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Vampyressa pusilla. By Susan E. Lewis and Don E. Wilson

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Vampyressa Thomas, 1900

Vampyrops (Vampyressa) Thomas, 1900:270. Type species Phyllostoma pusillum Wagner, 1843, by original designation. Vampyressa Miller, 1907:156, first use of name in generic sense.

CONTEXT AND CONTENT. Order Chiroptera, Suborder Microchiroptera, Family Phyllostomidae, Subfamily Stenodermatinae. The genus *Vampyressa* contains five species in two subgenera. The subgenus *Vampyressa* contains *V. melissa* and *V. pusilla*; the subgenus *Vampyriscus* contains *V. bidens*, *V. nymphaea*, and *V. brocki*. A key to the species follows (Peterson, 1968):

1	One pair lower incisors V. biden	s
	Two pair lower incisors	
2(1)	Third lower molar present	ı
	Third lower molar absent	
3(2)	Second lower molar approximately as long as wide with	
	high anterior and posterior cusps	ı
	Second lower molar longer than wide with low anterior	
	and posterior cusps	Ļ
4(3)	Forearm in adults more than 34 mm, greatest length of	
	skull more than 20 mm	ı
	Forearm in adults less than 34 mm, greatest length of	
	skull less than 20 mm V. brock	i

Vampyressa pusilla (Wagner, 1843)

Little Yellow-eared Bat

Phyllostoma pusillum Wagner, 1843:173. Type locality "Sapitiva," Rio de Janeiro, Brazil.

Vampyressa pusilla, Miller, 1907:156, first use of current name combination.

Vampyressa thyone Thomas, 1909:231. Type locality "Chimbo, near Guayaquil, Ecuador. Alt. 1,000'."

Vampyressa minuta Miller, 1912:25. Type locality "Cabima, Panama."

Vampyressa venilla Thomas, 1924:533. Type locality "San Lorenzo, 500'," Perú.

Vampyressa nattereri Goodwin, 1963:16. Type locality "probably Ipanema, district of São Paulo, Brazil."

CONTEXT AND CONTENT. Context as above. Goodwin (1963) recognized three subspecies of V. pusilla: V. p. pusilla, V. p. thyone, and V. p. venilla. Subsequently, Handley (1966:767) regarded V. pusilla as monotypic and described the subspecies characteristics as "age rather than geographic variables." In a more recent review of the species, Peterson (1968) recognized two subspecies, V. V. pusilla and V. V. pusilla.

DIAGNOSIS. Vampyressa pusilla usually can be distinguished from V. bidens by the number of lower incisors. Usually V. bidens has one on each side, but V. pusilla has two on each side, although Davis (1975) found two individuals of V. bidens from Perú with additional lower incisors. In V. pusilla, the third lower molar is absent, whereas it is present in V. melissa and V. bidens.

In two of the five species of Vampyressa, the tragus is hirsute on the lateral attachment; V. pusilla, V. melissa, and V. nymphaea lack this pilosity. The medial, distal extension of the tragus is finely serrated and more pronounced in V. pusilla and smooth and less pronounced in V. nymphaea and V. melissa (Peterson, 1968).

Vampyressa pusilla and V. melissa lack the dorsal stripe present in the other three congeners. The dorsal pelage of V. pusilla is paler and the facial markings not as well defined as those of the other species.

The interfemoral membrane of V. pusilla is narrower than that of V. nymphaea and V. brocki. The edge is nearly naked with

the exception of a small fringe in the center. The interfemoral membrane of *V. melissa* is more hirsute (Goodwin, 1963).

The forearm length of *V. pusilla* ranges from 30 to 32 mm (Goodwin, 1963), shorter than that of *V. melissa* and *V. nymphaea* (average forearm lengths 38 and 36 mm, respectively; Peterson, 1968).

GENERAL CHARACTERISTICS. Goodwin (1963:15) described *V. pusilla thyone* (Fig. 1) as follows: "Upper parts anteriorly Pinkish Buff grading to Sacardo's Umber or Sayal Brown on lower back; under parts rather darker than Light Buff; facial stripes white, the upper pair extending back to between ears. Skull with a short, broad rostrum, large, full braincase; upper incisors very unequal, the inner more than twice as high as outer; cutting edges bifid, separated by a space and converging distally but not in contact at tip; upper molars broader than long; lower incisors small, completely filling space between canines, their cutting edges faintly trifid." The skull (Fig. 2) is typical for the subfamily, and the dental formula is i 2/2, c 1/1, p 2/2, m 2/2, total 28 (Miller, 1907).

