fig. 1). In general, the muzzle is short, wide, and flattened; the noseleaf is well developed and lanceolate, the tip is pointed whereas the base resembles a horseshoe with a finely crenulated free margin. The rounded ears are about the size of the head; their internal margins are convex whereas the external margins are concave. The tragus is well developed, pointed, and crenulated along the internal margin. Wing membranes connect at the metacarpals, almost at the base of the phalanges. The calcar is short. The interfemoral membrane is strongly indented with the edge of the concavity touching at the knees. The thumb is long with a well-developed nail. The dorsal pelage is thick and long (5 to 6 mm). Sparse hairs cover the superior surface of the interfemoral membrane, the legs, and the digits of the feet. A fringe of fine hairs extends along the posterior margin of the interfemoral membrane. The digits of the feet are small with weak nails. The dorsum is yellow-brown to dark-brown whereas the venter is paler. The head has four broad white stripes (Fig. 1); two extend from the base of the noseleaf to the posterior edge of the ear and two occur on the cheek below the eye. A distinct white stripe extends along the dorsum from the occiput to the base of the interfemoral membrane.

The dental formula is i 2/2, c 1/1, p 2/2, m 3/3, total 32. Upper incisors are large, in contact, and oblique, each with a broad cusp projecting inward and slightly forward (Fig. 2). The outer upper incisors are small, approximately half the size of 11, conical, and straight. The lower incisors are small, equal in size, and bifid. The canines and premolars are similar to those of Artibeus. The surface of the crowns of the lower molars is almost smooth; M3 is reduced. The cranium is similar to that of Artibeus, although the rostrum is relatively longer and narrower.

In addition to reporting measurements of V. lineatus, Swanepoel and Genoways (1979) listed a number of other studies that contain mensural data (Allen, 1891; Chuna Vieira, 1942; Dobson, 1878; Elliot, 1904; Goodwin, 1946; Hershkovitz, 1949; Lima, 1926; Sanborn, 1955). Taddei (1979) reported statistically significant secondary sexual variation in samples from northwestern São Paulo, Brazil, for 2 of 18 cranial characters (palate width and basal length) and 5 of 18 external characters (forearm length, length of the metacarpal of digit III, length of the first phalanx of digit III, length of the third phalanx of digit III, and length of the metacarpal of digit IV). Willig (1983) examined morphometric variation within and between populations in northeast Brazil; 9 of 14 external characters (total length, hind foot length, forearm length, weight, length of digit I, length of digit III, length of digit IV, length of digit V, tibia length) and none of 16 cranial characters exhibited significant secondary sexual variation. Significant differences between populations from Caatingas and edaphic Cerrado habitats were obtained for four cranial characters (rostral breadth, breadth across the upper molars, upper molariform toothrow length, width of widest molar) and four external characters (hind foot length, forearm length, length of digit IV, length of digit V). Mean values (followed by standard deviations in parentheses) in mm (Willig, 1983), each based upon a sample of 20 individuals, for Caatingas males, Caatingas females, Cerrado males, and Cerrado females, respectively, are: total length, 64.40 (2.98), 67.85 (2.60), 63.55 (2.78), 66.70 (2.66); hind foot length, 11.20 (0.62), 11.60 (0.60), 11.55 (0.51), 11.90 (0.45); ear length, 18.05 (1.05), 18.15 (0.67), 17.80 (0.89), 18.15 (0.67);

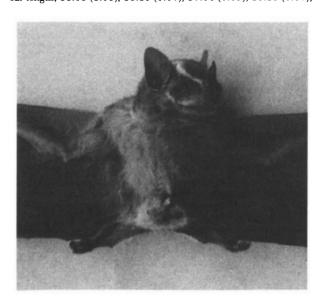


FIG. 1. Photograph of a live specimen of Vampyrops l. lineatus from northeast Brazil (photograph by M. R. Willig).

