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Systematics of *Vampyressa melissa* Thomas, 1926 (Chiroptera: Phyllostomidae), with descriptions of two new species of *Vampyressa*

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ABSTRACT

Vampyressa melissa is a poorly known phyllostomid bat listed as vulnerable by the International Union for Conservation of Nature (IUCN). Since its description in 1926, fewer than 40 *V. melissa* have been reported in the literature, and less than half of these may have been correctly identified. During revisionary studies of *Vampyressa*, we uncovered two previously unrecognized species related to *V. melissa*, all associated with higher elevation habitats (>1400 m), one from the Andes of Colombia (*Vampyressa sinchi*, new species) and the other from western Panama (*Vampyressa elisabethae*, new species) revealing that *V. melissa*, as traditionally defined, is a composite of at least three species. In this paper, we provide a restricted diagnosis for the genus *Vampyressa*, an emended diagnosis of *V. melissa*, and descriptions of the two new species. The separation of these frugivorous bats, previously identified as *V. melissa*, into three isolated upper-elevation species, each having restricted distributions further highlights their fragile conservation status.

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INTRODUCTION

Commonly known as “yellow-eared bats,” species of *Vampyressa* and their allies have been regarded as primarily or exclusively frugivorous (Gardner, 1977a); nevertheless, little is known about their feeding habits and ecology. The genus *Vampyressa* (sensu lato Simmons, 2005) has received much attention beginning with the recognition of its paraphyly as a result of the comprehensive morphological phylogeny developed by Wetterer et al. (2000). Gardner (1977b) illustrated the major chromosomal differences in *Vampyressa* (sensu lato) and Peterson (1968) recognized three distinct evolutionary lineages for *Vampyressa* (s.l.) as the subgenera *Vampyressa*, *Metavampyressa*, and *Vampyriscus*, a revision acknowledged in Koopman’s (1994) classification. Davis (1975), however, recognized two subgenera: *Vampyriscus* (with *Metavampyressa* a synonym) to include *V. bidens*, *V. brocki*, and *V. nymphaea*; and *Vampyressa* to include *V. pusilla* and *V. melissa*. More recent work has provided molecular support for treating *Vampyressa* and *Vampyriscus* as separate genera (Baker et al., 2003; Hoofer and Baker, 2006; Hoofer et al., 2008). This arrangement was recognized by Arroyo-Cabrales (2008a, 2008b) and is followed here. A summary of historical taxonomy and contents of *Vampyressa* and *Vampyriscus* since the three subgenera proposal of Peterson (1968) is provided in the table 1.

Revisionary work at the species level is scarce; a recent exception is that of Lim et al. (2003) who recognized *V. pusilla* and *V. thyone* as separate species. *Vampyressa melissa*, as restricted here, is among the rarer Neotropical stenodermatines. The species is restricted to Andean slopes (between 1180 and 2600 m) with fewer than 40 literature records attributed to this taxon, and even fewer specimens (approximately 20) actually deposited in museum collections. Oldfield Thomas (1926) described the species based on material collected in the northern region of Chachapoyas, Peru, by R.W. Hendee during the Godman-Thomas Expedition. Thomas (1926: 157) remarked that *V. melissa*, among the five species of *Vampyressa* recognized at that time, was “a very strongly marked species.” Goodwin (1963) noted the larger size of *V. melissa* as compared to other *Vampyressa*, along with other distinctive characters such as the hairy and fringed uropatagium, and the peculiar shape and relative size of its lower molars. Although *V. melissa* is indeed a distinctive species, easily recognizable upon close examination, various interpretations of the characters mentioned in the few published reports (e.g., Peterson, 1968), together with the lack of taxonomic keys and comparisons with closely related taxa, have contributed to many misidentifications.

Ongoing morphological and quantitative studies of *Vampyressa* have revealed that specimens previously identified as *V. melissa* actually represent three species, one from Central America and two (including *V. melissa*) from South America. The Central American form is represented by a small series of four specimens in the National Museum of Natural History, Washington, DC, collected in the early 1960s during a countrywide survey of the ectoparasites of Panamanian mammals. Another specimen from Panama was acquired by the National Museum in 1976.

A single specimen collected in the eastern Cordillera of Colombia in the 1970s by Kjell von Sneider and labeled as *Vampyressa melissa* (FMNH 114028) also differs from *V. melissa* (BMNH 26.5.3.4) and represents an undescribed South American form. We later discovered two additional specimens matching the characteristics of FMNH 114028.

TABLE 1. Historical taxonomy and contents of *Vampyressa* and *Vampyriscus* departing from the split into three subgenera proposed by Peterson (1968).

Peterson (1968) ^a	Davis (1975) ^a	Lim et al. (2003) ^c	Arroyo-Cabrales (2008a, b) ^f
<i>Vampyressa</i> ^b <i>melissa</i>	<i>Vampyressa</i> ^b <i>melissa</i>	<i>Vampyressa</i> ^b <i>melissa</i>	<i>Vampyressa melissa</i>
<i>Vampyressa</i> ^b <i>pusilla</i>	<i>Vampyressa</i> ^b <i>pusilla</i>	<i>Vampyressa</i> ^b <i>pusilla</i>	<i>Vampyressa pusilla</i>
<i>pusilla</i> ^c			
Synonym:		Synonym:	Synonym:
<i>natterii</i> ^d		<i>nattereri</i>	<i>nattereri</i>
<i>thyone</i> ^c		<i>Vampyressa</i> ^b <i>thyone</i>	<i>Vampyressa thyone</i>
Synonyms:		Synonyms:	Synonyms:
<i>minuta</i>		<i>minuta</i>	<i>minuta</i>
<i>venilla</i>		<i>venilla</i>	<i>venilla</i>
<i>Metavampyressa</i> ^b <i>brocki</i>	<i>Vampyriscus</i> ^b <i>brocki</i>	<i>Vampyriscus</i> ^b <i>brocki</i>	<i>Vampyriscus brocki</i>
<i>Metavampyressa</i> ^b <i>nymphaea</i>	<i>Vampyriscus</i> ^b <i>nymphaea</i>	<i>Vampyriscus</i> ^b <i>nymphaea</i>	<i>Vampyriscus nymphaea</i>
<i>Vampyriscus</i> ^b <i>bidens</i>	<i>Vampyriscus</i> ^b <i>bidens</i>	<i>Vampyriscus</i> ^b <i>bidens</i>	<i>Vampyriscus bidens</i>

^aClassification based on morphology.

^bSubgenus of *Vampyressa*.

^cSubspecies of *V. pusilla*.

^dIncorrect spelling of *Vampyressa nattereri* Goodwin (1963: 16).

^eClassification based on morphology and mtDNA data.

^fThe classification followed by this paper; supported by the molecular studies of Baker et al. (2003), Hoofer and Baker (2006), and Hoofer et al. (2008).

Herein, we report on our systematic study of these specimens previously identified as *V. melissa*. In addition, we provide a restricted diagnosis of the genus *Vampyressa*, a diagnosis and revised description of *V. melissa*, and descriptions of two previously undescribed species of *Vampyressa*.

MATERIAL AND METHODS

External and craniodental characters are based mainly on, but not restricted to, those defined by Tavares (2008) and Wetterer et al. (2000). Other anatomical features are derived from Giannini et al. (2006) and Giannini and Simmons (2007), or are described as follows:

Accessory cusp near apex of upper canine. A small “cusp” at the apex of the mediolateral ridge forming the lingual border of the longitudinal sulcus on posterior crown of upper canines. In most stenodermatines, the mediolateral ridge is complete to the tip of the canine. In *Vampyressa* (and *Mesophylla*) the mediolateral ridge is incomplete and terminates as a small subapical step on the posterointernal crown of the canine. *Ectophylla* has a similar accessory subapical cusp, which differs in that it is thicker and is at the apex of both the mediolateral and a secondary ridge along the lingual surface of the upper canine (Tavares, 2008: chars. 191 and 192).

Accessory medial foramen. A small foramen located either in the septum (medial flange of the palatine process of the premaxilla) separating incisive foramina, or located in the midline between premaxillae anterior to the incisive foramina. In all *Vampyressa* examined, this foramen is in the septum (illustrated herein).

Extension of caudal border of pterygoid. The caudal border of the pterygoid process extends posterolaterally across the basisphenoid toward the auditory bullae as a low ridge. This ridge passes anterior to the bony excrescences and forms the anterior margin of the eustachial groove. In *Vampyressa* this ridge is low and well separated from the foramen ovale; in some stenodermatines (e.g., *Vampyriscus*), the ridge may be more highly developed and better described as a flange; in others, this ridge may lie along the posterior border of the foramen ovale (e.g., *Platyrrhinus*) or on a bridge separating anterior and posterior segments of a large foramen ovale (e.g., *Chiroderma*).

Mesethmoid plate. There are differences among species of *Vampyressa* in the morphology of the mesethmoid plate visible in frontal view within the external nares (illustrated herein: fig. 5).

Posttympanic process. The posttympanic process is comprised of a ventral extension of the squamosal and lateral process of the exoccipital that covers the posterolateral rim of the otic capsule. In *Vampyressa* (and *Mesophylla*) these two bones are unfused, whereas in other vampyressine stenodermatids these bones are fused at least at the tips. The unfused condition as well as the subapical “cusp” on the canine is illustrated in figure 26A (*Mesophylla*) in Wetterer et al. (2000).

Sphenorbital foramen or fissure. In *Vampyressa*, this opening, posterior to the optic foramen, is either a discrete foramen or an elongate fissure (e.g., Giannini et al., 2006: fig. 11).