Baker et al. (1973), found no significant geographic differences among specimens from Central and South America for one external and eight cranial measurements. Mean and range (in parentheses) of external and cranial measurements (in mm) for 36 specimens from Colombia, Venezuela, and Ecuador are (Baker et al., 1973): length of forearm, 31.4 (29.3 to 33.2); greatest length of skull, 18.4 (17.5 to 19.3); zygomatic breadth, 10.7 (10.0 to 11.3); postorbital breadth, 4.6 (4.3 to 5.0); breadth of braincase, 8.2 (7.5 to 8.7); mastoid breadth 9.1 (8.6 to 9.6); length of maxillary toothrow, 5.8 (5.4 to 6.3); palatal length, 8.3 (7.7 to 9.0); breadth across upper molars, 7.7 (7.1 to 8.3). LaVal and Fitch (1977) reported the average mass for 27 specimens from La Selva, Costa Rica, to be 8.2 g.



Fig. 1. Vampyressa pusilla thyone from Costa Rica, Photograph by Richard K. LaVal.



Fig. 2. Dorsal, ventral, and lateral views of cranium, and lateral and dorsal views of mandible, of male *Vampyressa pusilla pusilla* from Vicosa, Minas Gerais, Brazil (USNM no. 395703). Greatest length of skull is 19.6 mm.

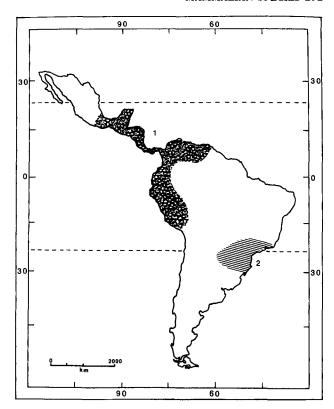


Fig. 3. Distribution of Vampyressa pusilla: 1, Vampyressa pusilla thyone; and 2, Vampyressa pusilla pusilla.

DISTRIBUTION. Vampyressa p. thyone ranges from southern Mexico (Oaxaca, Chiapas, Yucatan, Veracruz, and Campeche; Ramirez et al., 1983) south along the Caribbean coast of Central America through Guatemala, Belize (British Honduras), Honduras, Nicaragua, Costa Rica, and Panamá, then east through Colombia (Aellen, 1970) and Venezuela (Handley, 1976) and south through Ecuador and Perú (Fig. 3). V. p. pusilla is found in eastern Paraguay (Myers et al., 1983) and southeastern Brazil (Taddei, 1979). There is no fossil record for the species.

Koopman (1978) classified V. pusilla as both an Amazonian highland and lowland species in Perú, based on capture records above and below 1,000 m. Graham (1983) gave the elevational limits for 10 specimens of V. pusilla from Perú as 300 to 1,500 m. Handley (1976) reported an elevational range in Venezuela of 23 to 1,537 m, with 86% caught above 500 m. Specimens from Panamá in the National Museum of Natural History were taken from sea level to 854 m.

A specimen of *V. pusilla* was reported on a ship passing through the Bass Strait between Australia and Tasmania. Presumably the bat had boarded the vessel when it passed through the Panamá Canal (Hill and Smith, 1984).

FORM AND FUNCTION. In describing the gastric morphology of *V. pusilla*, Forman (1973) noted that the stomach closely resembles that of *Uroderma*, except for an extremely small cardiac vestibule. The stomach has an elongated pouch between the gastroesophageal junction and the left lateral terminus, which Forman (1973) designated as the fundic caecum. This caecum, along with a moderate terminal portion and small cardiac vestibule, gives the stomach a tubular appearance. The rugae are distributed diagonally in the fundic caecum and longitudinally within the remaining portions.

Brunner's glands are absent (Forman, 1971). The zone of pyloric glands in the terminal portion of the stomach is more extensive than in most stenodermines. Forman (1973) suggested that the pyloric mucosa produces an acid-neutralizing agent to protect the upper duodenum from ulceration.

Studier and Wilson (1983) reported average natural urine concentration of 359 mOsm/kg for two females from Panama. Sodium concentration was 5 mEq/1 and potassium was 33 mEq/1. All of these values are low for bats in general and even for

frugivorous bats as well (mean natural urine concentration for 148 samples of 13 species, 557 mOsm/kg; Studier and Wilson, 1983).

