ADDITIONAL BATS FROM THE MIDDLE MIOCENE LA VENTA FAUNA OF COLOMBIA

by

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Abstract

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By screenwashing sedimentary rocks from three localities in the middle Miocene Villavieja Formation, Río Magdalena valley, Huila Department, Colombia, we collected several fossils that add to the knowledge of bats in the ca. 12-13 million-year-old La Venta fauna. The new specimens represent an emballonurid, a noctilionid, three phyllostomids, a thyropterid, three molossids, and a probable vespertilionid, and they came from a level (Monkey Beds) bracketed by dates of 12.5 million and 12.2 million years. The first known upper molars of *Notonycteris magdalenensis* reaffirm this species' close relationship with *Vampyrum* and *Chrotopterus*, as does a new species of *Notonycteris* based on two lower molars and characterized by smaller size than *N. magdalenensis*. Two upper molars of a primitive nectar-feeding bat represent another new taxon of Phyllostomidae (Glossophaginae), a new genus and species which provides the only Tertiary record for this group. An additional but not yet identifiable molossid adds to the bat list, and an unidentified probable vespertilionid is the first of its family recorded in the fauna. The La Venta fauna now includes 14 species of bats, several of which are indeterminate.

Key words: bats, Chiroptera, Colombia, fossil, La Venta, Miocene, Tertiary.

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Resumen

En los yacimientos de rocas sedimentarias de tres localidades del Mioceno medio de la Formación Villavieja, valle del río Magdalena, departamento de Huila, Colombia, fueron recolectados varios fósiles de murciélagos que permiten ampliar el conocimiento de la Paleofauna que existió hace ca. 12-13 millones de años en la localidad La Venta. Los ejemplares representan seis familias y nueve especies, algunas de las cuales habían sido registradas previamente para esta localidad. Los primeros molares superiores conocidos de *Notonycteris magdalenensis* confirman su estrecha afinidad filogenética con *Vampyrum* y *Chrotopterus*. Se propone una especie nueva de *Notonycteris*, la cual se separa de *N. magdalenensis*, con base en dos molares inferiores y el tamaño más pequeño de la especie nueva. Dos molares superiores de un murciélago pequeño de hábitos nectarívoros representan un género y una especie nueva de Phyllostomidae (Glossophaginae o Lonchophyllinae), el cual a su vez es el único registro del Terciario para este grupo. Se registró un murciélago no identificado de la familia Molossidae y posiblemente un representante de Vespertilionidae, el cual sería el primer registro de la familia. La paleofauna de La Venta está representada hasta el momento por 14 especies de murciélagos: Emballonuridae (gen. et sp. indet., *Diclidurus* sp. indet.), Noctilionidae (*Noctilio albiventris*), Phyllostomidae (*Notonycteris magdalenensis*, N. nueva especie, *Tonatia* sp. indet., género y especie nuevas), *Thyropteridae* (Thyroptera lavali, T. cf. *T. tricolor*), Molossidae (*Mormopterus colombiensis*, *Eumops* sp. indet., *Potamops mascahehenes*, gen. et sp. indet.), ?Vespertilionidae (gen. et sp. indet.).

Palabras clave: Chiroptera, Colombia, fósil, La Venta, Mioceno, murciélagos, Terciario.

Introduction

In the middle Miocene, South America was situated near its present geographical position, with the northern part of the continent—including what is now Colombia—in the tropic zone near the equator. At that time, the Cordillera Central of the northern Andes was volcanically active and high with abrupt slopes, but the Cordillera Oriental was very low and discontinuous. Miocene sediments including the fossiliferous Honda Group were being shed continuously from the Cordillera Central across the low-lying area to the east. The Honda Group sediments represent a meandering and anastomosing river system with generally eastward-flowing channels (**Fields**, 1959; **Guerrero**, 1997).

The La Venta fauna of Colombia is one of the most diverse Cenozoic vertebrate paleofaunas in the New World tropics. It originates from Honda Group beds including the La Victoria and Villavieja formations in the Neiva Basin of the Río Magdalena, between the eastern and central cordilleras of the Andes Mountains in southwestern Colombia (**Guerrero**, 1997). A total of 154 taxa of fossil vertebrates in about 70 families have been found at La Venta, including a cartilaginous fish, about 25 bony fishes, two amphibians, 32 reptiles, five birds, and about 89 mammals (**Kay** & **Madden**, 1997; **Villarroel**, 1998, 2000). **Madden** et al. (1997) used the mammals to define the Laventan land mammal age. In addition to the lowland meandering river system indicated by the geology, the vertebrate fauna furthers the interpretation of the paleoenvironment. For example, diverse and abundant fossils of freshwater fishes, turtles and crocodilians indicate aquatic habitats, fossils of several kinds of arboreal monkeys indicate the presence of tropical rain forest, and various other kinds of mammals seem to indicate the presence of forests, forest/grassland mosaics, and open grasslands (**Kay** & **Madden**, 1997).

As is usual in fluvio-lacustrine beds containing vertebrate fossils, the remains of bats are rare in Honda Group beds. Most bats in the La Venta fauna were recovered from the Villavieja Formation; to date, only one fossil bat has been found in the La Victoria Formation (**Czaplewski**, 1997). In this paper we report newly collected and previously unreported fossils of bats from the La Venta fauna, all of which are from the Villavieja Formation.

Fossils of bats and other small vertebrates were collected by screenwashing rock matrix in the field and by picking and sorting specimens from the resulting concentrate under a microscope in the laboratory. The specimens described in this report are cataloged with permanent numbers of the Museo Geológico (IGM), of the Instituto Nacional de Investigaciones en Geociencias, Minería y Quimica (INGEOMINAS) in Bogotá, Colombia. “IGM-KU” field numbers are provided for a few specimens collected by IGM-Kyoto University teams. “IGM-DU” field numbers are provided for a few uncataloged specimens collected by IGM-Duke University teams. Measurements were made on a stereomicroscope using an ocular micrometer calibrated with a stage micrometer. All measurements are given in mm, to the nearest 0.05 mm. Abbreviations for measurements are *apl*, anteroposterior length; *tw*, transverse width; *trigw*, trigonid width; *talw*, talonid width. Dental terminology follows **Legendre** (1984:fig. 1). The phylogenetic relationships of some phyllostomines in this report were estimated by scoring 48 dental, cranial, and postcranial osteological characters in nine taxa of Phyllostominae and by analyzing the resulting data matrix using the computer-assisted phylogenetic analysis software program PAUP version 4.0b10 (**Swofford**, 2000; see Appendices 1 and 2 for character list and data matrix, respectively). A parsimony analysis was conducted using the bootstrap method with branch-and-bound search, with all characters unordered and of equal weight. Missing data were coded as "?". We used *Macrotus waterhousii* as an outgroup, based on the results of other recent studies such as **Baker** et al. (1989, 1997, 2000), **Wetterer** et al. (2000), and **Jones** et al. (2002).

Specimens reported herein include those collected by Duke University-IGM teams in 1988-1991 from Duke field localities 22 and CVP, and by Kyoto University-IGM teams during 1990-1993 at a field locality known as the Chepe site. Duke field locality 22, also known as San Nicolás, is about 7 km northeast of the village of Villavieja (see map in **Guerrero**, 1997:fig. 2.9). Stratigraphically, locality 22 is in the Monkey Beds, the basal unit of the Villavieja Formation (and its Baraya Member), which overlies the Cerbatana Conglomerate Beds, the uppermost unit of the La Victoria Formation (**Guerrero**, 1997:fig. 2.7C). Geochronological work indicates a range of dates for the Villavieja Formation from about 12.5 Ma to about 10.1 Ma (**Flynn** et al., 1997); the radiometric dates of 12.5 Ma from the Cerbatana Conglomerate Beds provide the lower limit of this range. The Duke field locality known as CVP (Capa Verde de Peces) is north of Quebrada La Venta in the Fish Bed, a thin, extensive mudstone unit thought to represent a lake or swamp deposit. The Fish Bed contains abundant fossils of fishes and less common fossils of other aquatic vertebrates (such as the manatee *Potamosiren magdalenensis*) and terrestrial vertebrates. The Fish Bed is low in the Baraya Member of the Villavieja Formation, above the Monkey Beds (**Guerrero**, 1997:fig. 2.8).

Kyoto University's Chepe site, also known as Cuzco, is about 4.5 km east of Villavieja between Quebrada La Venta and Quebrada Las Lajas. The Chepe site is in the uppermost Las Lajas Member (of **Takai** et al., 1992) of the Villavieja Formation. The Las Lajas Member of **Takai** et al. (1992) is equivalent to the upper part of the Baraya Member of **Guerrero** (1997) and **Villarroel** et al. (1996). The Baraya Member is overlain by the Cerro Colorado Member. The fossil bats from the Chepe site are stratigraphically the highest known in the Villavieja Formation and thus, geologically slightly younger than those from locality 22. No radiometric dates are available for the Las Lajas/upper Baraya Member, but **Guerrero** (1997) and **Flynn** et al. (1997) provided a date of 12.2 Ma from the San Francisco Sandstone Beds low in the overlying Cerro Colorado Member. This indicates the Chepe site fossils are slightly older than 12.2 Ma. The available radiometric dates neatly bracket the sites yielding the bat fossils in this report between 12.5 and 12.2 Ma. The only other locality in the Honda Group known to have produced a bat fossil (Duke locality 90; the type locality of *Potamops mascahehenes*; **Czaplewski**, 1997) is between 13.7 and 13.3 Ma (**Guerrero**, 1997; **Flynn** et al., 1997).