Specimens examined for this study are housed in the following collections:

AMNH	American Museum of Natural History, New York
BMNH	British Museum (Natural History) London, UK
CMUFLA	Coleção de Mamíferos da Universidade de Lavras, Lavras, Minas Gerais, Brazil
DZSJRP	Coleção de Chiroptera do Departamento de Zoologia de São José do Rio Preto, São Paulo, Brazil
FMNH	Field Museum of Natural History, Chicago, Illinois
IAvH	Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Villa de Leyva, Boyacá, Colombia
MEPN	Museo Escuela Politécnica Nacional, Quito, Ecuador
MHNUC	Museo de Historia Natural, Universidad del Cauca, Popayán, Colombia
MUSM	Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Peru
MZUSP	Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil
RMNH	National Museum of Natural History, Leiden, Netherlands
UMMZ	Museum of Zoology, University of Michigan, Ann Arbor, Michigan
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C.

For the morphometric analyses we measured 56 specimens of the five species of *Vampyressa* we recognize here (appendix). Our observations are based on adults, with the exception of a single individual (MUSM 8915) demonstrated as young by the retention of an upper left

deciduous premolar. The dental homology for premolars follows Miller (1907): first upper premolar (P3), second upper premolar (P4), first lower premolar (p2), and second lower premolar (p4). We recorded external and craniodental measurements in millimeters (mm) using digital calipers accurate to 0.01 mm; body mass is in grams (g). Standard external measurements (TL, total length; HF, hind foot length; E, ear length; and body mass) were taken from skin labels or database records. The abbreviation *s.u.* following the measurement of the foot of the holotype of *V. melissa* means *sine unguis* ("without claw") and was the standard practice in Europe for recording foot measurements. Measurements are defined as follows:

Total length (TL): Distance from the tip of the snout to end of the body.

Hind foot length (HF): Distance from the base of calcar to tip of the claw of longest toe.

Ear length (E): Perpendicular height from the ear notch to tip of the pinna without stretching.

Tragus length (TrL): Perpendicular height of tragus, measured from the notch to tip.

Forearm length (FA): Distance from the end of olecranon process to wrist (including carpals) with the wing folded.

Third metacarpal length (METIII): Distance from the wrist (including carpals) of the folded wing to distal end of third metacarpal.

Fourth metacarpal length (METIV): Distance from the wrist (including carpals) of the folded wing to distal end of fourth metacarpal.

Fifth metacarpal length (METV): Distance from the wrist (including carpals) of the folded wing to distal end of fifth metacarpal.

Tibia length (TiL): Distance from articulation with femur to articulation with foot (including tarsals).

Greatest length of the skull (GLS): Distance from the posteriormost point of occipital to the anteriormost surface of premaxillae (not including incisors).

Condylolincisive length (CIL): Distance from a line connecting the posteriormost margins of occipital condyles to the anterior face of upper incisor(s).

Condyllocanine length (CCL): Distance from the posterior margin of the occipital condyle to the anterior face of the canine.

Postorbital breadth (PB): Least breadth behind orbits, always posterior to postorbital bulge if present.

Interorbital breadth (IB): Least breadth measured across orbitals, always anterior to postorbital bulge if present.

Braincase breadth (BB): Greatest breadth of braincase.

Mastoid breadth (MB): Greatest breadth across mastoid region.

Zygomatic breadth (ZB): Greatest breadth across zygomatic arches.

Maxillary tooththrow length (MTRL): Distance from anterior face of upper canine to posteriormost margin of last upper molar.

Mandibular tooththrow length (MANDL): Measured from anterior face of lower canine to posterior margin of last lower molar. Includes m3 in *V. melissa* and *V. sinchi*, sp. nov.; m3 missing in *V. elisabethae*, sp. nov.

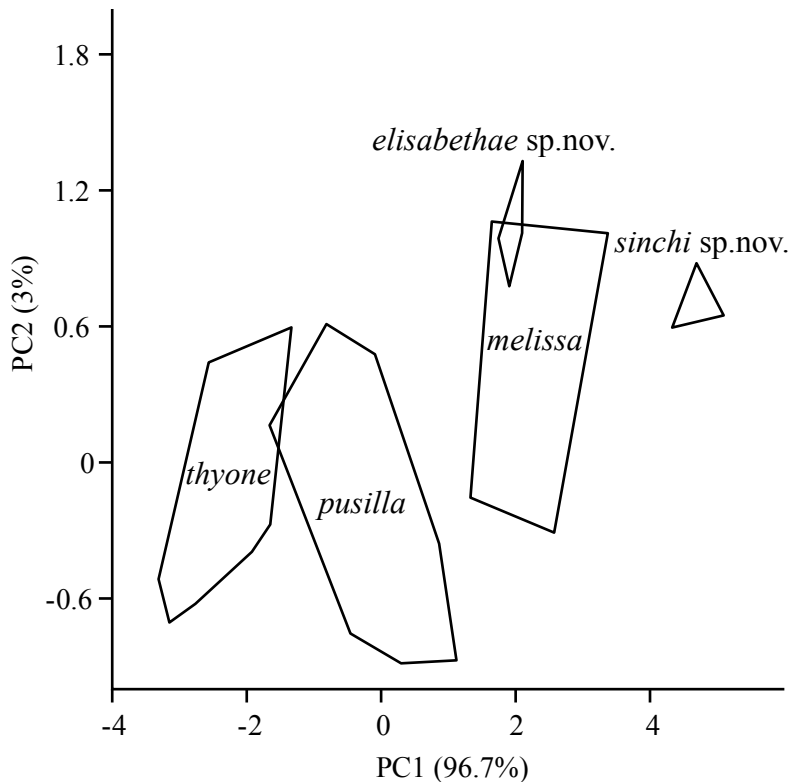


FIG. 1. Plot of components 1 and 2 extracted from the PCA analysis of external measurements from specimens of *Vampyressa*; the amount of the variation explained by each principal component is in parenthesis.

We tested for normality of the several samples of the univariate data using Shapiro-Wilk's tests (Shapiro and Wilk, 1965). Seventeen ANOVA and Tukey's tests for unequal sample sizes were used to compare measurements between groups within the *Vampyressa* complex of species (*V. melissa*, *V. sinchi*, sp. nov., and *V. elisabethae*, sp. nov.). We then included the selected external and skull measurements useful to discriminate between these groups to build correlation matrices, together with samples of all *Vampyressa* species currently recognized, and performed a principal-component analyses (PCA) for data reduction and visualization. Analyses were performed using Systat for Windows, version 11.0, and PAST (Hammer et al. 2001).

RESULTS

All external metric characters (FA, METIII, METIV, METV, TiL) and six skull metric characters (GLS, CIL, CCL, MB, ZB, and MTRL) were useful to discriminate among groups among *Vampyressa pusilla*, *V. thyone*, and the three forms of the *Vampyressa melissa* complex ($p < 0.01$).

Most of the variation was explained by the two first components in the PCA based on the five external metric characters for 55 specimens of *Vampyressa* (fig. 1). The bivariate plot of the

TABLE 2. Factor loadings for the components extracted from correlation matrices resulting from the principal-components analysis (PCA) of five external and six skull characters comparing all the species of *Vampyressa*.

External Characters	Axis					
	I	II	III	IV	V	VI
FA	0.42	0.31	-0.16	-0.84	0.01	–
METIII	0.43	0.10	0.75	0.12	0.48	–
METIV	0.42	0.33	0.17	0.30	-0.77	–
METV	0.41	0.32	-0.61	0.45	0.40	–
TiL	0.54	-0.82	-0.14	0.00	-0.09	–
Skull Characters						
GLS	0.39	-0.12	-0.01	-0.37	0.08	0.83
CIL	0.46	-0.10	0.28	-0.33	0.63	-0.44
CCL	0.46	-0.07	0.29	-0.22	-0.77	-0.25
MB	0.32	-0.02	0.49	0.78	0.09	0.19
ZB	0.39	0.86	-0.33	0.08	0.02	-0.03
MTRL	0.41	-0.49	-0.70	0.29	-0.01	-0.14

first and second components extracted from the external measurements showed a clear separation in size between the small (*V. pusilla* and *V. thyone*) and the large species of *Vampyressa* (*V. melissa*, *V. sinchi*, sp. nov., and *V. elisabethae*, sp. nov.). The samples of the *V. melissa* and *V. elisabethae*, sp. nov., showed some size overlap but *V. sinchi*, sp. nov., was clearly segregated from all the others (fig. 1). Along PC 1, all external metric characters varied equally and positively with size, but PC 2 loadings indicated that TiL was not proportional to FA, METIII, METIV, and METV (table 2).

The second PCA employing cranial dimensions for the same 55 specimens analyzed for external characters also resulted in the variation mostly explained by the two first components (fig. 2). Bivariate plots of the first and second components extracted for skull measurements (fig. 2) also showed clear separations in size between the small species of *Vampyressa* (*V. pusilla* and *V. thyone*) and the large *Vampyressa*, and within species of the *V. melissa*-like species (fig. 2). All skull metric characters varied equally and positively with size along PC I, but for skull characters, zygomatic breadth (ZB) was not proportional to the characters describing skull length (e.g., MTRL) and to the mastoid breadth (MT) as demonstrated by the variation along PC 2 (table 2).

Based on the morphometric results, and our study of several discrete characters that were variable within the larger “*V. melissa*” complex and between these larger species and *V. pusilla* and *V. thyone*, we recognized two new forms that are described and named below. To clarify the diagnostic characters defining *Vampyressa* (sensu stricto) and to distinguish *V. melissa* from other taxa diagnosed in this study, we provide emended diagnoses of both the genus *Vampyressa* and *V. melissa*.