McDaniel (1976), in describing the external anatomy of the brain, noted that the cerebrum is smooth with well-developed sulci and not domed, as in *V. nymphaea*. The inferior colliculi are exposed dorsally and the pseudotemporal lobes project ventrally at an angle. The cerebellum is simple with a low medial crest.

As part of a comprehensive study of the morphometrics of chiropteran wings, Smith and Starrett (1979) listed the mean overall aspect ratio for five specimens of *Vampyressa* (species not given) as 5.88 and the mean wing loading as 11.50 newtons/m².

ONTOGENY AND REPRODUCTION. Wilson (1979) suggested that the reproductive pattern of *V. pusilla* probably was bimodal polyestry, although data were incomplete. Pregnant females have been collected in January (Fleming et al., 1972), February (Jones et al., 1973; LaVal and Fitch, 1977), March (Jones et al., 1971), April (Fleming et al., 1972; LaVal and Fitch, 1977), June (Myers et al., 1983), July (Davis et al., 1964; LaVal and Fitch, 1977; Rick, 1968; Starrett and de la Torre, 1964) August (LaVal and Fitch, 1977; Valdez and LaVal, 1971), and November (Davis and Dixon, 1976). Lactating females have been collected in March (Fleming et al., 1972), April (Hall and Jackson, 1953), May (LaVal and Fitch, 1977) July, and August (Armstrong, 1969).

Peterson (1965:676) reported a 28 mm, 3.2 g embryo collected on 17 March in British Honduras that was "not quite full term." This exceeded one-half the length of the mother and approached one-half of her mass. These measurements suggest that V. pusilla has one of the highest offspring-to-mother size ratios of any species, but animals from Panama average about 10 g, which would provide the more normal ratio of about one-fourth.

ECOLOGY. Handley (1976:29) provided the following details on habitat use based on a collection of 115 specimens from Venezuela: "Caught in mist nets (99 percent) and by hand in a house (1 percent); near streams (5 percent) and other moist areas (73 percent), as well as in dry sites (22 percent); usually in evergreen forest (92 percent), and rarely in yards (5 percent), orchards (1 percent), croplands (1 percent), and swamps (1 percent)" V. pusilla also was collected over streams in gallery forests in Nicaragua (Jones et al., 1971), and in dense rainforests in Costa Rica (LaVal and Fitch, 1977). To account for the low incidence of recapture data for V. pusilla, LaVal and Fitch (1977) postulated that the species is either nomadic or has a proficiency for avoiding traps and mist nets after the first capture.

Vampyressa pusilla typically is found in the presence of Artibeus, Carollia, Sturnira, Vampyrops, and other species of Vampyressa (Davis, 1975; Davis and Dixon, 1976; Myers et al., 1983). Although this species is relatively rare, locally dense concentrations have been reported (Davis and Dixon, 1976).

Bonaccorso (1979) captured this species more frequently between 3 and 12 m than at ground level. He also frequently captured them along creeks on Barro Colorado Island in Panama.

Gardner (1977b) summarized the feeding habits of *V. pusilla* as totally frugivorous. They have been found with small amounts of plant material in their stomachs (Fleming et al., 1972; Starrett and de la Torre, 1964). Howell and Burch (1974) identified fruit from guano and stomach contents of *V. pusilla* to be that of *Acnistus* sp., a fruit-bearing tree cultivated near the collection site. Bonaccorso (1979) characterized the species as a common fig specialist, and reported 92% *Ficus yoponensis* in 13 fecal samples.

Webb and Loomis (1977) listed *V. pusilla* as host for four familes of mites (Sarcoptidae, *Chirnyssoides caparti*; Macronyssidae, *Macronyssoides* sp.; Spinturnicidae, *Periglischrus iheringi*; and Trombiculidae, *Trombicula dunni*), and one family of bat fly (Streblidae, *Neotrichobius delicatus*).

Periglischrus iheringi and Trombicula dunni were identified from V. pusilla in Panamá (Brennan and Yunker, 1966; Furman, 1966). Neotrichobius delicatus was reported from Venezuelan V. pusilla by Wenzel (1976) and Wenzel et al. (1966) described Neotrichobius stenopterus in part from Panamanian V. pusilla. Reed and Brennan (1975) reported Odontacarus tubercularis (Trombiculidae) from V. pusilla in Venezuela, and Brennan and Reed (1975) added Crotiscus desdentatus and Loomisia desmodus (both Trombiculidae), also from Venezuela.