Previously, **Takai** et al. (1991) described *Kiotomops lopezi* from the Kyoto site in the Monkey Beds at La Venta. They referred this taxon to the bat family Molossidae; however, it represents a marsupial (**F. J. Goin**, personal communication). Unlike molossids, the holotype M1 of *Kiotomops* lacks a talon, hypocone, mesostyle, and lingual cingulum. Like marsupials, it bears large stylar cusps B and D separated by a deep ectoflexus. As in many marsupials, the preparacrista runs from the paracone to stylar cusp B instead of connecting with the parastyle (stylar cusp A) to form a hooklike process as in molossids. The holotype molar also has a low, swollen ridge running from the protocone into the trigon basin (worn in the holotype) which does not occur in bat molars. Thus we remove *Kiotomops* from the list of La Venta bats and add it to the list of La Venta marsupials.

As in certain previously reported bat fossils from La Venta, several of the teeth described below lack much or all of their enamel yet retain the underlying dentine. This occurs in two new specimens of *Noctilio albiventris*, two of *Notonycteris magdalenensis*, one tooth of a new species of *Notonycteris*, the associated right and left lower jaw fragments of a *Tonatia*, several small molossid teeth, and several additional teeth not detailed in this report. These teeth probably were rendered enamelless by digestion within the gut of a crocodilian, the only known process by which the loss of enamel with preservation of dentine can occur (**Fisher**, 1981). Crocodilians are diverse and abundant in the La Venta fauna, with 5 families and 11 species reported by **Langston** (1965) and **Langston** & **Gasparini** (1997). Small crocodilians such as young caimans could have occasionally killed or scavenged bats, as modern crocodiles in Australia are known to do to megachiropterans (**Taylor**, 1979; **Webb** & **Manolis**, 1989) and microchiropterans (**Webb** et al., 1982:table 1). **Grahame Webb** (personal communication) has observed captive crocodilians in Australia snap bats out of the air as the bats flew low over water chasing insects, and notes that wild crocodilians do the same thing, even gathering beneath bat roosts wherever a colony is located in crocodilian habitat.

Systematic Paleontology

Class Mammalia

Order Chiroptera

Family Emballonuridae

Genus and species indeterminate

(Fig. 1; Table 1)

Material: IGM 252993, left C1 fragment.

Locality: Duke loc. 22

Description: The main cusp of this canine is broken and the resulting cross-section shows a hemiconical shape. The root is stouter than the main cusp. There is a prominent cingular cusp at the anterior medial corner. A labial cingulum leads from this cusp around the anterior side of the tooth but does not quite reach the midpoint of the labial side. Another prominent cingular cusp occupies the posterolingual corner, with a prominent posterior cingulum extending from it across the posterior of the tooth to its posterolabial portion. A less prominent cingulum on the lingual base of the crown connects the two cingular cusps.

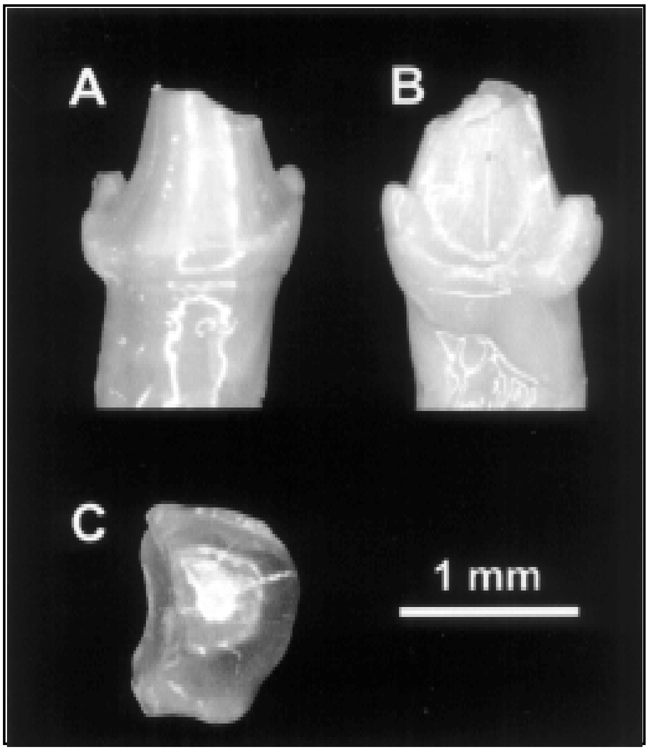

Figura 1. Emballonuridae: left C1 fragment (IGM 252993) in **A**, labial; **B**, lingual; and **C**, occlusal views.

The general configuration of the tooth is like that of various emballonurids except for Diclidurinae (which lack prominent anterior and posterior cingular cusps on the upper canine). The tooth represents an animal about the size of *Peropteryx kappleri*. Its anterior and posterior, sharp cingular cusps and overall morphology are similar especially to *Saccopteryx canescens*, *Centronycteris maximiliani*, *Cormura brevirostris*, and *Peropteryx kappleri* in the western hemisphere and *Coleura afra* in the eastern hemisphere. The tooth is less procumbent (canted forward) than in most Old World emballonurids (*Saccolaimus pluto*, *S. flaviventris*, *Taphozous nudiventris*, *T. peli*, *T. melanopogon*) but similar to *Coleura afra* and *Emballonura alecto* in its straight main cusp. It is less laterally compressed than in *Saccopteryx leptura*, *S. gymnura*, and *S. canescens*, *Rhynchonycteris*, *Peropteryx macrotis*, and *Emballonura alecto*. The development of a cingulum in the fossil is on the anterior (or actually, anteromedial), posterior, and lingual sides; no cingulum occurs on the labial side. The cingulum is rather sharp-edged by comparison with many modern emballonurids, in which it tends to be more rounded. The posterior cingular cusp is slightly more distally separated from the posterior crest of the main cusp and more securely situated on the cingulum than in most modern forms. The posterior cingulum is a sharp shelf with a slightly projecting (or widened) posterolabial portion. This configuration is very much like that in *Coleura afra* but has the more rounded and less-projecting configuration seen in this area of the tooth in New World emballonurid canines. Among New World forms, this area projects slightly in *S. canescens*, *Cormura brevirostris*, *Peropteryx kappleri*, *Balantiopteryx plicata*, and *Balantiopteryx io*. The fossil canine is rather intermediate in the development of the cingulum; it is less developed than in *Coleura afra* and more developed than in these just-mentioned New World taxa. The fossil canine differs from *Coleura* in lacking the labial portion of the cingulum and in having the lingual portion narrower and more rounded. The fossil differs from *Saccopteryx*, *Cormura*, *Peropteryx*, and *Balantiopteryx* in having wider and sharper anterior, lingual, and posterior cingula.

Table 1. Tooth measurements (in mm) of Miocene bats in the La Venta fauna, Villavieja Formation, Colombia. Parentheses indicate estimated measurements of broken specimens.

		UPPER TEETH				
taxon	IGM number	tooth	labial length	lingual length	tw	apl
EMBALLONURIDAE						
Gen. & sp. indet.	252993	C1	—	—	1.05	1.30
PHYLLOSTOMIDAE						
Notonycteris magdalenensis	90-C01	M2	3.55	3.40	4.40	—
Palynephyllum antimaster	252971	M1 or 2	1.40	1.05	1.30	—
	252863	M1 or 2	—	1.22	1.30	—
THYROPTERIDAE						
Thyroptera lavali	252979	M1	1.55	1.25	1.65	—
	252985	C1	—	—	0.75	0.95
	252970	M1 or 2	—	1.10	—	—
MOLOSSIDAE						
Eumops sp. indet.	9303	M1	2.30	1.85	3.10	—
Gen. & sp. indet.	250329	M1 or 2	—	1.30	—	—
	252969	M1 or 2	—	1.10	—	—
	90-235	M1 or 2	—	1.20	1.80	—

		LOWER TEETH				
	IGM number	tooth	tw	apl	trigonid width	talonid width
PHYLLOSTOMIDAE						
Notonycteris magdalenensis	252972	m1	—	3.00	1.90	2.00
Notonycteris sucharadeus	9305	m1	—	2.50	1.45	1.90
	252869	m2	—	2.85	1.70	1.80
Tonatia or *Lophostoma*	252980	m1	—	2.35	1.25	1.35
	“	m2	—	(2.40)	1.50	1.40
	252981	m2	—	(2.10)	1.40	1.30
	“	m3	—	2.00	1.10	0.90
	252983	m3	—	—	—	0.70
THYROPTERIDAE						
Thyroptera lavali	252978	m1	—	1.20	0.75	0.80
	“	m2	—	1.25	0.75	0.80
	SN-022-1a	m1 or 2	—	—	—	(0.90)
	SN-022-1b	m3	—	—	—	0.7
MOLOSSIDAE						
Gen. & sp. indet.	252987	m3	—	1.70	1.10	1.00
	252988	m1 or 2	—	1.60	1.00	1.20
	252989	m1 or 2	—	1.70	1.20	1.30
	250331	c1	1.20	1.30	—	—
	250332	p3	0.90	0.80	—	—
	250996	p3	0.90	0.90	—	—
	250338	p3	0.90	0.80	—	—
VESPERTILIONIDAE						
Gen. & sp. indet.	250339	m1 or 2	—	1.50	1.10	1.20

This specimen probably represents a new taxon of emballonurid, intermediate in at least a few characters of its upper canine between Old World and New World emballonurids. A *Diclidurus* sp. was previously reported in the La Venta fauna by **Czaplewski** (1997), but this new specimen represents a smaller bat and also does not have the canine morphology of *Diclidurus*.