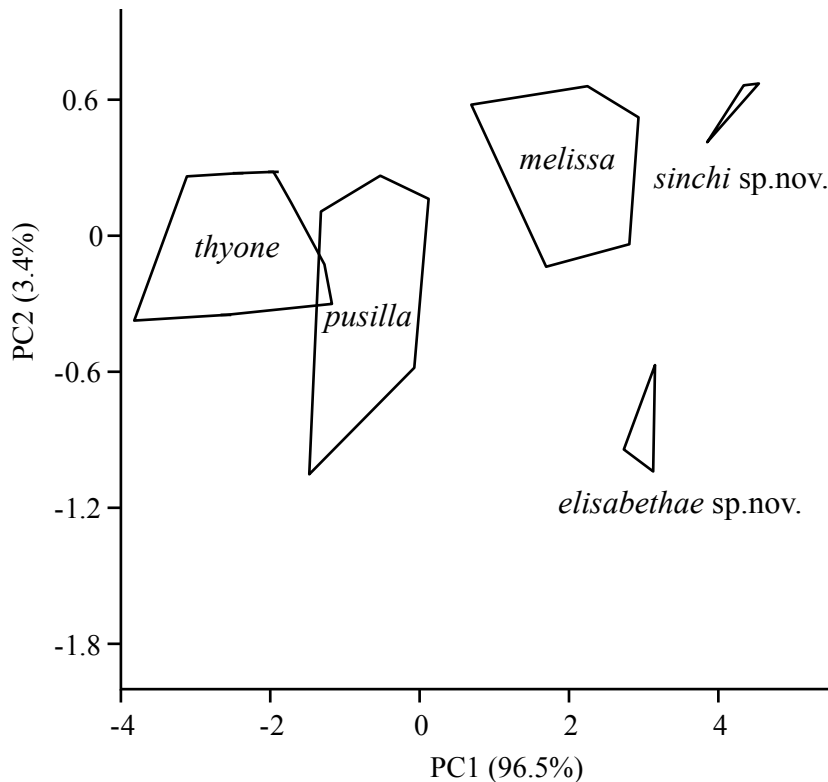


FIG. 2. Plot of components 1 and 2 extracted from the PCA analysis of skull measurements from specimens of *Vampyressa*; the amount of the variation explained by each principal component is in parenthesis.

SYSTEMATICS

CLASS MAMMALIA

ORDER CHIROPTERA

FAMILY PHYLLOSTOMIDAE GRAY, 1825

SUBFAMILY STENODERMATINAE GERVAIS, 1856

Genus *Vampyressa* Thomas, 1900

Phyllostoma Wagner, 1843: 366; part; not *Phyllostoma* Cuvier, 1800.

Artibeus: Tomes, 1860: 260; incorrect subsequent spelling, not *Artibeus* Leach, 1821.

Vampyressa Thomas, 1900: 270; type species *Phyllostoma pusillum* Wagner, 1843, by original designation; described as a subgenus of *Vampyrops* Peters, 1865.

Vampiressa Festa, 1906: 7; incorrect subsequent spelling of *Vampyressa* Thomas, 1900.

Vamqyressa Cabrera, 1958: 83; incorrect subsequent spelling of *Vampyressa* Thomas, 1900.

Vampiressa Silva, 1975: 52; incorrect subsequent spelling of *Vampyressa* Thomas, 1900.

Vampuressa Coimbra, Borges, Guerra, and Mello, 1982: 34; incorrect subsequent spelling of *Vampyressa* Thomas, 1900.

Vampiressa Montenegro and Romero-Ruiz, 2000: 646; incorrect subsequent spelling of *Vampyressa* Thomas, 1900.

Vapyressa Contreras-Vega and Cadena, 2000: 287; incorrect subsequent spelling of *Vampyressa* Thomas, 1900.

RESTRICTED DIAGNOSIS OF *VAMPYRESSA*: The following combination of characters defines the genus *Vampyressa* as currently constituted (five species recognized herein): Two pairs of white facial stripes; a dorsal stripe is lacking; interfemoral membrane usually conspicuously furred (hairs may be restricted to medial area) and often fringed; a tail is lacking; inner upper incisors relatively long, bifid or weakly trifid, and usually converging distally; accessory subapical “cusp” on upper canines; caniniform p2; p4 lacks a prominent anterior cingulum; second lower molar (m2) has a well-developed, high, and bladelike entoconid; septum (medial flange of palatine processes of premaxillae) between incisive foramina perforated by large accessory medial foramen; irregularly fenestrated palate, foramen ovale relatively small and located well anterior to the caudal extension of the pterygoid (the ridge forming the anterolateral border of the eustachial groove); portions of squamosal and exoccipital bones comprising posttympanic process unfused; dental formula $2/2, 1/1, 2/2, 2/2-3 \times 2 = 28-30$.

COMPARISONS WITH *VAMPYRISCUS*: *Vampyriscus*, which we recognize as a separate genus, includes three species (*Vampyriscus bidens*, *V. brocki*, and *V. nymphaea*). *Vampyriscus* can be distinguished from *Vampyressa* by the presence of a middorsal stripe (weakly developed in some *V. nymphaea* and absent in some *V. brocki*); lack of extensive fur and absence of a fringe of hair on interfemoral membrane; upper inner incisors long, pointed, and parallel in *V. brocki*, or unevenly bifid and convergent at the tips in *V. bidens* and *V. nymphaea*; normal crowns of upper canines (lack subapical cuspule); p2 not caniniform; p2 and p4 with well-developed anterior cingulae; entoconid of m2 not prominent as an elevated bladelike cusp; septum between incisive foramina narrow with a small medial accessory foramen in *V. bidens*, or very narrow and lacking the medial accessory foramen in *V. brocki* and *V. nymphaea*; palate comparatively flat with scattered small, porelike perforations (not obviously fenestrate as in *Vampyressa*); foramen ovale relatively large, adjacent to and partially occluded by high ridge of caudal extension of the pterygoid (in posterior view); bones comprising posttympanic process fused.

Vampyressa melissa Thomas, 1926

Melissa's Yellow-eared Bat

Figures 4–8

Vampyressa melissa Thomas, 1926: 157, type locality “Puca Tambo, Peru, altitude 7100’,” San Martín, Peru.

Vampyressa (Vampyressa) melissa: Peterson, 1968: 14; name combination.

TYPE MATERIAL: The holotype BMNH 26.5.3.4 consists of a relatively well-preserved skin and skull of an adult female from Puca Tambo (6°9’S, 77°16’W), Moyobamba, department of

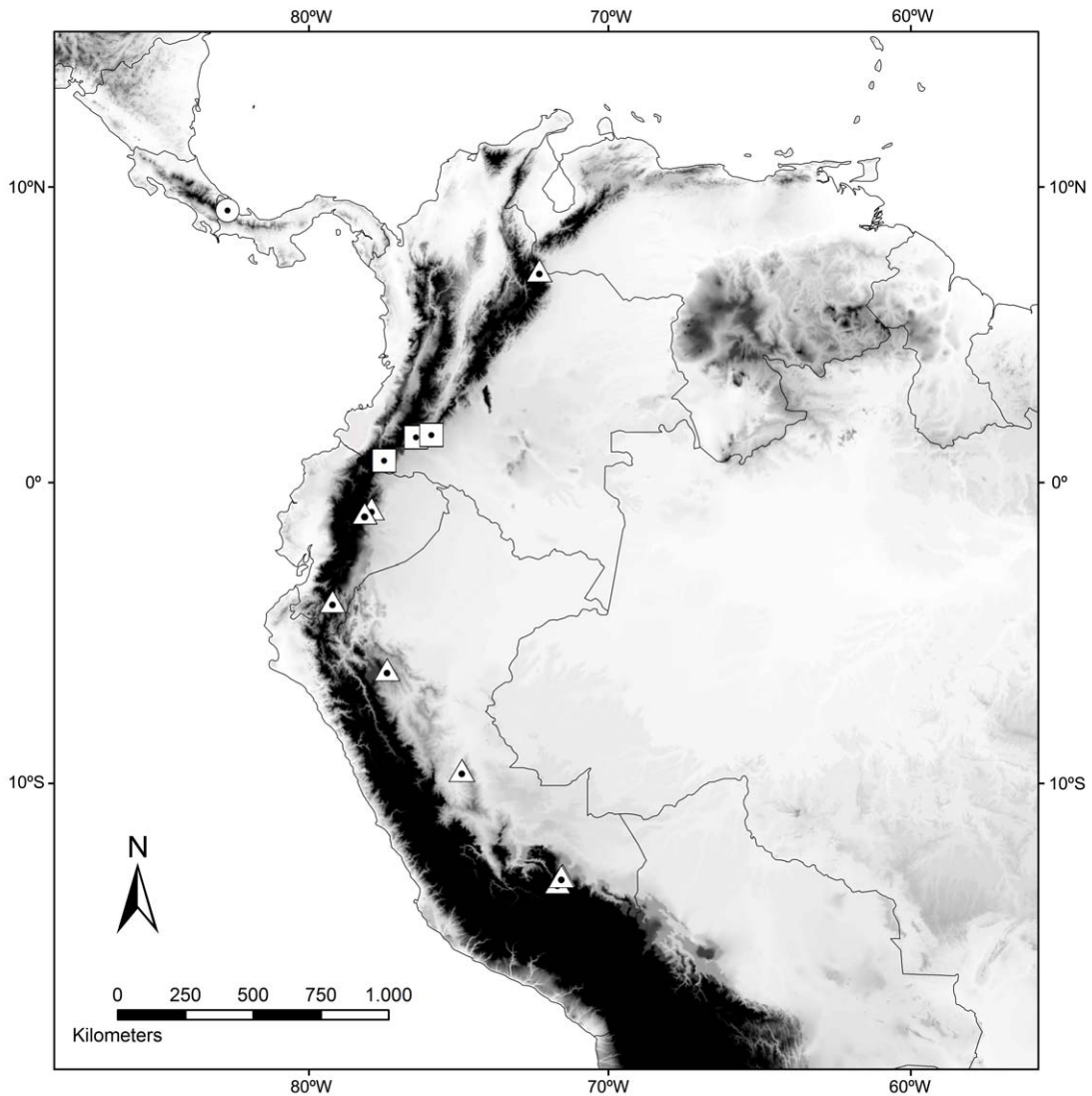


FIG. 3. Map showing collecting localities of *Vampyressa elisabethae*, sp. nov. (circle), *V. melissa* (triangles), and *V. sinchi*, sp. nov. (squares). Numbers refer to entries in the specimens examined list (appendix).

