

Taxonomic Status of the Cuban Vampire Bat (Chiroptera: Phyllostomidae: Desmodontinae: *Desmodus*)

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ABSTRACT.—The Cuban subspecies of vampire bat, *Desmodus rotundus puntajudensis* Woloszyn and Mayo, is redescribed and raised to the specific rank. *Desmodus puntajudensis* shares some cranial characters with two extinct species of vampire bats from North America, *D. stocki* and *D. archaeodaptes*. Characters that distinguish the Cuban species are skull with globose braincase, palate wide with posterior apex widely grooved at midline, zygomatic arch short and higher anteriorly, orbital region deeply excavated, pterygoid process reduced, paraoccipital process reduced and ventrally placed, occipital protuberance greatly projected, occiput high and facing postero-ventrally, and foramen magnum larger antero-posteriorly. An additional, nearly complete skull of *D. puntajudensis* is recorded from a Quaternary cave deposit at Cueva de Paredones, La Habana, Cuba, which represents the westernmost fossil locality for its paleodistribution in the Cuban archipelago.

KEY WORDS.—*Desmodus*, distribution, taxonomy, Cuba

INTRODUCTION

Fossil vampire bats of the genus *Desmodus* have been described from both North and South America (Jones 1958; Gut 1959; Morgan et al. 1988; see Ray et al. 1988, for a summary of fossil occurrences, and Trajano and de Vivo 1991; Cartelle and Abuhid 1994; Arroyo and Ray 1997; Czaplewski and Cartelle 1998; Pardiñas and Tonni 2000; and Czaplewski et al. 2003, for additional records). Two of these taxa, *Desmodus stocki* Jones 1958, and *D. draculae* Morgan, Linares and Ray 1988, are larger than *D. rotundus* (E. Geoffroy St. Hilaire 1810), the only living species of the genus (Jones 1958; Morgan et al. 1988). *Desmodus archaeodaptes* Morgan, Linares and Ray 1988, is within the size range of the living taxon and represents the oldest record, latest Pliocene (very early Irvingtonian), for any vampire bat in America (Morgan 1991). *Desmodus magnus* Gut 1959, from the late Pleistocene of Florida, is considered a junior synonym of *D. stocki* (Hutchison 1967).

Sanguivorous bats are known in the West Indies only from the fossil record of

Cuba (Ray et al. 1988; Morgan 2001). The first evidence of their occurrence on the island was established with a well-mineralized rostral portion of a skull from a cave deposit at Cueva Lamas, Santa Fé, La Habana Province (now Ciudad de La Habana) (Arredondo 1958; Koopman 1958). Koopman (1958) identified this specimen as *Desmodus rotundus murinus* Wagner 1840; an extant subspecies that inhabits Mexico and Middle America. A well preserved skull, apparently from the Holocene, recovered from a cave deposit at Punta Judas, Las Villas Province (now Villa Clara), was described as an extinct subspecies: *Desmodus rotundus puntajudensis* Woloszyn and Mayo 1974. Jiménez and García (unpublished data) referred a mandibular fragment and some postcranial elements to *Desmodus* from a Quaternary cave deposit at La Habana Province. Additional material of a vampire bat was recently collected from a cave deposit at the Alturas Habana-Matanzas, near Corral Nuevo, western Cuba (Johanset Orihuela pers. comm.).

While curating uncatalogued fossil material of bats at the paleontological collection of the Museo Nacional de Historia Natural, La Habana, Cuba (MNHNCu), I discovered

ms. received May 20, 2004; accepted October 10, 2005

one nearly complete skull of a vampire bat (Fig. 1) from a cave deposit at Cueva de Paredones, western La Habana Province; a locality near Cueva Lamas (ca. 25.5 km SW). Further comparisons with specimens

of *D. rotundus murinus*, and with the holotype skull of *D. r. puntajudensis*, show that the new material is referable to the latter taxon. Moreover, I distinguished cranial characters in the Cuban fossils of equal magnitude to those used to describe extinct species in *Desmodus*. While the generic allocation of the Cuban vampire bat is unquestionable (Woloszyn and Mayo 1974:259), its current specific position is erroneous. Herein, I redescribe the Cuban vampire bat and reconsider its taxonomic status.