Family Noctilionidae

Noctilio albiventris Desmarest 1818

Material: IGM 252975, right p4 missing most of its enamel; IGM 252976 nearly enamelless left p4.

Locality: Duke locality 22.

Discussion: These two teeth are both broken and lack most of their enamel. Nevertheless, the portions that remain are similar in size and shape to p4s of *Noctilio albiventris*. This species was recorded in the La Venta fauna by **Czaplewski** (1997), but the lower premolars had not been found previously.

Family Phyllostomidae

Subfamily Phyllostominae

Notonycteris magdalenensis Savage 1951 (Fig. 2; Table 1)

Material: IGM-KU 90-C01, complete right M2 (Fig. 2B-D); IGM 252973, right M1 or M2 lacking most of its enamel (Fig. 2A); IGM 252972, right m1 missing most of its enamel.

Localities: IGM-KU 90-C01 is from the Chepe site; IGM 252973 and 252972 are from Duke loc. 22.

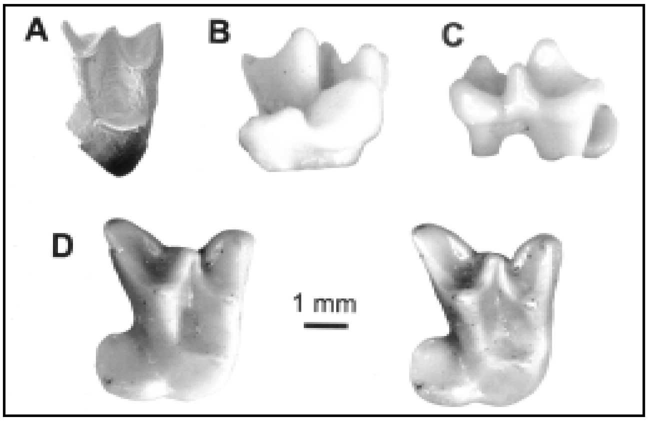

Figura. 2. Phyllostomidae: *Notonycteris magdalenensis*, **A**, enamelless right M1 or M2 (IGM 252973) in occlusal view; right M2 (IGM-KU 90-C01) in **B**, lingual; **C**, labial; and **D**, occlusal (stereopair) views.

Description and Discussion: The upper molars are the first known upper teeth of this species. One specimen (IGM 252973) is missing nearly all of its enamel and is relatively uninformative. However, the other upper molar, IGM-KU 90-C01, is in perfect condition. As in other phyllostomines, this M2 has a broad rounded talon with a low, crested hypocone at its lingual border near the protocone. The post-hypoconal crest continues as a cingulum along the lingual and posterior border of the talon, but weakens along the labial border. The postparacrista and premetacrista are shorter than the preparacrista and much shorter than the postmetacrista. Accordingly, the mesostyle is lingually situated relative to the parastyle and metastyle, so that the tooth appears strongly indented in its labial occlusal outline. The mesostyle is tall but anteroposteriorly short. The postmetacrista is about twice the length of the premetacrista. The paracingulum is reduced to a short remnant adjacent to the parastyle. The parastyle is prominent but barely hooked. The preprotocrista is very short and connects with the base of the paracone. The postprotocrista is somewhat longer and connects with the base of the metacone. There is no lingual cingulum. The metacingulum is weakly developed for a short distance lingual to the metastyle.

The M2 of *Notonycteris magdalenensis* is less derived than the same tooth in *Trachops*, *Chrotopterus*, and *Vampyrum*, but is more similar to those genera than to any other phyllostomids. In particular, it is most similar to *Chrotopterus* and somewhat less similar to *Vampyrum*. The M2 differs strongly from that of *Trachops* in being much larger and in having much less obliquely angled crests of the W-shaped ectoloph, an indented mesostyle, a much broader talon, a crested rather than cuspate hypocone, a weaker paracingulum, and a stronger metacingulum. It differs from *Vampyrum* in being much smaller and in having a more prominent mesostyle, relatively longer postparacrista and premetacrista, relatively shorter postmetacrista, less developed paracingulum, and taller, more prominent hypocone. It differs from *Chrotopterus* in being a little larger, and in having a relatively and absolutely lower unworn crown height, a relatively shorter postmetacrista, a relatively longer preprotocrista and postprotocrista, and a taller and more prominent hypocone.

Based on the parsimony analysis of morphological characters, *Notonycteris magdalenensis* and the new species of *Notonycteris* described below form part of a monophyletic clade with *Chrotopterus* and *Vampyrum* (Fig. 3) to the exclusion of *Trachops, Phyllostomus, Phylloderma*, and *Tonatia*. A sister relationship between *Chrotopterus* and *Vampyrum* is strongly supported, and the relationship of *Notonycteris* to these bats is moderately so.

Notonycteris sucharadeus sp. nov. (Figs. 4, 5A; Table 1)

Holotype: IGM-KU 9305, complete left m1 in small fragment of the dentary bone.

Hypodigm: The holotype plus IGM 252869, a right m2 missing enamel along its labial side, in a small fragment of dentary.

Type Locality and Horizon: The holotype is from the Chepe site (Cuzco); uppermost part of Las Lajas Member, Villavieja Formation, Honda Group; Middle Miocene, Laventan land mammal age (**Madden** et al., 1997).

Additional Locality: IGM 252869 is from Duke loc. 22, San Nicolás; Monkey Beds, Villavieja Formation.

Diagnosis: A *Notonycteris* smaller than *Notonycteris magdalenensis*, the only other species of the genus. Dimensions of the m1 in *N. sucharadeus* are about 77% to 84% of those in *N. magdalenensis*; measurements of the m2 are about 71% to 76% of those in *N. magdalenensis*.

Etymology: *souchos*, Greek, crocodilian; *arados*, Greek, a rumbling in the bowels; *-eus*, Greek, doer, agent, maker of. Based on the possibility that IGM 252869 passed through the gut of a crocodilian (see Introduction).

Description: These molars from two different localities represent a large phyllostomid. They are about three-fourths the size of the same teeth in *Notonycteris magdalenensis*, and are slightly smaller (73% to 87% of linear dimensions) than in *Chrotopterus auritus*. The holotype m1 is virtually undamaged but is fairly heavily worn. The m2 is moderately worn, but less so than the holotype.

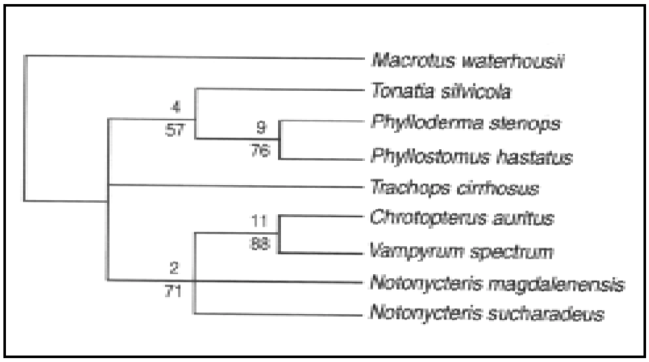

Figura. 3. Tree representing potential phylogenetic relationships among *Notonycteris* species and selected other Phyllostominae, based on unweighted parsimony analysis of 48 dental and osteological characters (see Appendices). Topology represents 50% majority-rule consensus of nine most parsimonious trees using bootstrap method with branch-and-bound search. Tree length = 73 steps; consistency index = 0.6800; retention index = 0.5102. Numbers above the branch lines are decay (Bremer support) values; numbers below the branches are bootstrap support values.

The m1 (Fig. 4C-E) appears relatively robust and low-crowned, with a talonid that is much wider than the trigonid. The paraconid is much lower and smaller than the metaconid. On the protoconid, the angle between the paracristid and protocristid is slightly less than 90°, forming a fairly open trigonid angle. There is also an angle within the paracristid such that the portion lingual to the notch in the paracristid (on the paraconid) is directed medially rather than forward. There is a relatively large hollow within the trigonid basin beneath the notch in the paracristid. The cristid obliqua meets the posterior wall of the trigonid beneath the notch in the protocristid. The talonid shows a nyctalodont configuration, with the postcristid forming a long sigmoid crest connecting to a strong, crested hypoconulid. A large interdental contact facet is present on the posterior of the tooth beneath the hypoconulid. The entoconid is large at its base and tall; it is separated from the postcristid/hypoconulid by a small V-shaped trough. The entoconid bears a relatively high entocristid that extends to the metaconid. The labial cingulum is tall with a smooth edge; it rises slightly into the labial basin between protoconid and hypoconid.

The m2 (IGM 252869; Fig. 4A-B) was previously illustrated and described by **Czaplewski** (1997:fig. 25.3 C, D) as follows (modified from the original): Enamel has been lost all along the labial base of the crown including all of the labial cingulum. The paraconid is well-developed and nearly as tall as the metaconid; the paracristid is relatively high. The talonid is slightly wider than the trigonid, and the talonid basin is deep and rounded. The cristid obliqua meets the trigonid below the notch in the protocristid. The postcristid is continuous with the hypoconulid, which in turn occurs as a curved ridge separated from the entoconid by a V-shaped groove. There is a small interdental contact facet on the distal cingulum beneath the hypoconulid. The entoconid is large, tall, and distinct, and is connected with the metaconid by a relatively high entocristid. The talonid crests (cristid obliqua and postcristid) lack carnassial-like notches at this stage of wear, although there is a relatively large hollow within the trigonid basin beneath the notch in each cristid.