San Martín, Peru, collected at 1480 m by R.H. Hendee (no. 408) on January 15, 1926, during the Godman-Thomas Expedition to Peru.

MEASUREMENTS OF THE HOLOTYPE: The following measurements (mm) of the holotype are from the skin label: TL 54, HF 10.5 *s.u.*, E 16. Additional measurements (mm) taken by one of us (V.C.T.) from the holotype are: FA 36.8, TiL 14.9, GLS 21.2, CIL 20.2, CCL 19.5, PB 5, IB 6.2, BB 8.9, BH 8.7, MB 10.4, ZB 12.5, MTRL 6.9, and MANDL 7.4.

DISTRIBUTION: As defined here, *Vampyressa melissa* is currently known from upper-elevation localities (1180–2763 m) in Andean Colombia, Ecuador, and Peru (fig. 3).

EMENDED DIAGNOSIS: A large *Vampyressa* (FA 34.5–37.7, $n = 9$; GLS 21.2–22.6, $n = 9$; table 3) with a broad skull (ZB 12.5–13.5, $n = 8$; table 3); anteriorly tapering rostrum; discrete orbi-

TABLE 3. External and craniodental measurements (mm), sample statistics,^a and dental formula (DF) of *Vampyressa melissa*, *V. pusilla*, and *V. thyone*.

	<i>V. melissa</i>	<i>V. pusilla</i>	<i>V. thyone</i>
Sex	6 ♀, 2 ♂	10 ♀, 7 ♂	10 ♀, 10 ♂
TL	61.3 ± 3.4 (58–66) 5	50.3 (48–53) 3	47.3 ± 4.7 (43–65) 20
HF	9.9 ± 0.9 (8.9–11.0) 7	8.8 ± 1 (6–9) 10	9 ± 0.9 (7–10) 20
E	16.1 ± 3.2 (13–22) 6	12.9 ± 1.7 (11.2–15.0) 9	14 ± 1 (12–16) 20
FA	36.7 ± 1.1 (34.5–37.7) 9	33.4 ± 0.6 (32.3–34.3) 16	30.6 ± 0.7 (29.3–32.3) 19
METIII	34.8 ± 2.0 (33.7–37.3) 9	32.4 ± 1.2 (29.9–34.2) 15	29 ± 0.7 (27–30) 19
METIV	34.8 ± 0.6 (34.1–37.0) 9	31.6 ± 0.7 (29.8–32.5) 15	28.9 ± 1 (27.1–32.3) 19
METV	36.6 ± 0.9 (35.1–38.2) 9	32.5 ± 0.9 (30.6–33.9) 15	30.2 ± 0.9 (28.7–32.3) 19
TiL	13.7 ± 0.6 (12.2–14.9) 9	12.4 ± 1 (10.6–13.7) 5	10.4 ± 0.5 (9.4–11.2) 19
GLS	21.8 ± 0.5 (21.2–22.6) 8	19.8 ± 0.4 (19.0–20.6) 15	18.2 ± 0.6 (17.1–19.2) 19
CIL	20.3 ± 0.5 (19.5–21.0) 8	18.1 ± 0.5 (17.6–19.4) 14	16.4 ± 0.6 (15.5–17.5) 19
CCL	19.6 ± 0.6 (18.7–20.5) 8	17.5 ± 0.5 (16.8–19.1) 15	15.9 ± 0.6 (14.9–17.0) 19
PB	5.2 ± 0.3 (4.6–5.7) 8	5.2 ± 0.2 (4.78–5.6) 15	4.7 ± 0.2 (4.4–5.0) 20
IB	6.2 ± 0.4 (5.4–6.6) 7	5.5 ± 0.2 (5.2–5.7) 10	5 ± 0.2 (4.5–5.2) 20
BB	9.3 ± 0.4 (8.8–10.0) 8	8.6 ± 0.23 (8.3–9.1) 14	8.2 ± 0.2 (7.7–8.6) 20
MB	10.6 ± 0.3 (10.3–11.0) 8	9.6 ± 0.3 (8.8–10.0) 15	9.1 ± 0.2 (8.6–9.4) 19
ZB	13 ± 0.3 (12.5–13.5) 8	11.5 ± 0.3 (11–12.1) 13	10.6 ± 0.4 (9.5–11.2) 20
MTRL	7.1 ± 0.4 (6.7–7.9) 8	6.6 ± 0.3 (6.1–7.3) 16	5.9 ± 0.3 (5.5–6.5) 20
MANDL	7.7 ± 0.3 (7.1–8.1) 8	6.9 ± 0.2 (6.5–7.3) 16	6.2 ± 0.3 (5.9–6.9) 20
DF	i 2/2, c 1/1, p 2/2, m 2/3	i 2/2, c 1/1, p 2/2, m 2/2	i 2/2, c 1/1, p 2/2, m 2/2

^a The sample mean plus or minus the standard error of the mean, the observed range (in parentheses), and the sample size are provided for each species.

tosphenoid foramina, well-developed postglenoid processes that project ventrally to the level of pterygoid processes; mesopterygoid fossa about as long as wide; large basioccipital-basisphenoid pits, and lacks a well-developed posterolabial cuspid on p4. *V. melissa* is larger than *V. pusilla* and *V. thyone*, but averages smaller in most dimensions than either of the new species described below.

REDESCRIPTION: *Vampyressa melissa* has sparse, long guard hairs conspicuous in the dorsal pelage; two pairs of pale facial stripes with the medial stripes extending above eyes from between ears to upper border of nasal horseshoe, and the lateral stripes extending below eyes from base of ears to upper corners of mouth. The pelage of the dorsum is uniformly brownish, a dorsal stripe is lacking. The noseleaf (lancet) is triangular, elongate, and with deep grooves separating the lateral flaps from the midrib; bicolored with most of lateral margins of the lancet and outer border of the horseshoe conspicuously pale yellow or cream color. The ear pinna is hairy from its base to halfway to the tip. The proximal two thirds of the forearm is densely furred.

All flight membranes are dark brown; the antebrachial membrane (propatagium) is narrow and the posterior plagiopatagium inserts on the hind limb at the base of the toe. The uropatagium is relatively narrow, its greatest breadth approximately half the length of



FIG. 4. Dorsal (A) and ventral (B) views of the skull of *Vampyressa elisabethae* (USNM 319283 [holotype]; male) from Bocas del Toro, Panama. Dorsal (C) and ventral (D) views of the skull of *V. melissa* (FMNH 174909; female) from Cuzco, Peru. Dorsal (E) and ventral (F) views of the skull of *V. sinchi* (FMNH 114028 [holotype]; female) from Nariño, Colombia. Scale bar = 5 mm.

the tibia; its posterior border has an inverted U-shape. Dorsal and ventral surfaces of the uropatagium are conspicuously haired and the posterior margin bears a paler fringe of hair