MATERIALS AND METHODS

I conducted comparisons with osteological material of *Desmodus rotundus murinus* from Yucatán, Mexico, at the collection of the Instituto de Ecología y Sistemática, La Habana, Cuba (CZACC: Colecciones Zoológicas de la Academia de Ciencias de Cuba). All fossils herein referred to *Desmodus puntajudensis* (see Referred material) were examined, with the exclusion of the rostral portion of skull (Museum of Comparative Zoology, Harvard University, Massachusetts, MCZ 4737), for which I used only the figure and description published by Koopman (1958). I also used for comparisons the original descriptions and illustrations of the fossil species *D. stocki* Jones (1958), *D. archaeodaptes*, and *D. draculae* (the latter two described by Morgan, Linares, and Ray 1988). Measurements were taken with a vernier caliper to the nearest 0.1 mm. Osteological terminology and measurements mainly follow DeBlase and Martin (1981) and Woloszyn and Mayo (1974).

SYSTEMATICS

Order Chiroptera

Family Phyllostomidae

Subfamily Desmodontinae

Genus *Desmodus* Maximilian

Desmodus puntajudensis Woloszyn and

Mayo 1974, *new combination*

(Figs. 1 and 2)

Desmodus rotundus murinus: Koopman 1958.

Desmodus magnus: Varona 1974.

Desmodus rotundus puntajudensis Woloszyn and Mayo 1974.

Desmodus rotundus?: Fischer 1977.

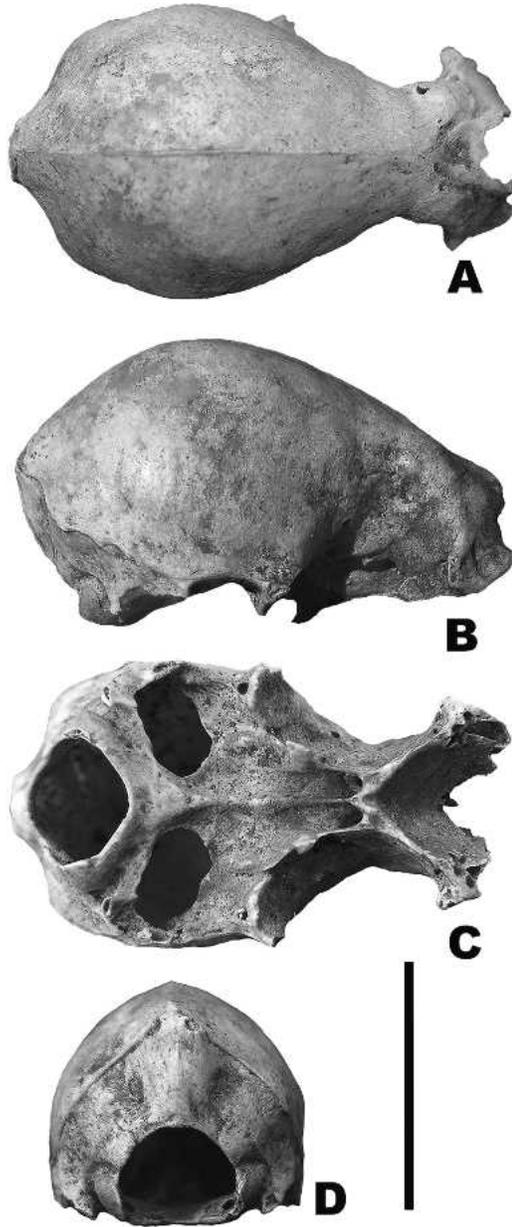


FIG. 1. *Desmodus puntajudensis* skull (MNHNCu 76.4713) from Cueva de Paredones, La Habana, Cuba, in dorsal (A), lateral (B), ventral (C), and posterior (D) views. Scale bar = 1 cm.