Aside from the difference in size, the m1 of *N. sucharadeus* differs from generally comparable phyllostomid genera as follows: The crown is relatively lower and more robust than in *Trachops*, and has a relatively larger paraconid. The trigonid angle is much less open than in *Vampyrum*, with a relatively larger metaconid, less reduced talonid

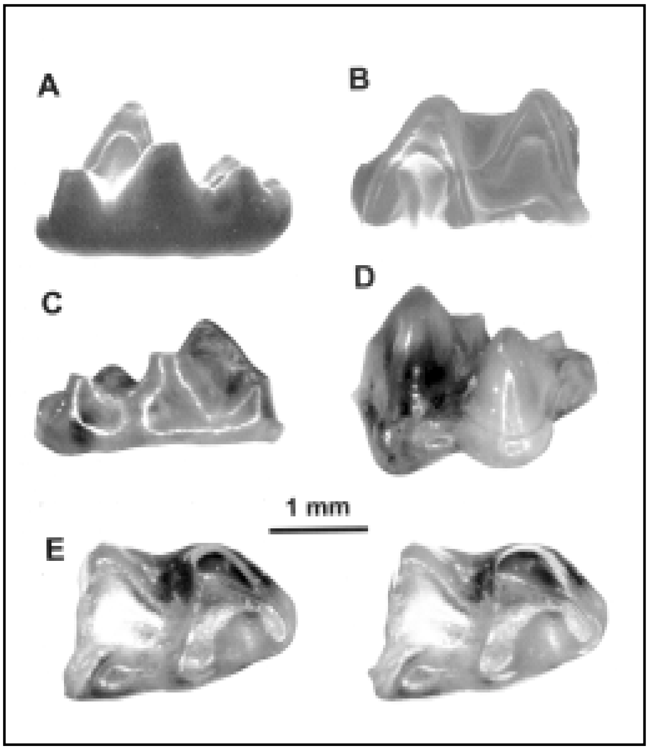

Figura. 4. Phyllostomidae: *Notonycteris sucharadeus* sp. nov., right m2 (IGM 252869) in **A**, lingual and **B**, occlusal views; left m1 (IGM-KU 9305, holotype) in **C**, lingual; **D**, labial; **E**, occlusal (stereopair) views.

(especially the hypoconid), and stronger entocristid. The m1 of *Notonycteris sucharadeus* has a less open trigonid angle than *Chrotopterus*, with a longer protocristid, less reduced talonid (especially the hypoconid) and longer cristid obliqua.

The fossil m2 has the following morphological differences relative to m2s of other phyllostomid genera (see also **Czaplewski**, 1997). The paraconid is nearly equal in height to the metaconid, relatively larger and higher than in *Trachops*. The talonid is not nearly as reduced in size relative to the trigonid as in *Vampyrum*. Although molar cusp deployment and crest morphology are quite similar to *Chrotopterus*, the molars of *N. sucharadeus* are relatively low-crowned compared with *Chrotopterus* (Fig. 5); the m2 of *N. sucharadeus* is 87% of the length of the m2 of *Chrotopterus*, but the height of its protoconid is only 73% of that of an equivalently worn m2 of *Chrotopterus*. The crests and cusps are also relatively more robust in *N. sucharadeus* than in *Chrotopterus*. Relative height of the crown of *N. sucharadeus* is similar to that of *N. magdalenensis*; length of IGM 252869 is approximately 76% and protoconid height is 74%, respectively, of equivalently-worn teeth of *N. magdalenensis*. The m1 and m2 talonids are less reduced in both species of *Notonycteris* than in *Chrotopterus*. Relative robustness of the teeth, cusp deployment, and crest morphology in *N. sucharadeus* are almost identical to those of *N. magdalenensis*.

Notonycteris sucharadeus is clearly most similar to its congener *Notonycteris magdalenensis*, and also very close to *Chrotopterus auritus* among living bats. Except for their smaller size, the two available teeth of *N. sucharadeus* are virtually identical to the same teeth in *N. magdalenensis*. The type m1 of *N. sucharadeus* has a relatively larger entoconid than that in the holotype m1 of *N. magdalenensis*. However, another partial m1 of *N. magdalenensis* (University of California Museum of Paleontology 39960; **Savage**, 1951) has the entoconid broken off, but its base indicates it was probably larger than the entoconid in the holotype of that species, and of the same relative size as the entoconid in *N. sucharadeus*; thus entoconid size may be individually variable. Also by comparison with *N. magdalenensis*, the m1 of *N. sucharadeus* has a slightly more robust paraconid and less prominent vertical swelling on the lingual face of the protoconid (descending from the apex of the protoconid into the trigonid basin).

Discussion: Several characters of the lower molars of *N. sucharadeus* are distinct from those of *Chrotopterus* and *Vampyrum*, including the relatively lower crown height, more robust crests and cusps, and less reduced talonids. In the upper molars (at least one M2 described above) of *N. magdalenensis*, distinctive features include the lower crown height, less slender cusps and crests, less obliquely oriented ectoloph crests, and shorter postmetacrista. These features seem to reflect a relatively primitive molar configuration in *N. sucharadeus*, as was also mentioned for *N. magdalenensis* by **Savage** (1951) relative to the configuration in the modern genera. **Freeman** (1988; 1998) and other authors have interpreted some of these dental features as functional adaptations for carnivory in extant *Trachops cirrhosus, Chrotopterus auritus, Vampyrum spectrum*, and other bats. The molar characters of *N. sucharadeus* suggest that it was probably similar in dietary habits to *N. magdalenensis* and that both species of *Notonycteris* were less specialized for carnivory than modern carnivorous phyllostomids.

Phylogenetic analysis: The parsimony analysis of dental-osteological characters in *Notonycteris sucharadeus, N. magdalenensis*, and several other phyllostomines resulted in nine equally parsimonious trees of 73 steps (Fig. 3). The clade comprised of *Chrotopterus* and *Vampyrum* received relatively strong bootstrap support

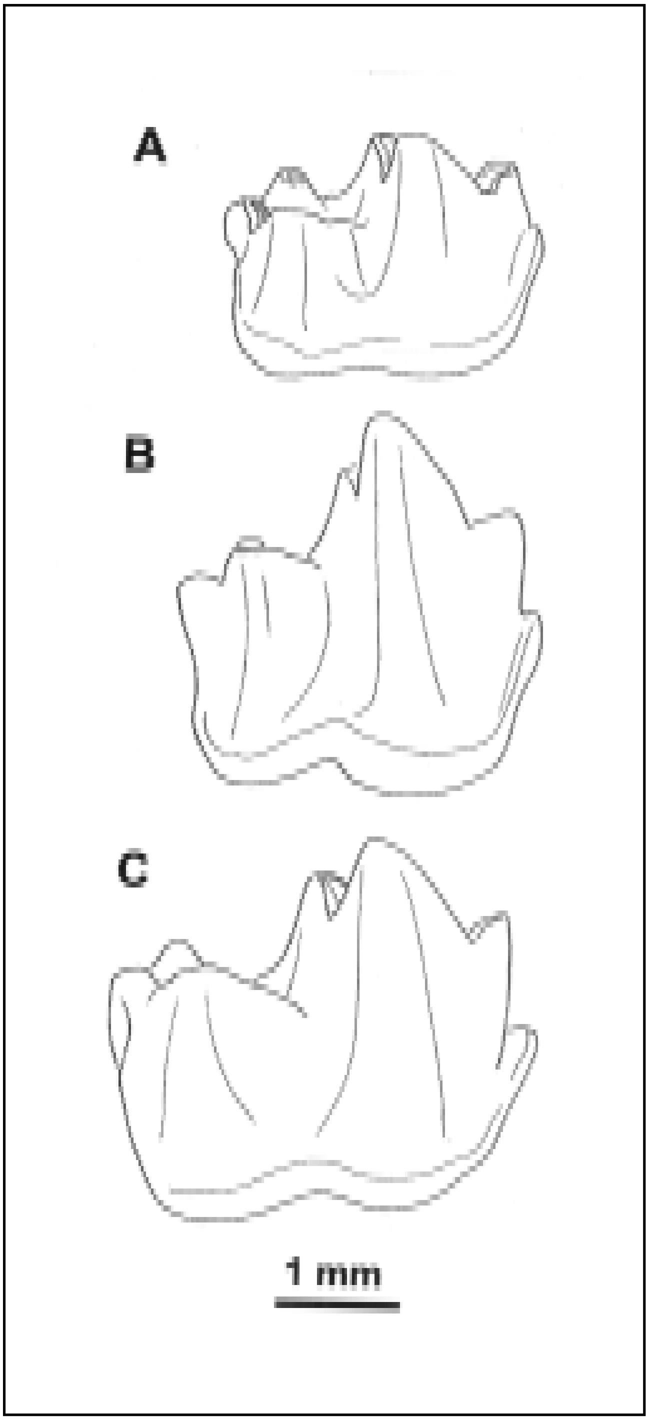

Figura. 5. Phyllostomidae: Outline drawings in labial view comparing the unworn or little-worn crowns of the m2s of **A**, *Notonycteris sucharadeus* (IGM 252869); **B**, *Chrotopterus auritus* (modern specimen, USNM 530910, male, Peru); and **C**, *Notonycteris magdalenensis* (IGM 252865, left m2 [reversed; Czaplewski, 1997]). Note the squat stoutness of the two species of *Notonycteris* compared to the more slender cusps and relatively higher crown in *Chrotopterus*.

and a high decay value indicating a close relationship between these two taxa. The two species of *Notonycteris* clustered with *Chrotopterus* and *Vampyrum*, but bootstrap support for this relationship was moderate. The placement of *Trachops* was equivocal relative to this clade and the other taxa examined. It is interesting to note that the two species of *Notonycteris* did not necessarily appear in the analysis as sister taxa, despite being identical in all available character states. The reason for failure to disclose a more solid sister relationship is incompleteness of the data for one of the fossil taxa. *Notonycteris sucharadeus* is known only by two teeth, so the data for this species are very incomplete (13 of 48 characters; 27% complete). By comparison, the data for *N. magdalenensis*, which is known from several jaws, teeth, and postcranial bones (**Savage**, 1951), are much more complete (31 of 48 characters; 65% complete). As a result, the identical character states make it impossible to distinguish the two *Notonycteris* species (except for their difference in size, which is not included in the phylogenetic data).