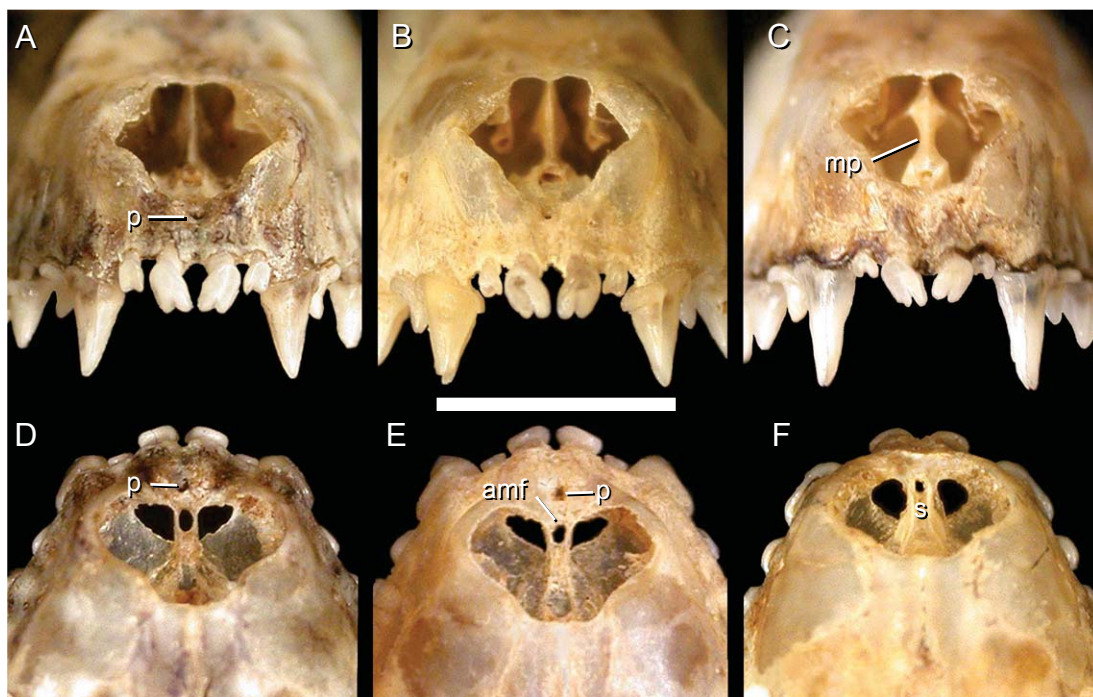
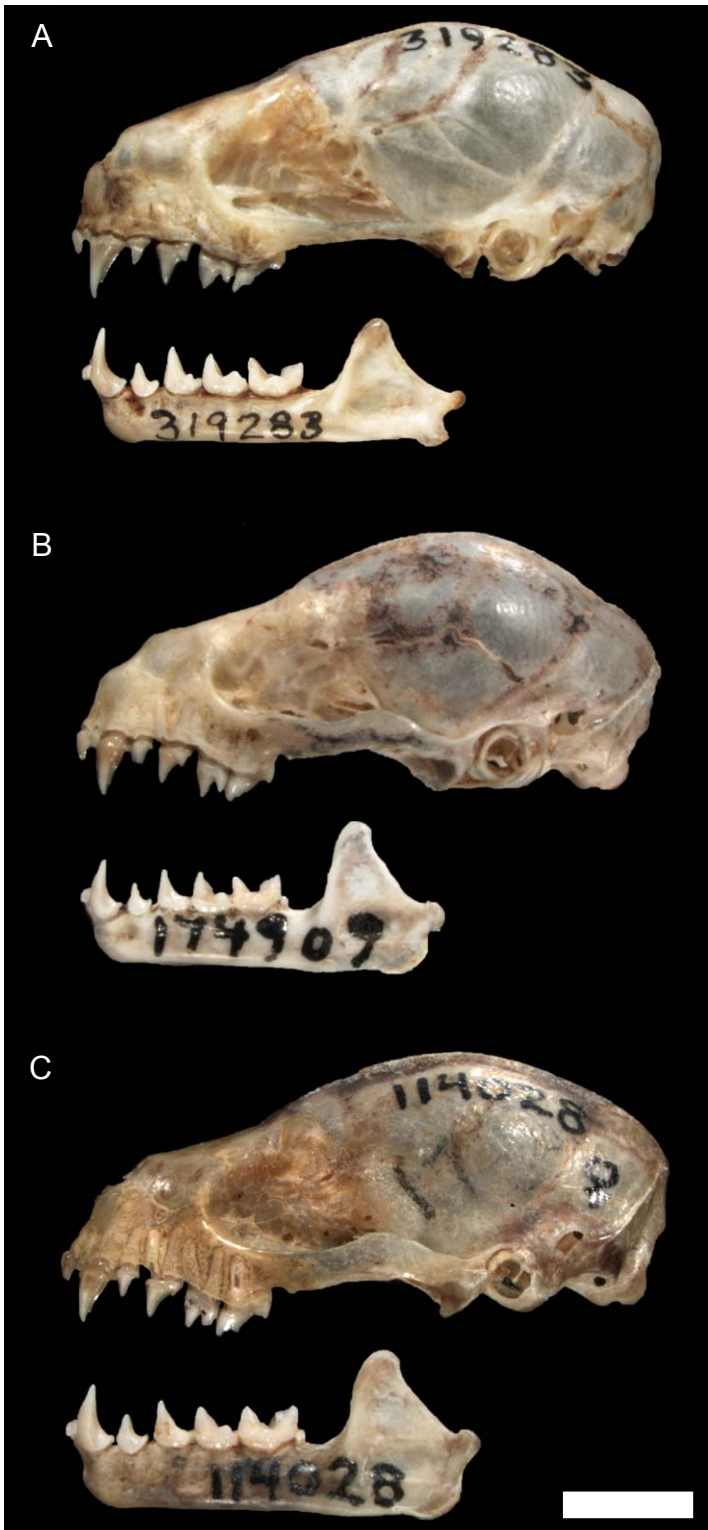


FIG. 5. Frontal view and dorsal view of external nares of the skulls of *V. melissa*, USNM 548310 (A, D); *V. sinchi*, sp. nov., FMNH 114028 [holotype] (B, E); *V. elisabethae*, sp. nov., USNM 319285 (C) and USNM 319284 (F). Abbreviations: **amf**, accessory medial foramen; **mp**, mesethmoid plate; **p**, median premaxillary pit; **s**, septum between incisive foramina. Scale bar = 5 mm.

that is longest toward the midline; lower legs, adjacent uropatagium, and dorsal surface of feet densely covered with reddish-brown hair.

The skull is robust; the rostrum is elevated anteriorly from a horizontal plane connecting ventral surfaces of occipital condyles and crown apices of last upper molars; premaxillae inclined posteriorly at approximately 60° from the horizontal plane (fig. 6B). The angle of the forehead with the rostrum is not abrupt (~150°) and the forehead slopes smoothly to the rostrum in lateral outline. The ventral margin of the external nares is V-shaped and bears a small medial pit (fig. 5A, D). The external nares are emarginate dorsally (nasals comparatively short; fig. 5D). The rostrum tapers anteriorly and the postorbital constriction is narrower than interorbital breadth (fig. 4C). The sagittal crest is low, but well developed; the posterior border of the skull (inteparietal region) is not conspicuously inflated (fig. 6B). The dorsoventrally thin septum separating the triangular-shaped incisive foramina is perforated by a large accessory medial foramen (fig. 5D). The lightly and irregularly fenestrate hard palate is conspicuously domed behind the incisive foramina. The shape of the emargination of the posterior border of palate is variable, yet the mesopterygoid fossa is approximately as long as wide (figs. 4D, 8A). A discrete orbitosphenoid foramen is present. The hamular process of the pterygoid and the foramen ovale are approximately even with (on same lateral plane as) the robust postglenoid process. The paired basioccipital-basisphenoid pits are long and extend anterior to anterior margin of bullae. The caudal



extension (ridge) of each pterygoid is directed posterolaterally and well separated from medium-sized bony excrescences (fig. 8A). The foramen magnum is rounded in outline.

Crowns of upper incisors (I1s) are large, approximately evenly bilobate, converge apically, and have well-separated roots; outer upper incisors (I2s) also are bilobate, but much smaller, extending to or slightly beyond cingulae of upper canines (fig. 5A), and anterior portions are visible in dorsal view of the skull. There are two subequal and weakly bifid lower incisors on each side of the mandible.

The upper canine (C) is about twice the length of P4, and has a conspicuous small "cusp" at the apex of the medio-lateral ridge forming the lingual border of the longitudinal sulcus on its posterior crown. P3 is about a half or less the size of P4, which is nearly triangular, has a well-developed labial cingulum and a small posterior cuspule paired with a smaller cuspule on the postero-labial cingulum. The lower

FIG. 6. Lateral views of the skull and lower jaw of (A) *Vampyressa elisabethae* (USNM 319283 [holotype]; male). Lateral views of the skull and lower jaw of (B) *V. melissa* (FMNH 174909; female). Lateral views of the skull and lower jaw of (C) *V. sinchi* (FMNH 114028 [holotype]; female). Scale bar = 5 mm.

TABLE 4. External and craniodental measurements of the type series of *Vampyressa sinchi*, sp. nov. Measurements are in millimeters, except weight, in grams.

Character	Holotype FMNH 114028 ♀	Paratype MHNUC 1514 ♀	Paratype IAvH 2282 ♂
Weight	–	–	16 g
TL	70	70	68
HF	13	11	11.6
E	–	17	18
FA	40.5	41.5	39.1
METIII	40.0	38.0	39.0
METIV	38.2	38.6	37.9
METV	38.9	40.3	38.8
TiL	15.0	15.9	15.1
GLS	23.7	23.6	23.3
CIL	22.7	22.3	21.9
CCL	22.0	21.6	21.3
PB	5.3	5.3	5.5
IB	6.3	5.6	6.0
MB	11.2	11.4	10.8
ZB	14.2	14.8	13.9
MTRL	7.6	7.5	7.7
MANDL	8.8	8.7	8.7

canine (c) has a well-developed posterior cingulum; p2 strongly resembles the lower canine, although less than half its size; p4 has a ridge along the posterior crown of the major cusp that extends across the heel of the tooth to the posterior cingulum, but lacks a discrete posterolabial cuspid (figs. 6B, 7A).

The first upper molar (M1) has a relatively well-developed protocone, paracone, and smaller metacone. The second upper molar (M2) has a rudimentary protocone, a much-reduced metacone, and a small protoconule behind the large paracone. The first lower molar (m1) is quadrate in occlusal outline, with a large protoconid and a small blunt hypoconid. The second lower molar (m2) has a long metaconid that is twice the size of the protoconid and a large, L-shaped (bladelike) entoconid approximately the same size as the metaconid. Thomas (1926: 1) commented on the lower molars of *V. melissa*: “Its ... peculiarly shaped m1, and the unusual development of the characteristic cusps on m2 all readily distinguish it from the other species of the genus [sensu lato].” A small peglike m3 is present.

COMPARISONS: Previously, *V. melissa* was compared with presumed congeners *Vampyriscus bidens* and *V. nymphaea*. Goodwin (1963: 23), for example, briefly redescribed the holotype of *V. melissa* and commented that the skull was “about like that of *Vampyriscus nymphaea* but more robust.” However, these two taxa along with *Vampyriscus brocki* are not species of *Vampyressa* and need not be compared herein (see diagnosis for *Vampyressa*).