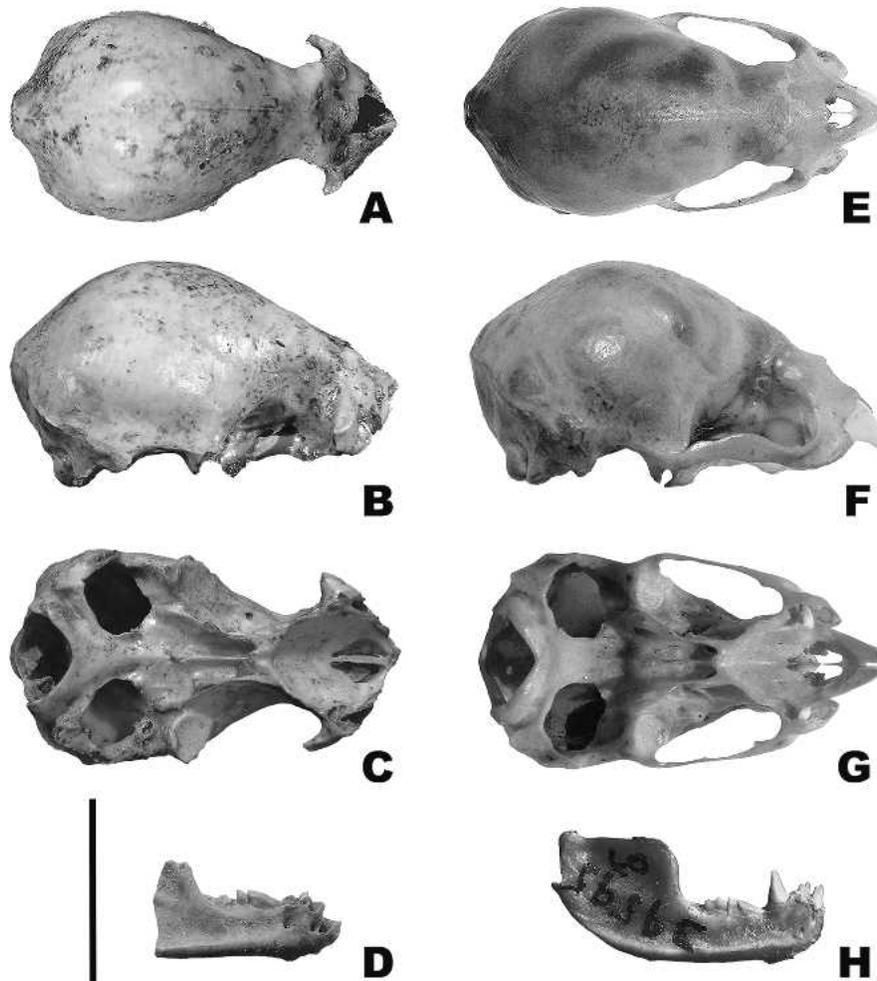


FIG. 2. Skull and jaw of *Desmodus puntajudensis* (A-D) (holotype skull, IG ACC 7999/401 [CZACC unnumbered]; referred mandibular ramus, CZACC 1.5546), in comparison with the equivalent elements in *D. rotundus* (E-H). Skulls in dorsal (A, E), lateral (B, F) and ventral (C, G) views. Mandibular rami in lateral (D-H) view. Scale bar = 1 cm.

Holotype.—A nearly complete skull (formerly in the collections of the Instituto de Geología, Academia de Ciencias de Cuba, IG ACC 7999/401; now at CZACC, without number); collected by Angel Graña in March 1970.

Type locality.—Cueva del Centenario de Lenin, Punta Judas, Villa Clara Province (formerly Las Villas), Cuba (see Mayo 1970, and Woloszyn and Mayo 1974, for the description and age of the deposit).

Referred material.—Holotype. Cueva de Paredones, Ceiba del Agua, Municipality of Caimito, La Habana: a nearly complete

skull, lacking the anterior part of the palate and both zygomatic arches (MNHNCu 76.4713), collected by Emilio Alfaro and Reinaldo Rojas in 1991. Cueva Lamas, Santa Fé, Ciudad de La Habana: rostral portion of skull (MCZ 4737), collected on 21 January 1951 by Oscar Arredondo and Manuel Rivero de la Calle. Cuevas Blancas, Aguacate, Quivicán, La Habana: right mandibular ramus with p1, p2 and part of m1 present (CZACC 1.5546); pelvis (CZACC 1.5543); right humerus (CZACC 1.5547); right (CZACC 1.5545) and fragmentary left (CZACC 1.5544) femora, collected on 8

January 2001 by Osvaldo Jiménez and Elvis García.