Tonatia Gray 1827 or *Lophostoma* D'Orbigny 1836

Tonatia or *Lophostoma* species indeterminate. (Fig. 6; Table 1)

Material: The following specimens were found in association with one another in a small amount of rock matrix during the screenwashing process. They probably represent the right and left lower jaws of an individual bat that was eaten and its teeth partly digested by a crocodilian because most of the teeth lack enamel (see Introduction): IGM 252980 left dentary fragment with roots of p4 and m1-m2; IGM 252981 right dentary fragment with m2-m3; IGM 252982, right m1 trigonid; IGM 252983, left m3 talonid.

Description and Discussion: In IGM 252981, the depth of the dentary on the labial side below the anterior root of m2 is 1.90 mm, the lingual depth of the dentary below the anterior root of m2 is 3.10 mm. Other measurements are provided in Table 1. Many of the morphological features present in the dentine cores of the teeth are similar to those of *Notonycteris* and extant insectivorous-omnivorous phyllostomines. The trigonid of the m1s is more widely open (greater than 90°) than that in the m2s. The talonids of both m3s retain enamel. The m3 talonid is much narrower than the trigonid and is oblong and lophate with no distinguishable cuspids. The specimens indicate a bat smaller in most dimensions than *Notonycteris sucharadeus* and about the size of the extant species *Tonatia bidens*. The m1s of this set of specimens are narrower overall and have a much more open angle between the paracristid and protocristid on m1 than in *Notonycteris magdalenensis* and *N. sucharadeus*. The m1s are a little

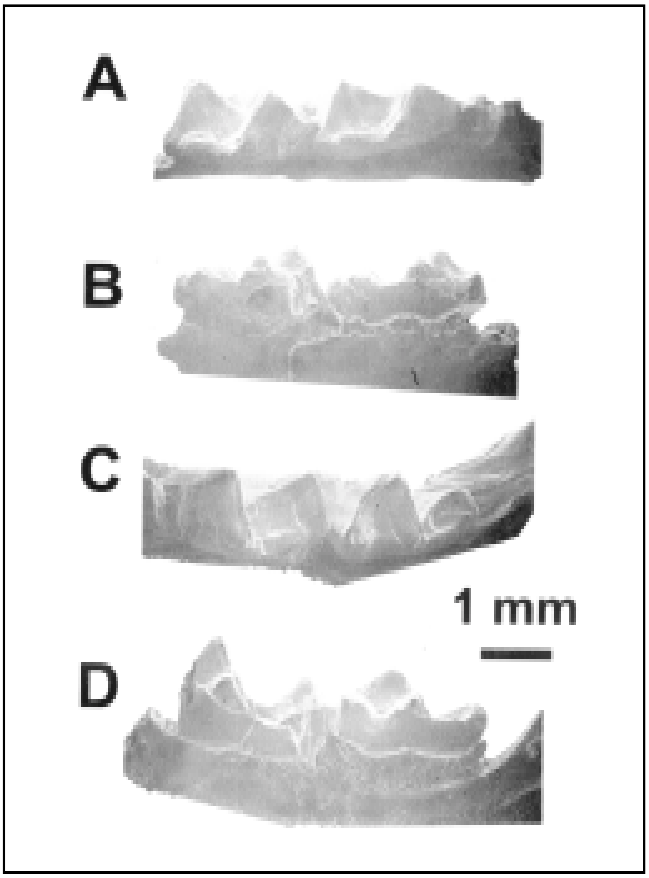

Figura. 6. Phyllostomidae: *Tonatia* or *Lophostoma*, left m1-m2 (IGM 252980) in **A**, occlusal and **B**, lingual views; right m2-m3 (IGM 252981) in **C**, occlusal and **D**, lingual views.

bit smaller than the holotype m1 of *N. sucharadeus*, and the m2s are much smaller than the m2 of *N. sucharadeus*.

In IGM 252980 each of the two roots of p4 retains a small, portion of the crown (from which the enamel has been lost; see Introduction), indicating a relatively large and long p4 with a ventrolabial border that was bilobed, as in the larger species of *Tonatia* and *Lophostoma* and unlike the unilobed p4 in *Macrophyllum* and smaller extant species of *Lophostoma* (see **Lee** et al., 2002, for the use of *Lophostoma*). The fossil teeth and jaws are much smaller than *Phylloderma* or any species of *Phyllostomus*. The molars are less trenchant (more robustly built with relatively inflated crowns and thick crests) than in *Lonchorhina*, *Macrophyllum*, *Micronycteris*, *Mimon*, and *Trinycteris*. The molars in the fossils also have less acute trigonid and talonid angles than in *Lonchorhina*, *Macrophyllum*, and *Mimon*. The m1 has a transversely wider trigonid with a less open angle than in *Chrotopterus*, *Glyphonycteris*, *Macrotus*, *Trachops*, and *Vampyrum*. In the qualitative features that are preserved, these fossils represent a phyllostomine most similar to *Tonatia* and *Lophostoma*. Unfortunately, the lack of enamel to show morphological details of the teeth precludes further work until more and better specimens can be found.

An isolated upper molar of *Tonatia* of an indeterminate species was previously reported in the La Venta fauna from the Fish Bed; it was said to be slightly smaller than *T.* (=*Lophostoma*) *silvicola* (**Czaplewski**, 1997). The new specimens from Duke locality 22 discussed above are about the same size and might represent the same species.

Subfamily Glossophaginae

Palynephyllum gen. nov. (Fig. 7; Table 1)

Type Species: *Palynephyllum antimaster*

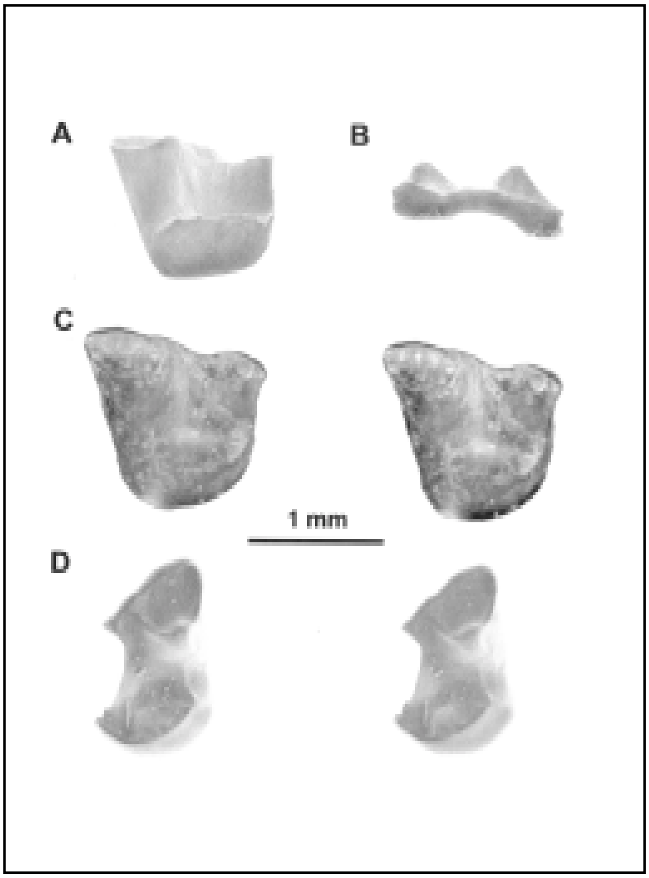

Figura. 7. Phyllostomidae: Glossophaginae: *Palynephyllum antimaster* new genus and species, right M1 or M2 (IGM 252971, holotype) in **A**, lingual; **B**, labial; and **C**, occlusal (stereopair) views; **D**, partial left upper molar (IGM 252863) in occlusal (stereopair) views.

Diagnosis: M1 or M2 small; talon and hypocone absent; lingual outline in occlusal view nearly semicircular; lingual cingulum absent; W-shaped ectoloph relatively primitive by comparison with most extant Glossophaginae (including Lonchophyllini), with relatively strong paracone and metacone, moderately reduced stylar shelf, short, anteriorly hooked parastyle, low and slightly elongate mesostyle formed in part by small gap between the labial ends of the postparacrista and premetacrista; styles do not bulge labially except for labial cingulum posterior to parastyle; slight crest posterior to mesostyle continuous with labial cingulum anterior to metastyle.