FIG. 7. Rami of *V. melissa*, USNM 548310 (A) and *V. elisabethae*, sp. nov., USNM 319284 (B). Note spiculelike m3 in *V. melissa* (lacking in *V. elisabethae*) and posterolabial cusp on p4 in *V. elisabethae* (lacking in *V. melissa*). Scale bar = 5 mm.

Vampyressa melissa is considerably larger than either of the other two known species of *Vampyressa* (contrast measurements of *V. melissa* with those of *V. pusilla* and *V. thylene* in table 3). *V. melissa* does merit comparison with each of the two new taxa described below (see those sections for comparisons).

During research on her doctoral dissertation, the lead author realized that Colombian specimens identified as *V. melissa* from upper elevations in the Andes were larger and more robust than *V. melissa*, and appeared to be undescribed. Here we describe this species as:

***Vampyressa sinchi*, new species**

Quechuan Yellow-eared Bat

Figures 4–6, 8–10

Vampyressa melissa: Lemke et al., 1982: 231.

Vampyressa melissa: Alberico et al., 2000: 55 (part).

HOLOTYPE: An adult female (FMNH 114028; figs. 4E–F, 5B, 5E, 6C, 8B, 9A) collected at Llorente (0°46'40" N, 77°21'50" W; 1700 m), municipio de Córdoba, departamento de Nariño, Colombia, by Kjell von Sneider (original number: 1736) on May 10 1971. The holotype is preserved as a skin and skull (table 4).

PARATYPES: An adult female (MHNUC 1514, fig. 10) caught at San Juan de Villalobos (1°33'18" N, 76°18'19" W; 1620 m), Vereda La Esmeralda, Santa Rosa, departamento de Cauca, Colombia, in the Caquetá River basin, eastern Colombian slopes of the eastern Andes by H.E. Ramírez-Chaves on 5 May 2005; and an adult male (IAvH 2282) collected in Parque Nacional Natural Cueva de los Guácharos (1°38' N, 75°58' W, 1900 m), Acevedo, departamento de Huila, Colombia, by T.O. Lemke (Lemke et al. 1982) see table 4.

DISTRIBUTION: Known only from the type series from the eastern slope of the Central Cordillera (Llorente) and eastern slopes of the Eastern Cordillera (San Juan de Villalobos and Parque Nacional Cueva de los Guácharos) of the Andes in Colombia (fig. 3).

ETYMOLOGY: A Quechuan word, *sinchi* conveys the meaning “robust and strong.” The name honors the Quechuan people of Colombia (the Ingas), and indicates the robustness of this species, the largest *Vampyressa* known. The name is to be treated as a noun in apposition.

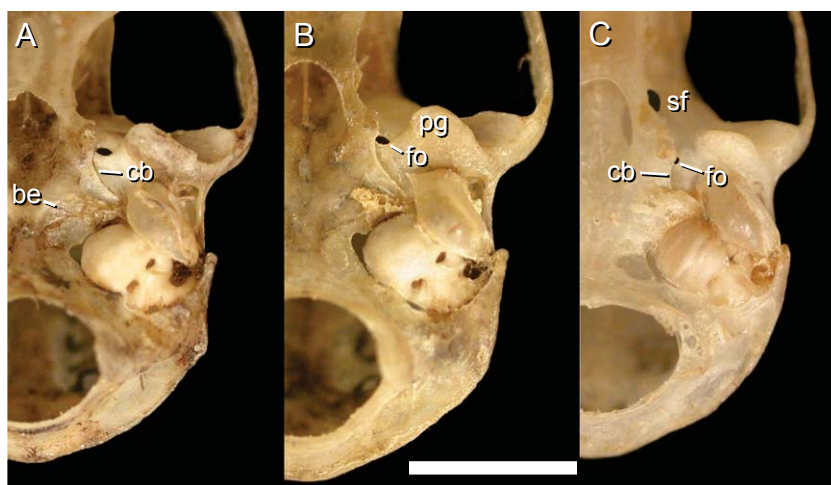


FIG. 8. Partial views of the basicranial region of *V. melissa*, USNM 548310 (A); *V. sinchi*, sp. nov., FMNH 114028 [holotype] (B); *V. elisabethae*, sp. nov., USNM 319282 (C). Abbreviations: **be**, bony excrescence; **cb**, extension of caudal border of pterygoid; **fo**, foramen ovale; **pg**, postglenoid process; **sf**, orbitosphenoid fissure. Scale bar = 5 mm.

DIAGNOSIS: *Vampyressa sinchi* is similar to *V. melissa*, but larger in most dimensions with few overlapping measurements (tables 3–4, figs. 1, 2, 4E, 4F, 6C). The skull, including dentition, is larger and more robust than any other known species of *Vampyressa*. The strongly developed postglenoid processes extend below the level of pterygoid processes; the mesopterygoid fossa is longer than wide; the ventral surface of the postdental extension of the palate is flat, its margins comparatively sharp, and bears small winglike projections on each side at approximately the level of the orbitosphenoid foramen.

DESCRIPTION: *Vampyressa sinchi* has pale brown to dark-beige dorsal pelage; the darker dorsum contrasts with the paler venter; short, sparse guard hairs on the head and dorsum; forearm densely haired proximally for about two thirds of its length; the uropatagium is narrow (about half the length of the tibia in dried skins), furred on both surfaces, and has a sparse fringe of hairs along its entire posterior margin but longest toward the midline; tibia, adjacent uropatagium, and foot conspicuously covered with reddish-brown hairs similar to the condition in *V. melissa*. The third and fifth metacarpals are similar in length and the fourth metacarpal averages shorter than the third and fifth. Otherwise, *V. sinchi* is very similar externally to *V. melissa* as described in that account.

The skull of *Vampyressa sinchi* (figs. 4E, 4F, 6C) also is similar to *V. melissa*, but more robust, and larger in most dimensions with few overlapping measurements (tables 3–4). The medial, incisor-bearing anterior premaxillae of *V. sinchi* are inclined at approximately 60° from the horizontal plane. The external nares are emarginate dorsally; the ventral margin is V-shaped between the roots of the upper inner incisors and bears a medial pit (figs. 5B, 5E). The nasals are relatively short resulting in a comparatively longer narial opening (deeper dorsal emargination, fig. 5E). The mesethmoid plate is not swollen and its anterior edge is thin (fig. 5B).

The rostrum is elevated above the horizontal plane connecting occipital condyles and the tips of the last upper molars. The septum between the incisive foramina is dorsoventrally thin

TABLE 5. External and craniodental measurements of the type series of *Vampyressa elisabethae* sp. nov. (in mm)

Character	Holotype USNM 319283 ♂	Paratype USNM 319282 ♀	Paratype USNM 319284 ♂	Paratype USNM 319285 ♂	Paratype USNM 520851 ♂
TL	—	58 ¹	—	—	53 ²
HF	9.3 ¹	10.9 ¹	9.7 ¹	10.5 ¹	10.5 ²
E	—	—	—	—	16 ²
FA	37.8	36.8	36.2	37.8	37.2
METIII	35.5	35.6	35.4	35.2	34.7
METIV	35.7	35.4	35.5	35.3	35.2
METV	37.0	37.2	36.1	36.5	36.1
TiL	12.3	12.7	12.4	12.4	12.9
GLS	22.9	22.9	22.9	23.0	22.9
CIL	21.4	21.3	21.6	21.6	21.5
CCL	20.7	20.7	20.8	20.8	20.8
PB	5.2	5.2	5.4	5.3	5.3
IB	6.3	5.9	6.0	6.1	5.7
BB	9.3	9.0	9.1	9.2	9.4
MB	10.9	10.6	10.7	10.9	11.0
ZB	12.6	12.0	12.0	12.1	12.4
MTRL	7.8	7.7	7.7	7.9	7.7
MANDL	8.6	8.3	8.5	8.1	8.4

¹Measurements from dried skin.²Measurements from fluid-preserved specimen.

and perforated by a large accessory medial foramen (fig. 5E). The lightly and irregularly fenestrated palate is conspicuously domed behind the incisive foramina. The sagittal and lambdoidal crests are low, but well developed; the interparietal-supraoccipital region is not conspicuously inflated. The mesopterygoid fossa is longer than wide; basioccipital-basisphenoid pits are sharply defined, deep, and extend well anterior to the anterior level of the auditory bullae.

The upper inner incisors (I1s) are subequally bilobed and convergent at the tips. The dentition is similar to that of *V. melissa*, but more massive throughout with stronger cingular development.

COMPARISONS: *Vampyressa sinchi* is larger than all other *Vampyressa* known (figs. 1–2, tables 3–4; Tavares et al., 2008) and tends to have longer fur and a darker dorsum. Among species of *Vampyressa*, *V. sinchi* is most similar to *V. melissa* from which it differs primarily in larger size; heavier, more robust dentition; unevenly bilobed upper inner incisors, deeper dorsal emargination of anterior nares, longer than wide mesopterygoid fossa, and a distinctly larger and longer postglenoid process that extends below the level of the hamular process of the pterygoid.