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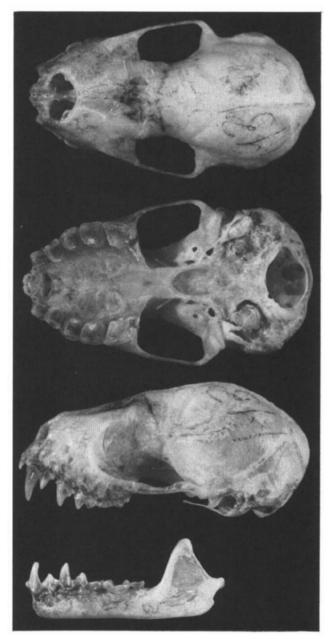


Fig. 2. Dorsal, ventral, and lateral views of cranium and lateral view of lower jaw of Vampyrops l. lineatus (M. R. Willig field number 1931 8), from O Aeroporto de Crato, Crato, Ceará. Greatest length of skull is 18.9 mm (photograph by N. Olson).

tragus length, 7.15 (0.75), 7.35 (0.59), 7.30 (0.57), 7.10 (0.72); forearm length, 47.20 (1.94), 47.45 (2.04), 46.00 (1.12), 47.20 (1.06); length of digit I, 10.65 (0.75), 10.95 (0.76), 10.60 (0.75), 11.10 (0.64); length of digit III, 96.80 (3.49), 97.10 (3.70), 94.00 (2.64), 97.35 (2.41); length of digit IV, 70.95 (2.04), 71.90 (2.55). 69.35 (2.03), 71.05 (1.93); length of digit V, 65.75 (1.94), 67.25 (2.86), 64.35 (1.90), 66.10 (1.65); tibia length, 18.00 (0.46), 18.35 (0.88), 17.95 (0.76), 18.50 (0.83); calcar length, 4.75 (0.85), 4.30 (0.57), 4.25 (0.44), 4.30 (0.47); noseleaf length, 6.95 (0.76), 7.00 (0.86), 6.85 (0.88), 7.25 (0.64); greatest length of skull, 24.32 (0.46), 24.40 (0.37), 24.38 (0.56), 24.41 (0.35); condylobasal length, 21.90 (0.44), 22.00 (0.46), 21.83 (0.61), 21.89 (0.38); zygomatic breadth, 14.32 (0.34), 14.37 (0.40), 14.25 (0.37), 14.17 (0.39); postorbital constriction, 6.26 (0.19), 6.29 (0.20), 6.23 (0.18), 6.22 (0.25); mastoid breadth, 12.12 (0.26), 12.22 (0.31), 12.21 (0.24), 12.16 (0.32); breadth of braincase, 10.51 (0.29), 10.56 (0.26), 10.56 (0.23), 10.58 (0.16); rostral breadth, 7.46 (0.26), 7.42 (0.31), 7.03 (0.36), 6.86 (0.21); height of braincase, 11.48 (0.23), 11.42 (0.31), 12.44 (0.29), 12.36

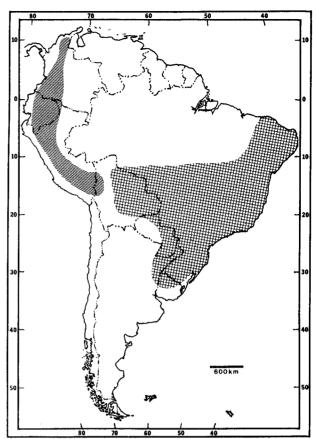


Fig. 3. Distribution of *Vampyrops lineatus* (principally after Koopman, 1983). Subspecies are *V. l. lineatus* (crosshatch) and *V. l. nigellus* (diagonal).

(0.24); breadth across upper molars, 10.19 (0.23), 10.40 (0.31), 10.17 (0.25), 10.13 (0.25); breadth across upper canines, 6.05 (0.22), 6.15 (0.23), 6.09 (0.15), 6.02 (0.21); length of maxillary toothrow, 8.59 (0.33), 8.75 (0.32), 8.76 (0.28), 8.62 (0.27); length of upper molariform toothrow, 7.09 (0.26), 7.16 (0.28), 7.05 (0.21), 7.98 (0.20); width of widest molar, 2.51 (0.11), 2.53 (0.13), 2.42 (0.14), 2.45 (0.16); greatest length of mandible, 16.62 (0.41), 16.74 (0.28), 16.49 (0.45), 16.49 (0.32); length of mandibular toothrow, 9.53 (0.26), 9.60 (0.33), 9.54 (0.25), 9.46 (0.26); and length of coronoid process, 5.69 (0.25), 5.87 (0.25), 5.76 (0.29), 5.74 (0.21). Mean weights (g) followed by standard deviations in parentheses for the same series are 23.93 (1.32), 26.44 (3.73), 23.10 (1.78), 26.48 (2.90).