Emended diagnosis.—A small species of *Desmodus* having a skull with globose braincase; palate wide, with posterior apex widely grooved at midline; zygomatic arch shorter, higher in its anterior part; orbital region short and deeply excavated; pterygoid process reduced; paraoccipital process reduced and ventrally placed; occipital protuberance greatly projected; occiput high, facing postero-ventrally; foramen magnum larger antero-posteriorly, caudally oriented, and with ventral margin rounded. Some of the cranial measurements exceeding the size range of *D. rotundus*.

Description and comparisons.—The cranium much smaller than that of the two large extinct species, *D. stocki* and *D. draculae*, and similar in size (but more delicate) to that of *D. archaeodaptes*, and *D. rotundus*, but with some measurements exceeding the size range of the living species (Table 1). *Desmodus puntajudensis* differs from *D. rotundus* in the following characters. Dorsal view: the skull is proportionally wider (longer and thinner in *D. rotundus*). In Silva 1979, Plate 9E, the photograph of the holo-

type shows distortion, as is elongated), with a well defined sagittal crest; facial region much shorter and also wider with nasal reduced and depressed (longer and thinner facial region, nasal larger and more upturned in *D. rotundus*); supraorbital bridge relatively wider (thinner proportionately in *D. rotundus*); braincase globose (less inflated in *D. rotundus*). Lateral view: the zygomatic arch is shorter, higher in its anterior part (longer, higher at center in *D. rotundus*) (the zygomatic arch is lacking in the holotype; see Woloszyn and Mayo 1974, for illustration, description, and measurement of this structure); orbital region short and deeply excavated, with rostral and caudal surfaces (of the concavity) much expanded and flattened (larger and less excavated orbital region, with inflated, more irregular and restricted rostral and caudal surfaces in *D. rotundus*); edge defined by the tympanic cavity straight (rounded in *D. rotundus*); paraoccipital process reduced and ventrally oriented (larger and caudally in *D. rotundus*); occipital protuberance greatly projected postero-ventrally (much less projected, or ventrally located in *D. rotundus*). Ventral view: the palate is shorter

TABLE 1. Cranial and mandibular measurements (mm) of *Desmodus* species. Sequence is: range (mean) sample size.

Character	<i>D.</i>				
	<i>puntajudensis</i>	<i>rotundus murinus</i> ^b	<i>stocki</i> ^b	<i>archaeodaptes</i> ^b	<i>draculae</i> ^b
Total length of skull	22.34 ^{a*}	22.7-24.3 (23.7) 30	26.5-28.2 (27.3) 6	—	31.2
Breadth of rostrum	6.0-6.2 (6.1) 2	5.5-6.5 (6.0) 30	7.1-7.6 (7.4) 6	—	9.2
Breadth of palate measured to external borders of fossa canini	6.5, 6.65 ^a	6.19-6.23 (?) 10 ^a	—	—	—
Interorbital constriction	5.1-5.2 (5.1) 2	5.1-5.8 (5.5) 30	5.9-6.2 (6.1) 9	5.8	5.7-6.7 (6.2) 2
Mastoid breadth	11.6-12.0 (11.8) 2	12.0-13.1 (12.5) 30	13.5-14.5 (14.1) 8	12.4	15.2-15.5 (12.6) 2
Breadth of braincase	12.0-12.1 (12.0) 2	11.5-12.5 (11.9) 30	13.6-14.2 (13.8) 11	12.3	14.5-14.8 (14.6) 2
Height of braincase	11.4-11.7 (11.5) 2	11.1-12.6 (11.9) 30	13.2-13.8 (13.5) 10	12.0	13.4-14.8 (14.1) 2
Breadth of foramen magnum	5.1, 5.13 ^a	4.85-5.20 (5.08) 10 ^a	5.3-5.8 (5.6) 9 ^c	—	—
Height of foramen magnum	5.0, 5.05 ^a	4.25-4.80 (4.51) 10 ^a	—	—	—
Length of mandibular tooth row	4.5	4.4-5.0 (4.7) 30	5.1-5.4 (5.3) 16	—	8.3-8.5 (8.4) 2

^aFrom Woloszyn and Mayo (1974).