Like *V. melissa*, *V. sinchi* has sloping premaxillae (approximately 60° from horizontal plane) that bear a pit located in the midline between roots of upper inner incisors; narrow anterior margin of mesethmoid plate (fig. 5E); anteriorly tapering rostrum; dorsoventrally thin septum separating wider than long incisive foramina and perforated by a large accessory medial foramen;

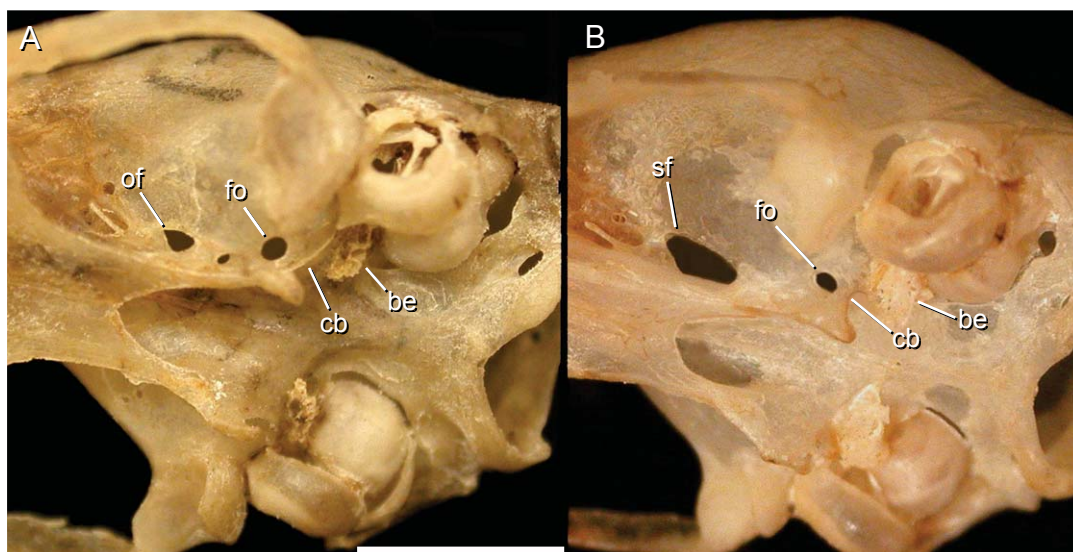


FIG. 9. Oblique views of the basicranial region of *V. sinchi*, sp. nov., FMNH 114028 [holotype] (A); *V. elisabethae*, sp. nov., USNM 319282 (B). Abbreviations: **be**, bony excrescence; **cb**, extension of caudal border of pterygoid; **fo**, foramen ovale; **of**, orbitosphenoid foramen; **sf**, orbitosphenoid fissure. Scale bar = 5 mm.

conspicuously domed hard palate behind incisive foramina; orbitosphenoid foramina (fig. 9A); foramen ovale and ventral projection of hamular process of pterygoid on same lateral plane as the base of the postglenoid process (fig. 8B); large basisphenoid-basioccipital pits that extend well anterior to anterior surfaces of auditory bullae; caudal ridge from pterygoid well separated from comparatively small bony excrescences (located on basisphenoid anteromedial to auditory bullae) (fig. 8B); rounded foramen magnum; robust mandibular rami and angular process. Like *V. melissa*, in *V. sinchi* the outer upper incisors are visible from above; p4 has a posterior ridge that extends down from the crown of the major cuspid and across heel to the posterior cingulum, and p4 also lacks a posterolabial cuspid. *V. sinchi* and *V. melissa* are the only species of *Vampyressa* that retain the spiculelike last lower molar; the dental formula is $2/2, 1/1, 2/2, 2/3 \times 2 = 30$.

The late Charles O. Handley, Jr., acquired four specimens of a large *Vampyressa* from the Bocas del Toro region in the 1960s during fieldwork in Panama related to a countrywide survey of the ectoparasites of vertebrates, primarily mammals. Although cataloged as *Vampyressa melissa*, Handley (1966: 767) reported these specimens as “*Vampyressa* species,” but never got around to describing them. An additional specimen from the same region was acquired by Robert K. Ender in 1976. These specimens are described here as:

***Vampyressa elisabethae*, new species**

Elisabeth's Yellow-eared Bat

Figures 4–9

Vampyressa species Handley, 1966: 767.



FIG. 10. Photograph of an adult female *Vampyressa sinchi* (MHNUC 1514) captured at San Juan de Villalobos, Caquetá River basin, eastern Colombian slopes of the Eastern Cordillera, collected at 1620 m. Photograph by Ofelia Mejía-Egas.

HOLOTYPE: An adult male (USNM 319283; figs. 4A–B, 6A) caught in evergreen forests of Rancho Mojica, upper Changena River, ± 20 miles [32.2 km] SSW of Changuinola ($9^{\circ}6' N$, $82^{\circ}34' W$; 1463 m), Provincia Bocas del Toro, Panama, by Vernon J. Tipton (original number 8006) on 13 September 1961. The holotype is preserved as a skin and skull (table 5).

PARATYPES: The skins and skulls of one adult female (USNM 319282; figs. 8C, 9B) and two adult males (USNM 319284 [figs. 5F, 7B], 319285 [fig. 5C]) caught at Rancho Mojica, upper Changena River, ± 20 miles SSW of Changuinola ($09^{\circ}6' N$, $082^{\circ}34' W$, 1463 m), Provincia Bocas del Toro, Panama (original numbers V.J. Tipton 8006, 8120, 8122). A fluid-preserved specimen of a male (USNM 520851), with skull removed, collected by Robert K. Enders at “Fish Camp” ($08^{\circ}58' N$, $082^{\circ}40' W$, 1494 m), Bocas del Toro, Panama on 26 March 1976.

DISTRIBUTION: Known only from provincia de Bocas del Toro, Panama (fig. 3).

ETYMOLOGY: The name *elisabethae* honors the legacy of the late Elisabeth Klara Victoria Kalko in the study of the natural history, ecology, conservation, vocal recognition, and behavior of bats.

DIAGNOSIS: A large *Vampyressa* (FA 36.2–37.8, $n = 5$; GLS 22.9–23.0, $n = 5$; table 5) having a relatively long, narrow skull (ZB 12.0–12.6, $n = 5$; table 5) with nearly parallel sides of the rostrum. Externally and dentally similar in appearance and size to *V. melissa* and *V. sinchi*, *V. elisa-*

bethae has a swollen anterior margin of mesethmoid plate (fig. 5C); dorsal contour of external nares not deeply emarginate (fig. 5F); an orbitosphenoid fissure (instead of a discrete foramen, figs. 4B, 9B); caudal border of pterygoid extending posteriorly as a low ridge over basisphenoid to near contact with the large bony excrescence (figs. 8C, 9B); laterally ovoid foramen magnum; unequally bilobate to weakly trilobate upper inner incisors (fig. 5C); a small cuspid on postero-labial crown of p4 (fig. 7B); m3 absent; dental formula $2/2, 1/1, 2/2, 2/2 \times 2 = 28$.

DESCRIPTION: *Vampyressa elisabethae* is closely similar in color pattern and other external features to both *V. melissa* and *V. sinchi*, although slightly smaller than *V. sinchi* and averaging equal to or slightly larger than *V. melissa*. On average, *V. elisabethae* has slightly paler dorsal pelage (pale ochre and yellowish brown to beige) than do either *V. melissa* or *V. sinchi*. The forearm is densely furred for a little more than its proximal half, and dorsal and ventral surfaces of the propatagium and plagiopatagium are hairy along sides of the body. The dorsal and ventral uropatagium, legs, and feet are sparsely furred, except toward the ventral midline of the uropatagium, where the fur is especially dense and long. The uropatagium lacks a conspicuous fringe of hair along the entire posterior margin. Like *V. melissa* and *V. sinchi*, the uropatagium is relatively narrow, its greatest breadth measuring less than half the length of the tibia. The third and fourth metacarpals are subequal, and the fifth metacarpal is longer than either the third or fourth. The tibia is short (12.3–12.9, $n = 5$) relative to the overall size of the bat.

Vampyressa elisabethae is cranially and dentally similar to *V. melissa* and *V. sinchi*, but can be distinguished by its relatively longer, narrower skull; nearly parallel sides of the rostrum; nearly straight profile of frontals and rostrum in lateral view (fig. 6A); less convergent upper toothrow; and narrower zygomatic breadth (ZB 12.0–12.6, $n = 5$). The anterior plane of pre-maxillae is near vertical (80°) from the horizontal plane of skull; the rostrum is aligned with the cranium (tips of canines and second upper molars on same horizontal plane as ventral surfaces of occipital condyles); lower margin of anterior external nares U-shaped and lacking a medial pit between roots of upper inner incisors; anterior margin of mesethmoid plate swollen (fig. 5C); dorsal contour of external nares not deeply emarginate (fig. 5F); an orbitosphenoid fissure present (figs. 4B, 9B); incisive foramina comparatively round with medial septum dorsoventrally thick and perforated by a comparatively small accessory medial foramen; palate not conspicuously domed behind incisive foramina; short, shallow basioccipital-basisphenoid pits; caudal border of pterygoid extending posteriorly as a low ridge to near contact with large bony excrescence on basisphenoid; foramen magnum laterally ovoid (fig. 8C); ventral surface of postdental palate weakly depressed (indented) along ventral midline and its lateral margins rounded along at least part of their length; foramen ovale and pterygoid process located behind medial base of postglenoid process; each dentary is proportionally slender, dorsoventrally narrow, has a low coronoid process, and a small articular process that is close to the small angular process; upper toothrows not strongly convergent anteriorly; unequally bilobate to weakly trilobate upper inner incisors; upper outer incisors not easily visible in dorsal view of the skull; a posterolabial cuspid present on p4, but lacking a medial ridge from major anterior cuspid to cingulum on heel; m3 absent; the dental formula is $2/2, 1/1, 2/2, 2/2 \times 2 = 28$.