Etymology: from *palynein*, Greek, to sprinkle, and *phyllon*, Greek, leaf; on the presumption that this species occasionally stuck its nose into flowers and dusted its noseleaf with pollen.

Palynephyllum antimaster sp. nov.

Holotype: IGM 252971, right M1 or M2.

Hypodigm: The holotype plus IGM 252863, partial left M1 or M2, lacking paracone.

Type Locality and Horizon: Duke loc. 22, San Nicolás; Monkey Beds, Villavieja Formation, Honda Group; Middle Miocene, Laventan land mammal age (**Madden** et al., 1997).

Diagnosis: As for the type and only species.

Etymology: *antis*, Quechua, Andes Mountains; *master*, Greek, searcher.

Description and Comparisons: The type specimen is virtually identical to IGM 252863 except for being a contralateral tooth and intact. The broken specimen was previously described by **Czaplewski** (1997). The fossils are approximately the size of the M2 in extant *Anoura caudifer* and *Lonchophylla handleyi*. The overall aspect presented by these fossils is that of a bat intermediate between typical insectivorous/omnivorous phyllostomines and derived nectar-feeding bats. The similarity in the shape of the ectoloph, styles, and stylar shelf to those of phyllostomines (with short preparacrista and labial outline angled inward anteriorly) suggests the fossils may represent M1s rather than M2s, but this is not certain without more complete toothrows. There are no wear facets on either of the teeth.

The four commissures of the ectoloph are present and formed of relatively sharp-edged crests. The postmetacrista is longest, followed by the postparacrista, premetacrista, and a short preparacrista. The commissures make a W-shape that is not elongated by comparison with some genera of glossophagines such as *Leptonycteris*. There is a slight gap between the labial ends of the postparacrista and premetacrista, with attendant anteroposterior lengthening of the mesostyle. The paracone is nearly as tall as the metacone. The protocone is large, with a preprotocrista that curves labially to meet the anterior base of the paracone, and a postprotocrista that extends posteriorly and then drops off, not reaching the base of the metacone and leaving the trigon valley barely open posteriorly. Lingual cingulum, paracingulum (mesial cingulum), and metacingulum (distal cingulum) are completely absent. A low parastyle with a very short, anteriorly directed crest is present. Another small crest extends posteriorly from the parastyle to form a labial cingulum along the stylar shelf , but this cingulum does not reach the mesostyle. This portion of the stylar shelf bulges slightly labially in occlusal view, with a small indentation behind it and ahead of the mesostyle. An additional small crest extending posteriorly from the mesostyle dresses the stylar shelf between mesostyle and metastyle. There is no labial emargination in the occlusal outline between mesostyle and metastyle. Talon and hypocone are absent.

Discussion: The two available teeth of *P. antimaster* are the oldest known teeth representing a glossophagine, and the only presumably nectar-feeding bat from the Tertiary period in the western hemisphere. Obviously, these two teeth are less than ideal for describing a new genus. Compounding this problem to some extent is the variability in tooth morphology within many extant species of nectar-feeding phyllostomids (**Phillips**, 1971). Nevertheless, the relatively primitive configuration of the upper molars of *P. antimaster* allows us to differentiate this new taxon from known glossophagines (as well as all other Phyllostomidae) as given below, yet precludes meaningful phylogenetic analysis of it. Moreover, despite the poor sample, the geological age of the La Venta fossils also suggests they represent a previously unnamed taxon, which justifies their formal recognition. The biological significance and phylogenetic relationships of extant nectar- and pollen-feeding phyllostomids are actively being studied by many researchers (e.g., **Gimenez** et al., no date; **Norberg** & **Rayner**, 1987; **Norberg** et al., 1993; **Helversen**, 1993; **Fleming**, 1993; **Fleming** et al., 2001; **Freeman**, 1995, 1998, 2000; **Schnitzler** et al., 1998; **Solmsen**, 1998; **Winter**, 1998, 1999; **Winter** et al., 1998; **Baker** et al., 2000; **Rojas-Martinez** et al., 2000; **Wetterer** et al., 2000; **Carstens**, 2001; **Valiente-Banuet**, 2002); but clarification of the phylogenetic relationships of *P. antimaster* must await the discovery of more and better fossils.

The upper molars of *P. antimaster* lack the extreme specializations for frugivory in *Ametrida, Ardops, Artibeus, Ariteus, Brachyphylla, Centurio, Chiroderma, Dermanura,* *Ectophylla, Enchisthenes, Phyllops, Platyrrhinus, Pygoderma, Sphaeronycteris, Stenoderma, Sturnira, Uroderma, Vampyressa, Vampyriscus,* and *Vampyrodes*. They lack the large talon seen in M1 and M2 of *Chrotopterus, Glyphonycteris, Lampronycteris, Lonchorhina, Macrophyllum, Macrotus, Micronycteris, Mimon, Neonycteris, Notonycteris, Phylloderma, Phyllostomus, Tonatia, Trachops, Trinycteris,* and *Vampyrum*. The fossils are much less reduced than upper molars in *Carollia, Choeronycteris, Choeroniscus, Desmodus, Diaemus, Diphylla, Erophylla, Hylonycteris, Lichonycteris, Musonycteris, Phyllonycteris, Platalina, Rhinophylla,* and *Scleronycteris*. They lack the distinct small talons of *Monophyllus redmani* and the elongated, flattened ectolophs of *Monophyllus plethodon*. They also lack the elongated and flattened W-shaped ectolophs of *Leptonycteris*.

The La Venta fossils most closely resemble the M1 and M2 of several primarily nectarivorous genera of phyllostomids recognized by **Phillips** (1971) as having relatively unspecialized teeth, *Lonchophylla, Lionycteris, Anoura,* and *Glossophaga*. Of these, the M1 and M2 of *P. antimaster* differ from *Lonchophylla* in lacking a small talon and having a less flattened and elongated W-pattern of the ectoloph. The fossils have a much less labially-protruding metastyle than on M1 and M2, and a less flattened and elongated ectoloph on at least the M1, than in species of *Glossophaga*. Unlike *Anoura*, the La Venta fossils have no hint of a talon, a short labial cingulum posterior to the parastyle, and a postparacrista and premetacrista that contribute equally to a much less prominent mesostyle. (In contrast, *Anoura* species have at least a very rudimentary talon that lends a "squared-off" bulge to the posterolingual border of the M1 and M2, a long labial cingulum extending posteriorly from the parastyle, and the postparacrista does not reach the mesostyle but the premetacrista forms a tall and labially-protruding mesostyle.) *Palynephyllum antimaster* has a stronger and taller postparacrista and premetacrista that extend to the mesostyle, and a relatively shallower trigon basin than in *Lionycteris*, and on M1 also a longer preparacrista.

Family Thyropteridae

Thyroptera lavali Pine 1993. (Fig. 8; Table 1)

Material: IGM 252978, left dentary fragment with m1-m2; IGM 252979, right M1; IGM 252970, left M1 or M2 fragment; IGM 252985, enamelless left C1; IGM-DU SN-022-1a, talonid of left m1 or m2 missing labial cingulum; IGM-DU SN-022-1b, left dentary fragment with talonid of m3.

Locality: Duke loc. 22.

Description: On IGM 252978, dentary depth (on labial side from lower edge of anterior alveolus of m1 to bottom edge of dentary) measures 1.00. Other measurements are given in Table 1. Compared to the two thyropterids previously reported from the La Venta fauna (*T. lavali* and *T.* cf. *T. tricolor*; **Czaplewski**, 1996, 1997), these new specimens represent the larger species, *T. lavali*. Only a talonid fragment of a lower molar and three upper teeth were previously known for *T. lavali*. The lower molars in IGM 252978 have small, carnassial-like notches in the cristid obliqua, postcristid, and a weak one on the entocristid. The talonids are myotodont (**Menu** & **Sigé**, 1971). The m1 hypoconid and hypoconulid are damaged, but the hypocristid in both molars clearly runs from hy-

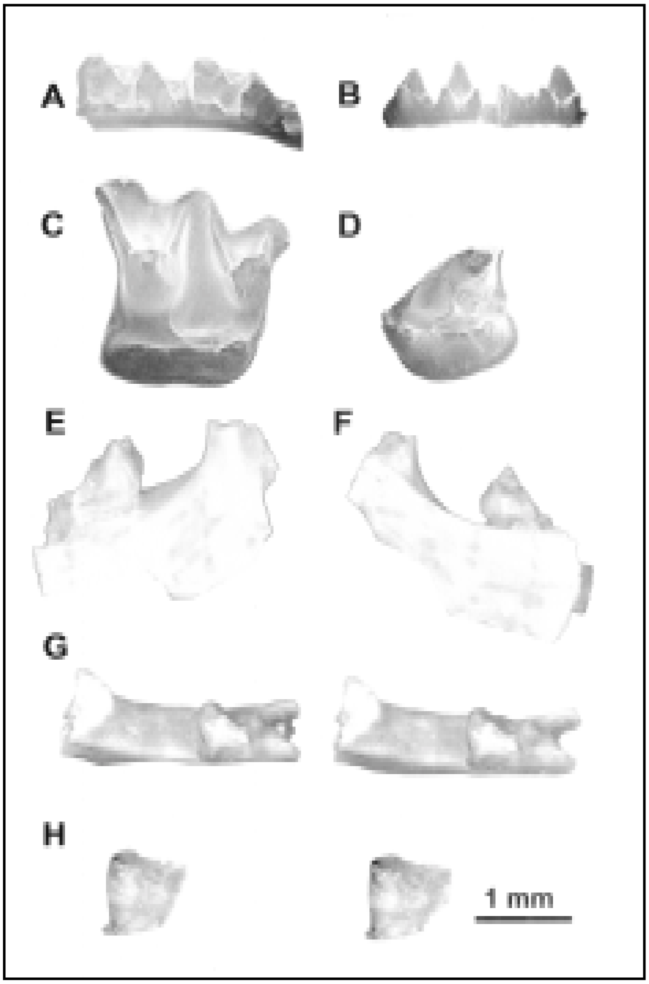

Figura. 8. Thyropteridae: *Thyroptera lavali* left dentary fragment with m1-m2 (IGM 252978) in **A**, occlusal, and **B**, lingual views. **C**, right M1 (IGM 252979) in occlusal view. **D**, left M1 or M2 fragment (IGM 252970) in occlusal view. Left dentary fragment with talonid of m3 (IGM-DU SN-022-1b) in **E**, labial; **F**, lingual; and **G**, occlusal (stereopair) views. **H**, talonid of left m1 or m2 (IGM-DU SN-022-1a) in occlusal (stereopair) views.

poconid to metaconid, with only a tiny weak ridge running perpendicularly from the postcristid down to the hypoconulid in the m2. For this reason the fragment can be referred to the Thyropteridae, which have myotodont lower molars, rather than the Furipteridae or Natalidae, which have nyctalodont lower molars.