^bFrom Morgan et al. (1988).

^cFrom Jones (1958).

?Mean not calculated by authors.

*Approximate measurement, as the holotype seems to be abraded since the original description.

and wider, and its floor forming a nearly rounded concavity (cup-like), where the midline suture is not defined (larger and thinner palate, floor with more flat plates converging in a well defined, angulated midline in *D. rotundus*); posterior apex of palate widely grooved at midline and projected horizontally (forming a distinct angle with the remaining palate), placed on a flat and wide, plate-like surface (not grooved in *D. rotundus*); interorbital constriction more noticeable, because of distinct outline angle of the much shorter anterior portion of the braincase (much less noticeable in *D. rotundus*); pterygoid process reduced, with lateral orientation of the pterygoid apophysis (larger, more caudally oriented pterygoid apophysis in *D. rotundus*); articular surface of glenoid fossa continued (antero-superiorly and medially) by a very flat surface (surface reduced, inflated, and in a different plane in *D. rotundus*); postglenoid process short and wide (longer, more pointed in *D. rotundus*); foramen magnum with a round ventral margin (angulated at midline in *D. rotundus*). Posterior view: the occipital region is more projected posteriorly; supraoccipital greatly inflated along midline, between the foramen magnum and the occipital protuberance (much less inflated in *D. rotundus*), with two distinct, very deep depressions at both sides (shallow surface, much less depressed in *D. rotundus*); occiput high, narrow, and facing postero-ventrally (lower and wider, facing more caudally in *D. rotundus*); caudally ori-

ented foramen magnum, larger antero-posteriorly, and with dorsal margin high and rounded (ventrally located, greater transverse diameter in *D. rotundus*).

The single known mandibular fragment (distal half of right ramus CZACC 1.5546) is robust, with a tooth row length within the lower size limit recorded for *D. rotundus* (Table 1); the ventral border is straight (more rounded in *D. rotundus*).

The known postcranial elements are in general within the lower size limit recorded for *D. rotundus* as well, where the femur is relatively more robust distally than in the living species (Table 2).

Measurements.—See Tables 1 and 2. Additional measurements, comparisons, and statistical analysis can be found in Koopman (1958), Woloszyn and Mayo (1974), and Silva (1979).

DISCUSSION

The Cuban vampire bat, *Desmodus puntajudensis*, shares some cranial characters with two fossil species described from North America, *D. stocki* and *D. archaeodaptes* (see Jones 1958; Morgan et al. 1988; and Morgan 1991, for detailed descriptions). The globose braincase and the broad palate resemble those of *D. stocki*; the caudally-oriented foramen magnum is similar to that of *D. archaeodaptes*. The shorter and blunted postglenoid process is in accordance with these two taxa, as well. In the

TABLE 2. Measurements (mm) of the humerus and femur of *Desmodus puntajudensis*, *D. rotundus*, and *D. stocki*. Sequence is: range (mean) sample size.

Character	<i>D. puntajudensis</i>	<i>D. rotundus</i>	<i>D. stocki</i>
Humerus			
Total length	33.4	32.4-42.4 (37.0) 19 ^a	39.3-47.5 (43.6) 42 ^c
Proximal width	4.6	4.4-5.6 (4.9) 19 ^a	5.8-6.8 (6.3) 47 ^c
Distal width	5.2	4.8-5.9 (5.4) 19 ^a	6.4-7.3 (6.8) 52 ^c
Thickness of shaft	1.9	1.7-2.4 (2.1) 15 ^a	2.0-2.9 (2.5) 56 ^c
Femur			
Proximal width	3.7	3.3-4.1 (3.7) 16 ^b	4.2-4.8 (4.5) 24 ^b
Distal width	3.5	2.9-3.6 (3.2) 16 ^b	3.6-4.0 (3.8) 13 ^b
Thickness of shaft	2.5-2.7 (2.6) 2	1.9-2.6 (2.2) 16 ^b	3.0-3.4 (3.2) 13 ^b

^aFrom Morgan et al. (1988).