COMPARISONS: *Vampyressa elisabethae* needs no comparison with the much smaller *V. pusilla* and *V. thyone*. Although externally similar to *V. melissa* and *V. sinchi*, *V. elisabethae*

has somewhat paler pelage, less hairy feet and uropatagium (except ventrally near midline), and shorter tibiae. The skull is conspicuously narrower and the anterior premaxillae more vertically oriented (near 80° from the horizontal plane versus approximately 60° in *V. melissa* and *V. sinchi*). The anterior nasal cavity is considerably different in that the ventral margin in *V. elisabethae* is U-shaped and lacks a medial pit (V-shaped with a medial pit between roots of upper inner incisors in the other two taxa), less emarginate upper border (deeper emargination in *V. melissa* and the much more deeply emarginate border in *V. sinchi*; fig. 5), and swollen anterior margin of the conspicuously thicker mesethmoid plate (plate thinner in *V. melissa* and *V. sinchi*; fig. 5). The sphenorbital opening in the cranium is a fissure in *V. elisabethae* in contrast with all other species of *Vampyressa* in which the opening is a foramen. The morphology of the anterior palate differs between *V. elisabethae*, *V. melissa*, and *V. sinchi* (fig. 5) and the palate is domed behind the incisive foramina in *V. melissa* and *V. sinchi*, but not domed in *V. elisabethae*. The foramen magnum is transversely ovoid in *V. elisabethae*, but more rounded in all other *Vampyressa*. Each dentary is massive, the coronoid process high, and both articular and angular processes are larger and not particularly close together in *V. melissa* and *V. sinchi* (fig. 6B–C), whereas in *V. elisabethae* each dentary is proportionally more slender, dorsoventrally narrow with a low coronoid process, and the smaller articular process is closer to the smaller angular process (fig. 6A).

Vampyressa melissa and *V. sinchi* obviously are closely related as reflected by their close similarity. *V. elisabethae* is not as closely related to these two species, nor is it closely related to *V. pusilla* and *V. thyone* based on its clearly distinctive features. Nevertheless, all known species of *Vampyressa* share the same major dental features, particularly the caniniform p2 and the characteristic well-developed, high, and bladelike entoconid on m2.

NATURAL HISTORY AND CONSERVATION

Vampyressa melissa was listed as vulnerable by the most recent IUCN Global Mammal Assessment because of presumed population decline and shrinkage in distribution inferred from habitat degradation and conversion (Tavares et al., 2008). The recognition that the populations previously identified as *V. melissa* comprise three distinct species reinforces the perception of threatened status. These three species of frugivorous bats are uncommonly encountered, and occur in fragmented, higher-elevation habitats. One Ecuadorian specimen of *V. melissa* (USNM 548310) was pregnant when captured on 12 February 1983 with a fetus having a crown-to-rump length of 27 mm.

The rarity of *Vampyressa melissa* and its allies constrains study of their variation and obviously hinders the possibility of gaining knowledge about their biology. On the other hand, *V. melissa* has been recorded in three instances from 1970 to 1990 in habitats described as disturbed. Gardner (1976) and Patton et al. (1982) reported collecting Peruvian specimens of *V. melissa* in lower-elevation humid forest of different secondary stages along the eastern slope of the Andes, and one Ecuadorian specimen came from a disturbed forest habitat (Albuja-V.,

1991). The supposed first specimen of *V. melissa* reported from Colombia, collected in highland cloud forest (Lemke et al., 1982), is actually *V. sinchi*.

The distribution of each of the three large *Vampyressa* species suggests fidelity to a particular high elevational range, an unusual pattern among stenodermatines. Graham (1983) reported elevational limits for *V. melissa* in Peru as 1000–1800 m, based on the scanty information available at that time. These species appear to be distributed at elevations above 1200 m and possibly range as high as or higher than 2600 m. Because these bats are frugivores, the primary factor limiting their distribution is the year-round availability of consumable fruit. That factor alone places these species in jeopardy because of continued habitat conversion and destruction at the elevations where these *Vampyressa* occur.

AUTHOR CONTRIBUTIONS

This report was redrafted by V.C.T. based on her revisionary work of *Vampyressa* (s.s.) as part of her doctoral dissertation. A.L.G. prepared figures 5, 7, 8, and 9; wrote most of the description of the new species from Panama; and contributed to the redraft the manuscript. H.E.R.C. provided measurements and observations on the paratypes of *V. sinchi* housed in the Colombian museums, and contributed with natural history information in a previous draft. P.M.V. prepared figures 3, 4, and 6, and contributed to the analyses.

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APPENDIX

SPECIMENS EXAMINED

The following list includes all the specimens used in this study, with their respective localities. See Material and Methods for abbreviations.

Vampyressa elisabethae, sp. nov. (5): PANAMA: *Bocas del Toro*: Changuinola, 20 miles SSW, upper Changena River, Rancho Mojica, 9°06' N, 82°34' W (USNM 319282, ♀; 319283, ♂ [holotype]; 319284, ♂; 319285, ♂); Fish Camp, 8°58' N, 82°40' W (USNM 520851, ♂).

Vampyressa melissa (11): COLOMBIA: *Norte de Santander*: Parque Natural Tamá, 7°06' N, 72°13' W (IAvH 6761, ♂). ECUADOR: *Pastaza*: Mera, 1°22' S, 78°01' W (USNM 548310, ♀). *Napo*: Cantón Archidona, Parroquia Cotundo, Río Urcusiqui, 0°49' S, 77°47' W (MEPN 5392, ♀). *Zamora-Chinchipe*: km 30 vía Loja-Zamora, Estación Científica San Francisco, 03°53' S, 79°05' W (MEPN 7578, ♂). PERU: *Cuzco*: Bosque de las Nubes, carretera Paucartambo-Pillcopata, km 150, Puente Union, 13°22' S, 71°61' W (MUSM 8914, ♀); Quitacalzón, carretera Paucartambo-Pillcopata, Puente at km 163, 12°99' S, 71°45' W (MUSM 8915, juvenile ♂; MUSM 8916, ♀); Paucartambo, Consuelo, 15.9 km SW Pillcopata, 13°02' S, 71°49' W (FMNH 174909, ♀). *Huanuco*: Cerros del Sira, 9°30' S, 74°47' W (AMNH 233761, ♀; AMNH 233769, ♂). *San Martín*: Moyobamba, Puca Tambo, 6°9' S, 77°16' W (BMNH 26.5.3.4, ♀ [holotype]).

Vampyressa pusilla (17): BRAZIL: *Minas Gerais*: APA Coqueiral, 21°11' S, 45°26' W (CMUFLA 165, ♀; CMUFLA 166, ♀); Apolo 21, Raposos, 19°57' S, 43°48' W (CMUFLA 167, ♂; CMUFLA 569, ♂); Lavras, 21°14' S, 44°59' W (CMUFLA 484, ♀; CMUFLA 530, ♀); Minduri, 21°39' S, 44°36' W (CMUFLA CPM 26, ♀); Viçosa, 20°44' S, 42°50' W (USNM 395703, ♂). *São Paulo*: Cananéia, 25°01' S, 47°55' W (MZUSP 22215, sex unknown); Ilha Anchieta, 23°31' S, 45°02' W (MZUSP 29438, ♂); Ilha do Cardoso, 25°11' S 47°59' W (MZUSP 27729, ♀; 28132, ♀); Mirassol, Sítio Progresso, 20°49' S, 49°31' W (DZSJRP 3920, ♂); Varjão do Guaratuba, 23°45' S, 45°53' W (MZUSP 21081, ♀); Ipanema, 23°27' S, 47°35' W (RMNH

17256, ♂). PARAGUAY: *Paraguarí*: Parque Nacional Ybycuí, 26°01' S, 57°03' W (UMMZ 133730, ♀; 133731, ♂).

Vampyressa sinchi, sp. nov. (3): COLOMBIA: *Cauca*: Santa Rosa, Vereda La Esmeralda San Juan de Villalobos, 1°33'18" N, 76°18'19" W (MHNUC 1514, ♀). *Huila*: Acevedo, Parque Nacional Natural Cueva de los Guácharos, 1°38' N, 75°58' W (IAvH 2282, ♂). *Nariño*: Córdoba, Llorente, 0°46'40" N, 77°21'50" W (FMNH 114028, ♀ [holotype]).

Vampyressa thyone (20): COLOMBIA: *Antioquia*: 24 km S and 22 km W, near La Tirana, 520 m, ca. 7°18' N, 75°05' W (USNM 499464, ♀; 499466, ♂; 499467, ♀). *Meta*: Finca "El Buque," Villavicencio, 4°09' N, 73°39' W (USNM 507198, ♂). COSTA RICA: *Puntarenas*: Corcovado N.P., Osa Peninsula, Quebrada Camaronal, Sirena, 8°33' N 83°35' W (USNM 565811, ♂). ECUADOR: *El Oro*: Puente de Moromoro, 1 km SW, 920 m, 3°44' S, 79°44' W (USNM 513466, ♀; 513467, ♀; 513469, ♀). PANAMA: *Canal Zone*: Barro Colorado Island, 09°09' N, 79°51' W (USNM 514966, ♀; 514967, ♂); Bohio Peninsula, 09°11' N, 79°50' W (USNM 503634 ♀; 503629, ♂; 503632, ♂; 503633, ♂; 503636, ♂). PERU: *Cuzco*: *Pagoreni*, 465 m, 11°42' S, 72°54' W (USNM 582870, ♂). VENEZUELA: *Apure*: Nulita, Selvas de San Camilo, 29 km SSW of Santo Domingo, 24 m, 7°19' N, 71°57' W (USNM 4407, ♀). *Yaracuy*: Minas de Aroa, Bolívar R.R., 10°25', 68°54' W (USNM 440660, ♂; 440733, ; 440734, ♀; 440736, ♀).

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