IGM 252970 has a strong metaloph and paraloph, but the paraloph is broken along part of its crest. Both metaloph and paraloph are long, sinuous, and extend around the trigon basin toward the summit of the protocone. The paracone and most of the ectoloph are missing except for the metacone. There is a moderate-sized talon with a long, curved ridgelike crest including a small hypocone along its length. This hypoconal crest is a continuation of the postprotocrista. A complete lingual cingulum is present.

Family Molossidae

Eumops Miller 1906

Eumops sp. indet. (Fig. 9; Table 1)

Material: IGM-KU 9303, left M1.

Locality: Chepe site.

Description: The specimen is large, about the size of the same tooth in *Eumops glaucinus*. The preprotocrista is continuous with the paracingulum. No paraloph is present, but the base of the paracone is very close to the narrow paracingulum. There is a short, distinct metaloph that does not connect with the postprotocrista. The postprotocrista is virtually continuous with the metacingulum except for a tiny gap. The lingual cingulum is high and strong; it extends from the anterior wall of the protocone to the posterior wall of the tooth below the lingual end of the metacingulum, with only a small interruption on the posterolingual corner of the talon and hypocone. The tooth bears a moderately large talon with a conical or hemiconical hypocone that is welded onto the posterior wall of the protocone except for the portion near the hypocone apex. There is a short, small pre-hypoconal crest between the summit of the hypocone and the posterior wall of the protocone just below the level of the postprotocrista. A minute post-hypoconal crest appears at the interruption in the talon cingulum.

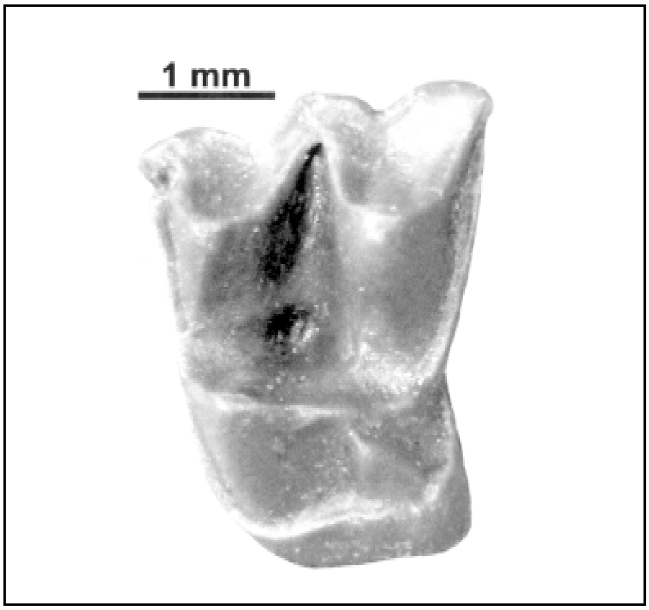

Figura. 9. Molossidae: *Eumops* sp. indet. left M1 (IGM-KU 9303) in occlusal view.

Czaplewski (1997) referred an isolated left M1 or M2 (IGM 184794) from the Fish Bed in the Villavieja Formation to *Eumops* sp. indeterminate; the specimen is broken and lacking some of its enamel such that it is not possible to see many details of the occlusal surface. IGM 184974 now appears to represent an M2 of the same taxon as this new, complete M1 (IGM-KU 9303). Besides size, the two teeth share the tall and continuous lingual cingulum, similar shape of the talon and hypocone, robustness, and other features. In the characters that are preserved in the broken tooth (IGM 184794), the only apparent difference is that the new, unbroken tooth has a short metaloph. There are relatively strong labial cingula along the stylar shelf and small indentations in the occlusal outline of the tooth between the parastyle and mesostyle, and between the mesostyle and metastyle. The old and new fossil specimens from La Venta clearly represent a *Eumops*; they were compared with all known species of *Eumops* except *E. maurus* and *E. patagonicus*, as well as all other genera in the family. No extinct species of *Eumops* have yet been described. Among the extant species, the La Venta fossils differ—especially in the posterolingual quadrant (postprotocrista-talon-hypocone region) of the tooth—from *Eumops auripendulus, E. bonariensis, E. dabbenei, E. hansae, E. trumbulli,* and *E. underwoodi*. The La Venta fossils are most similar in shape to the upper molars of *E. glaucinus* and *E. perotis*, and in size to *E. glaucinus*, but two isolated teeth are insufficient to confidently assign them to a species.

Genus and species indeterminate. (Fig. 10; Table 1)

Material: IGM 250329 lingual fragment of left M1 or M2 (Fig. 10 O); IGM 252969, enamelless broken left M1 or M2; IGM-DU 90-235 enamelless broken left M1 or M2; IGM 252987, right dentary fragment with m3 (Fig. 10 K,

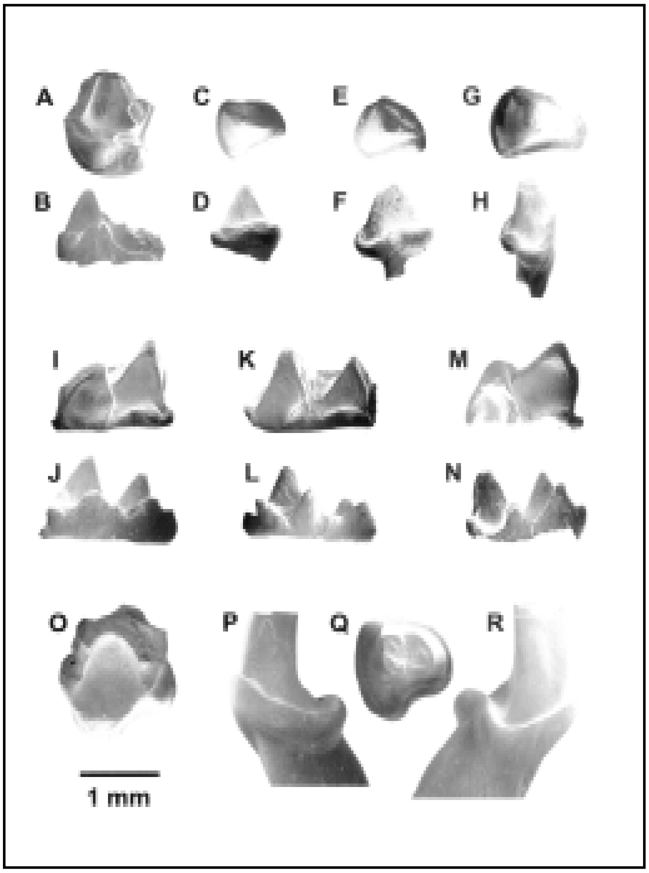

Figura. 10. Molossidae: Genera and species indeterminate: *Nyctinomops*-like left M1 or M2 fragment with long paraloph and metaloph (IGM 250277) in **A**, occlusal and **B**, posterior views. Left p3s: IGM 250338 in **C**, occlusal and D, posterior views; IGM 250996 in **E**, occlusal and **F**, posterior views; IGM 250332 in **G**, occlusal and **H**, posterolingual views. Right m1 or m2 (IGM 252989) in **I**, occlusal and **J**, lingual views. Right m3 (IGM 252987) in **K**, occlusal and **L**, lingual views. Right m1 or m2 (IGM 252988) in **M**, occlusal and **N**, lingual views. **O**, left M1 or M2 fragment (IGM 250329) in occlusal view. Right lower canine missing ti (IGM 250331) in **P**, lingual, **Q**, occlusal, and **R**, labial views.

L); IGM 252988, right m1 or possibly m2 (Fig. 10 M, N); IGM 252989, right m1 or possibly m2 (Fig. 10 I, J); IGM 250331, right c1 missing tip (Fig. 10 P, Q, R); IGM 250332, left p3 (Fig. 10 G, H); IGM 250996, left p3 (Fig. 10 E, F); IGM 250338, left p3 (Fig. 10 C, D).

Localities: IGM 250329, 252969, 252987, 252988, 252989, and IGM-DU 90-235 are from Duke loc. 22. IGM 250331, 250332, 250996, and 250338 are from the Fish Bed.