BEHAVIOR. Davis and Dixon (1976) recorded nocturnal activity patterns of a population of *Vampyressa pusilla* near Iquitos,

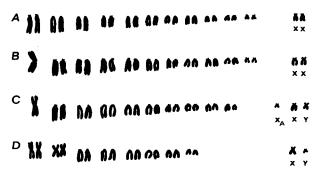


FIG. 4. Representative karyotypes of Vampyressa pusilla thyone (Gardner, 1977a). A) 2n = 23-24, FN = 22; female; Villavicencio, Intend. Meta, Colombia; USNM 507191. B) 2n = 22-23, FN = 22; female; Santa Elena, Dept. Huánuco, Peru; LSUMZ 14235. C) 2n = 22-23, FN = 22; male; Santa Elena, Dept. Huánuco, Peru; LSUMZ 14234. D) 2n = 18, FN = 20; Central America (Baker et al., 1973).

Perú, where most captures occurred between 1830 and 2000 h, although bats were captured occasionally throughout the night. Bonaccorso (1979) also found them more active during the first 2 h after sunset.

The roosting habits of *V. pusilla* are not well know. Davis and Dixon (1976) reported that they did not use buildings of a nearby village for daytime roosts, although the species was found in unusually high concentrations in and near the village. Hall and Jackson (1953: 645) disturbed a female *V. pusilla* when they, "had pushed aside bushes that partly obstructed the trail." Timm (1984) reported a single male *V. pusilla* roosting under a cut *Philodendron* sp. leaf in Costa Rica. The bat presumably had cut the veins of the leaf near the base, causing (p. 167), "the entire margin of the leaf to collapse downward forming a pyramid-shaped tent." Similar construction of tents by other species of bats has been reported (Timm, 1984).

GENETICS. Two chromosomal races of V. pusilla were described by Baker et al. (1973). The first, from Honduras and Nicaragua, has a diploid number (2n) of 18 and a fundamental number (FN) of 20, apparently with an XX/XY sex-determining system (Fig. 4). Six pairs of autosomes are acrocentric and two are metacentric or submetacentric. The X chromosome is small and subtelocentric; and Y is the smallest chromosome of the complement and has a small second arm. A second chromosomal morph, from Colombia, is radically different, with 2n = 24 in females and 2n = 23 in males (Fig. 4). The FN is 22 if all autosomes are considered uniarmed. Two pairs of autosomes have small, distinct second arms. There are no metacentric or submetacentric autosomes. In males three chromosomes in the complement are distinctly different from others in size and shape. This signifies a sex-determining system other than XX/XY.

Baker et al. (1973) also showed that these chromosomal differences were not reflected in morphology. There was no significant geographical variation for one external and eight cranial measurements.

The Colombian chromosomal morph of V. pusilla is similar to that of Mesophylla macconnelli (2n = 21/males, 22/females; FN = 24). In addition, the sex-determining system appears to be similar (Baker et al., 1973). Baker (1973) proposed a line of evolution consisting of Chiroderma, Vampyressa, Mesophylla, and Ectophylla within the Stenoderminae, evolving from a theoretical primitive karyotype of 2n=30 or 32, FN=56 or 60. Along this line, V. pusilla and M. macconnelli would be the karyotypically most derived species. Baker et al. (1973) modified this proposal, recognizing that M. macconnelli and the Colombian morph of V. pusilla have a similar sex-determining mechanism yet differ in cranial morphology and dentition. They postulated (p. 8) that these species evolved from a common ancestor with the derived sex-determining mechanism (where the Y has probably been translocated to an autosome) and the Central American karyotype has "undergone additional alterations that have resulted in a sex-determining system appearing as the classical XX/XY." Baker et al. (1973) proposed a closer relationship between V. pusilla and M. macconnelli than between V. pusilla and V. nymphaea or V. brocki.

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Gardner (1977a:300-302) presented a third karyotype of V. pusilla from Perú with 2n = 22 in males, 23 in females, and FN = 22 (Fig. 4). The chromosomes are described as follows: "Autosomes: 1 unpaired large metacentric and 9 pairs of mediumsized to small acrocentrics. The female has an additional pair of autosomes, the smallest in the complement, here considered to be acrocentric for the determination of FN, although each bears a very short second arm. The male possesses an unpaired acrocentric, which for descriptive purposes is considered with the sex chromosomes. Sex chromosomes: the X is considered to be a medium-sized subtelocentric because it is unpaired in the male and is comparable in size to the X in other Vampyressa. The male, in addition to the X and the small acrocentric mentioned previously, possesses a small submetacentric, which I presume represents the Y chromosome translocated to one of the smallest autosomes." It differs from the Colombian karyotype of Baker et al. (1973) by having a large, unpaired metacentric autosome and lacking one pair of acrocentrics. The unpaired chromosomes in males may differ slightly between the two chromosomal forms, but are essentially similar.