^bFrom Morgan (1991).

^cFrom Hutchison (1967).

general configuration of the cranium, *D. puntajudensis* resembles *D. stocki* rather than the remaining species of the genus, but it is similar to *D. rotundus* and *D. archaeodaptes* in the weakly inflated postero-medial process of the basisphenoid. The following qualitative characters indicate that *D. puntajudensis* is not a subspecies of *D. stocki*: braincase narrower (extremely broad in *D. stocki*); zygomatic arch short and robust (slender, thin, and delicate in *D. stocki*; see Morgan 1991); paraoccipital process reduced and ventrally deflected (caudally-oriented in *D. stocki*); occiput narrower and higher (broad and lower in *D. stocki*); foramen magnum ovoid, facing posteriorly with dorsal margin high and rounded (hexagonal in shape, ventrally located in *D. stocki*).

In Cuba, mammals such as sloths, monkeys, and large rodents, as well as large birds, were the most reasonable prey for *D. puntajudensis* (Arredondo 1958; Koopman 1958; Woloszyn and Mayo 1974). Morgan et al. (1988:918) suggested that the configuration of the postglenoid process, coupled with the larger articulating surface for the mandible, are indications of more freedom of movement of the lower jaw in the extinct vampire bats than in *D. rotundus*; presumably as a result of specialization in some kind of donors. The relatively robust femur of *D. puntajudensis* suggests a somewhat different mode of locomotion than in the living species, as in the case of *D. stocki* (Morgan 1991).

The extinction of *Desmodus puntajudensis* seems to have occurred during the Holocene, probably after the total extinction of the "megafauna" (Woloszyn and Mayo 1974). The specimens of *Desmodus* identified by Jiménez and García (unpublished data) are Holocene in age (^{14}C), providing more evidence for the postglacial occurrence of these bats in Cuba.

The skull MNHNCu 76.4713, referred herein to *D. puntajudensis*, is the second recovered in the island, it is well mineralized, and may be as old as the one from Cueva Lamas. Cueva de Paredones is the westernmost locality known in the distribution of this endemic species (see Morgan and Ot-

tenwalder 1993, for discussion of the age of the deposit in Cueva de Paredones).

Woloszyn and Mayo (1974:261) commented about the possibility that the Cueva Lamas material represents the endemic *Desmodus rotundus puntajudensis*, instead of the living *Desmodus rotundus murinus*. Although the rostral portion MCZ 4737 is very fragmentary in nature and was not available for direct comparison in this study, some characters, e.g. shorter and wider palate, a more noticeable interorbital constriction, and a distinct outline defined by the anterior portion of the braincase of *D. puntajudensis* are evident in the ventral view of the figure published by Koopman (1958); therefore, herein being referred as to the endemic *D. puntajudensis*.

Although Varona (1974:30-31) erroneously referred the fossil from Cueva Lamas to the extinct species *Desmodus magnus* (= *stocki*) (see also Gut 1959:537), he apparently noted the similarities with the North American vampire bat when he stated: "especie [*D. stocki*] con la que, a mi entender, guarda mayor afinidad" ("from my view point, species [*D. stocki*] which it shares more affinity"). This statement seems logical today.

Acknowledgments.—Osvaldo Jiménez Vázquez assisted during revision of fossil and comparative material at the Instituto de Ecología y Sistemática, La Habana, and kindly provided for study new collected specimens of the Cuban Vampire Bat. I thank Gilberto Silva Taboada for his comments on an early version of the manuscript. Julie Craves of the University of Michigan-Dearborn edited the English version of the manuscript. I wish to thank Gary S. Morgan and two anonymous reviewers for providing helpful comments on the manuscript.

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