**DISTRIBUTION.** The genus *Vampyrops* occurs from subtropical South America north to southern Mexico (Fig. 3). The two recognized subspecies of *V. lineatus* are not parapatric (Anderson et al., 1982). *Vampyrops l. nigellus* occurs along the Andes from northern Colombia south through Equador and Peru to western Bolivia. *Vampyrops l. lineatus* occurs from northeastern Brazil across to central Bolivia and south through eastern Paraguay and northeastern Argentina to northern Uruguay. There is no known fossil record.

ONTOGENY AND REPRODUCTION. Although the family Phyllostomidae is characterized by a single young per litter, the presence of a developed corpus luteum in each ovary of nulliparous females of *V. lineatus* suggests the possibility of occasional twinning in this species (Taddei, 1976). Taddei (1973) obtained mensural data on a neonate within 24 h of parturition, the measurements (in mm, and mass in g) and percentage of maternal size, respectively, follow: head and body length 46.5, 68.3; ear length, 14.5, 74.3; tragus length, 4.5, 69.2; forearm length, 27.0, 58.0; length of digit I, 6.5, 86.6; length of digit III, 21.0, 48.8; tibia length, 12.0, 68.5; foot length, 10.5, 95.4; weight, 8.30, 30.8. Embryologic development has not been examined otherwise.

Peracchi and Albuquerque (1971) captured pregnant females

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in December, January, and March in the Brazilian state of Rio de Janeiro. Taddei (1973, 1976) obtained pregnant females in all months except April in southwestern São Paulo state, Brazil; lactating specimens appeared from November to May. A protracted reproductive season and polyestry, indicated by simultaneously pregnant and lactating females in November and December, characterized the São Paulo population. Willig (1985) defined reproductive patterns in two well-delineated populations from northeast Brazil. Differences in the annual reproductive cycle between Caatingas and edaphic Cerrado populations were not evident. A biomodal distribution of pregnancy began in the early dry season (July) and terminated early in the rainy season (February-March). Pregnancy was no longer observed by the end of the rainy season. A bimodal distribution of lactation also was evident; lactating females were first observed at the end of the dry season (October) and continued to be captured into the middle of the rainy season.

FORM AND FUNCTION. Specimens from Bahia were reported by McNab and Morrison (1963) to contain relatively large salivary glands (1.3 to 2.5% of body mass) compared to other phyllostomids (for example, *Chiroderma villosum*, 0.6% of body mass). McNab (1982) reported that *V. lineatus* maintains body temperature independently of ambient temperatures to at least 10°C, with body temperature elevating in response to increases in environmental temperature beyond 30°C.

ECOLOGY AND BEHAVIOR. Based upon the works of Ruschi (1953) and McNab (1969), Gardner (1977a) defined the diet of this species as including fruits and insects, especially sphingid moths. McNab and Morrison (1963) occasionally captured V. lineatus near sapotes (Achras zapota) but did not report if the fruit was actually consumed. Taddei (1973) reported that Carica papaya, Cecropia, Chlorophora tinctoria, Ficus enormis, Ficus sp., and Syzygium jambos composed the natural diet in northwestern São Paulo state, Brazil; banana and honey water were consumed in captivity. McNab and Morrison (1963) previously reported a preference in captivity for papaya over banana. Willig (1983) suggested that Vismia was an important dietary component on the Chapada do Araripe in Ceará state, Brazil, because it was the dominant food item in stomachs and feces examined. The observations of Sazima and Sazima (1975) and Sazima (1976) expanded the reported feeding niche of V. lineatus to include nectarivory; Musa acuminata and Lafoensia pacari flowers often were exploited by V. lineatus on Serra do Cipó, in the Brazilian state of Minas Gerais. Sazima and Sazima (1975) further detailed the feeding behavior of the species. Specimens arrived at flowering Lafoensia at dusk, made one or two short passes and inserted their heads, while in flight, into the corolla. When the flower was inclined horizontally, V. lineatus suspended itself by the thumbs alone from the base of the flower. When the flower was vertical, V. lineatus also supported itself by anchoring the feet on the branch supporting the inflorescence. A sequence of rapid head movements followed, during which time individuals lapped nectar and pollen. Each visit lasted from 0.5 to 1.5 s. Stages of floral development previous to anthesis were exploited also. Group and solitary foraging was observed, the latter more common on plants with few available flowers.