In his analysis of the evolution of Vampyressa, Gardner (1977a) noted that the range of diploid numbers in the subgenus Vampyressa is much larger than that in Vampyriscus (14 to 24 and 24 to 26, respectively) and that the fundamental number displayed by Vampyressa is at least one-half that of Vampyriscus (20 to 24 and 44 to 48, respectively). By plotting FN against 2n, he derived a theoretical ancestral karyotype of 2n = 26, FN = 24. From this karyotype, the Central American karyotype can be derived with two tandem and two Robertsonian fusions. Gardner (1977a) postulated that because this chromosomal configuration has a normal XX/XY arrangement, it must have developed before the South American karyotypes with multiple sex-determining mechanisms. The Colombian morph of V. pusilla can be derived with one tandem fusion and a Y-autosome fusion of the ancestral karyotype. The unpaired metacentric in the Peruvian form could be either a Robertsonian fusion or an isochromosome.

The generic phylogeny proposed by Gardner (1977a) is fundamentally different than that of Greenbaum et al. (1975), who postulated an ancestral karyotype of 2n=30, FN=56, most similar to that of V. nymphaea (2n=26, FN=48). As Gardner (1977a) interpreted this, V. brocki (2n=24, FN=44) would have evolved from this karyotype with pericentric inversions of two autosomal chromosomes and a centric fusion. The Colombian form of V. pusilla then could have evolved with 11 additional pericentric inversions. Thus, the subgenus Vampyriscus would have been the predecessor of the nominate subgenus. Gardner (1977a) cited the retention of the maximum number of molars and incisors in V. melissa as evidence that from a morphological view, it is the least derived Vampyriscus, rather than the reverse.

With Gardner's (1977a) theoretical ancestral karyotype, V. melissa (2n = 14, FN = 24) can be derived through a series of six Robertsonian fusions. V. brocki would have evolved through 11 inversions and one tandem fusion. Vampyressa nymphaea can be derived with 12 inversions.

Gardner (1977a) also doubted the close relationship between V. pusilla and Mesophylla macconnelli as proposed by Baker et al. (1973). His argument was that this close relationship would imply either the inclusion of Mesophylla in the genus Vampyressa, at least as a subgenus, or formation of three genera: Vampyressa, including pusilla and melissa; Vampyriscus, including nymphaea, bidens, and brocki; and M. macconnelli. The close morphological similarities among species included in the genus Vampyressa do not support either option. Gardner (1977a) stated that it is premature to grant a close relationship between V. pusilla and M. macconnelli on the basis of chromosomal similarities until the evolution of the sex-determining system is better understood.

Myers et al. (1983) reported the karyotype of three specimens of V. p. pusilla from Paraguay as 2n=20 and FN=36. This karyotype is distinct from any of those reported for V. p. thyone. The sex-determining system was not described.

REMARKS. Peterson (1968) recognized three subgenera in *Vampyressa*, with *V. bidens* in the subgenus *Metavampyressa* on the basis of having only one lower incisor on each side. Davis (1975) found a variable number of lower incisors in the population of *V. bidens* he studied and questioned their separation into a distinct subgenus. He recommended that *Metavampyressa* be considered a junior synonym of *Vampyriscus*.

Baker et al. (1973) did not recognize subspecies in Vampyressa pusilla on the basis of karyotypic and morphometric data. All of the localities they studied, however, (Colombia, Honduras, Nicaragua, Ecuador, Venezuela, and Panamá) were in the range that Peterson (1968) cites for V. p. thyone. No specimens from Paraguay or Brazil, the range of the nominate subspecies, were examined. Myers et al. (1983) reported a karyotype for three specimens from Paraguay (V. p. pusilla) unlike any known from V. p. thyone.

The name Vampyressa is derived from the Serbian Wampira and literally means small vampire. This comes from the propensity of early naturalists to regard all Neotropical bats as vampires. Pusilla

is from the Latin pusillus meaning small or petty.

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