Willig (1983) reported unequal sex ratios for populations in northeast Brazil. Moreover, he suggested that male V. lineatus maintained small harems of 7 to 15 females in small granitic caves. Similar roosting colonies from 6 to approximately 20 individuals also were reported by Peracchi and Albuquerque (1971). They observed the smaller groups roosting under leaves of the palm, Livistona oliviformis, and larger groups roosting under Syagrus picrophylla leaves. Taddei (1973) observed eight individuals roosting beneath a Dracaena leaf (approximately 3 mm in height) and two individuals in a bromeliad 12 m off the ground.

Vampyrops lineatus has been captured with Anoura geoffroyi, Artibeus concolor, A. fimbriatus, A. jamaicensis, A. lituratus, Carollia perspicillata, Chiroderma doriae, C. vellosum, Chrotopterus auritus, Desmodus rotundus, Diphylla ecaudata, Eptesicus brasiliensis, E. diminutus, E. furinalis, Eumops auripendulus, E. bonariensis, E. glaucinus, E. perotis, Furipterus horrens, Glossophaga soricina, Histiotus velatus, Lasiurus borrealis, L. cinereus, L. ega, Lonchophylla mordax, Micronycteris megalotis, M. minuta, Mimon crenulatum, Molossops abrasus, M. planirostris, M. temminckii, Molossus ater, M. molossus, Myotis albescens, M. nigricans, M. riparius, M. ruber, M. simus, Natalus stramineus, Neoplatymops mattogrossensis, Noctilio al-



Fig. 4. A single diploid chromosomal complement of a male  $V.\ l.\ lineatus$  (Univ. Michigan number 125428); the sex chromosomes are in the lower right corner.

biventris, N. leporinus, Peropteryx macrotis, Phyllostomus discolor, P. hastatus, Promops nasutus, P. occultus, Pteronotus davyi, Pygoderma bilabiatum, Saccopteryx leptura, Sturnia lilium, Tadarida brasiliensis, T. laticaudata, Tonatia bidens, T. brasiliense, T. silvicola, Trachops cirrhosus, Uroderma magnirostrum, and Vampyressa pusilla (Myers, 1982; Taddei, 1973; Willig, 1983).

GENETICS. Figure 4 illustrates a single diploid chromosomal compliment from a male V. l. lineatus from Paraguay (courtesy of P. Myers). The chromosomal morphology is identical to that reported for V. l. nigellus (as V. nigellus by Gardner, 1977b) and all other congeners (Baker, 1979; Baker et al., 1982). The only variation in chromosomal morphology that has been documented for the genus Vampyrops is that the Y chromosome of some species (V. brachycephalus, V. dorsalis, and V. helleri) is submetacentric, whereas in other species (V. infuscus, V. l. nigellus, and V. vittatus), it is acrocentric (Baker, 1979; Baker et al., 1982; Gardner, 1977b). The condition of the Y chromosome of V. l. lineatus is acrocentric like that of V. l. nigellus reported by Gardner (1977b). The karyotype of V. lineatus and all reported congeners consists of a diploid number of 30 with a fundamental number of 56. Electrophoretic analyses involving V. lineatus have not been reported.

REMARKS. The English vernacular name, Geoffroy's Rayed Bat, is derived from a literal translation of the French vulgar name, "Phyllostome raye," written on the wing of the type specimen by Geoffroy. The generic name Vampyrops is derived from the combination of the Russian root "vampyr" meaning a vampire and the Greek root "ops" meaning appearance. The specific epithet is derived from the Latin root "linea" meaning a line. Thus, the scientific name Vampyrops lineatus means a vampire-appearing bat with a line

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