Discussion: These teeth show the general morphology of molossids as described in detail by **Legendre** (1984). Several taxa may be represented among these isolated teeth and fragments. Some could possibly belong to *M. colombiensis* (especially the lower molars, premolars, and/or canine, none of which has ever been found in association with diagnostic *M. colombiensis* upper molars). Other isolated teeth included here (the upper molars) certainly do not represent *M. colombiensis* because they lack that species' diagnostic features.

The upper molar fragments are in the same size range as *Mormopterus colombiensis* but they represent a different molossid. The ectoloph is broken on all three specimens and the enamel has been lost (digested away; see Introduction) on two of them, as in several other La Venta bat fossils. The protocones appear more compressed (anteroposteriorly shorter) than in *M. colombiensis*. They each have a metaloph that extends to the postprotocrista rather than toward the protocone as in *M. colombiensis*. There is a small talon with a hemiconical (instead of slender and rather cylindrical) hypocone with a summit that is merged into the postprotocrista (i.e., the apex of the hypocone is not separate and distinct). The hypcone meets the postprotocrista at about the same point as the metaloph does. The talon and hypocone are situated farther labially than in *M. colombiensis*. Because of breakage and loss of enamel, these three upper molar fragments are not identifiable beyond the family level. The configuration of the paraloph and metaloph in these upper molars also does not resemble the derived condition in M1 and M2 of *Nyctinomops* nor the intermediate condition in *M. colombiensis* (compare, for example, IGM 250329 with IGM 250277, previously recorded by **Czaplewski** [1997] as *M. colombiensis* but not previously illustrated; Fig. 10 O, A, B).

Among the lower molars, the m3 IGM 252987 represents a bat slightly larger than IGM 252988 in having a wider trigonid. In IGM 252987 the hypoconulid is reduced to nothing and the postcristid connects with the entoconid, the only cusp remaining at this corner of the talonid. The m1 or m2 IGM 252988 is clearly myotodont whereas IGM 252989 is clearly nyctalodont. Thus, more than one taxon is present among these isolated lower molars.

The p3s are similar in shape to p3s of *Mormopterus kalinowskii* and *M. phrudus* but much larger than in those extant species. They also resemble the p3s of *Nyctinomops* species.

Among these specimens of indeterminate small molossids, all of the upper molars and lower molars were found in Duke loc. 22, whereas the isolated canine and premolars were found in the Fish Bed. To date, all known specimens of *M. colombiensis* have been found in the Fish Bed (**Czaplewski**, 1997). It is possible that the difference in depositional environments between the Fish Bed (shallow aquatic) and loc. 22 (paleosol beneath forest) are reflected in a difference in the small molossids found in each. Thus, the canine and premolars found in the Fish Bed might represent *M. colombiensis*, and the teeth from loc. 22 definitely represent some other taxon. However, without associated toothrows and upper and lower teeth it is not yet possible to determine the taxa to which any of these teeth belong.

Family ?Vespertilionidae

Genus and species indeterminate. (Fig. 11; Table 1)

Material: IGM 250339, left m1 or m2.

Locality: Duke locality CVP (Fish Bed; **Guerrero**, 1997).

Discussion: This tooth has a myotodont configuration of the talonid, and the talonid is much wider than the trigonid. These characters are typical of Vespertilionidae and also found in certain Molossidae. Compared to Molossidae with myotodont molars, IGM 250339 has straighter crests (cristid obliqua, postcristid, entocristid), not sigmoidal crests as in *Mormopterus colombiensis*. The tooth has the trigonid and talonid more or less perpendicular to the long axis of the toothrow, not canted at an oblique angle as in molossids. Also unlike molossids, the talonid (especially its lingual side) in this molar is not shifted labiad relative to the trigonid. Given these features, the tooth probably represents a vespertilionid, but without more complete material it is not diagnostic below the family level.

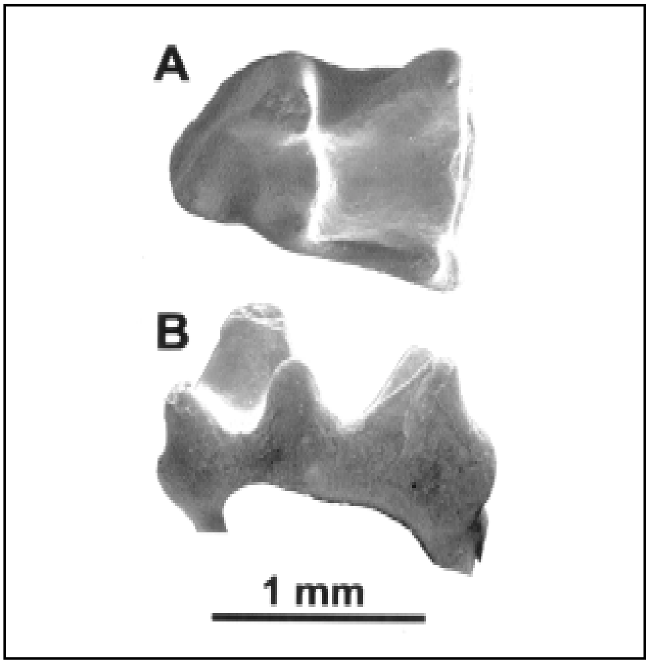

Figura. 11. ?Vespertilionidae: left m1 or m2 (IGM 250339) in **A**, occlusal and **B**, lingual views.

Family incertae sedis

Material: IGM 252986, periotic (Fig. 12).

Locality: Duke loc. 22.

Discussion: This specimen is rather poorly preserved and consists mainly of the cochlea. The semicircular canals are broken away and all that remains of them are mineralized internal molds of the ampulla and short segments of the lumen near the bases of one or two of the semicircular canals. The inner spiral chamber appears to make about two to two and one-fourth turns within the cochlea. There is a relatively large anteromedian flange on the promontorium that does not coincide with the position of the apical turn of the cochlea. The fenestra cochleae is relatively small and oval; its long diameter is less

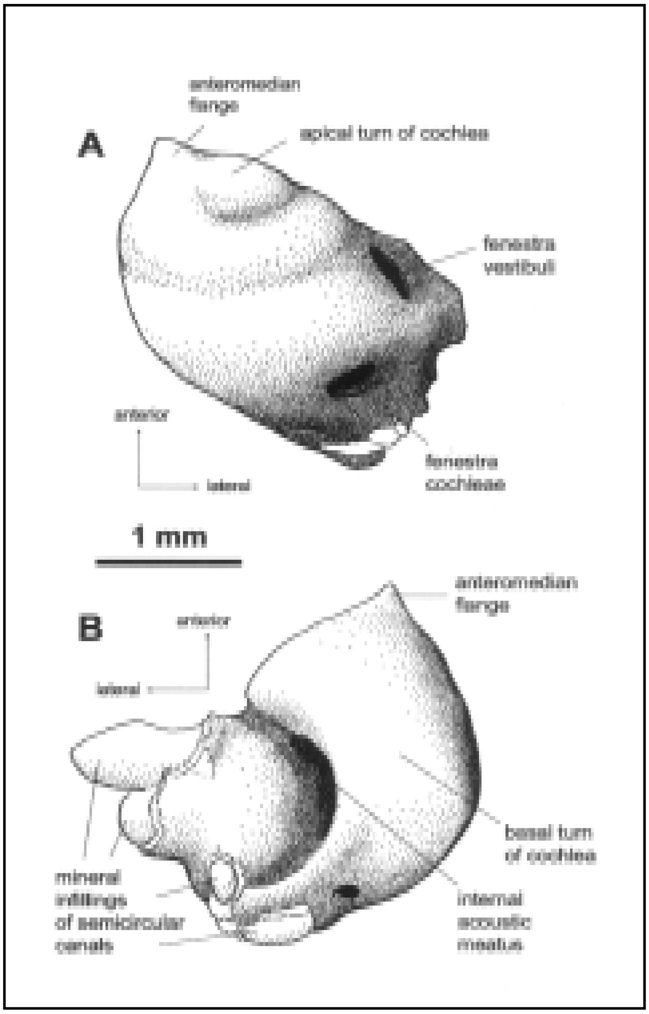

Figura. 12. Microchiroptera: family indeterminate, periotic bone (IGM 252986) in **A**, ventral view and **B**, dorsal (endocranial) view.

Table 2. Updated list of bat taxa in the La Venta fauna.

- Emballonuridae
    - *Diclidurus* sp. indet.
    - genus and species indet.
- Noctilionidae
    - *Noctilio albiventris*
- Phyllostomidae
    - *Notonycteris magdalenensis*
    - *Notonycteris sucharadeus*
    - *Tonatia or Lophostoma sp. indet.*
    - *Palynephyllum antimaster*
- Thyropteridae
    - *Thyroptera lavali*
    - *Thyroptera cf. T. tricolor*
- Molossidae
    - *Mormopterus colombiensis*
    - *Eumops sp. indet.*
    - *Potamops mascahehenes*
    - *genus and species indet.*
- Vespertilionidae
    - *genus and species indet.*

than that of the fenestra vestibuli. Little can be said about this specimen other than noting that it has the general morphology of periotics of Microchiroptera. Too few specimens of periotics dissected from modern bat crania were available from the variety of families that would be needed in order to make meaningful comparisons with the fossil, or attempt to assign the fossil to a family.

Discussion

Modern ecological communities of mammals in the Neotropics are very rich in species of bats. This, of course, is true across the broad variety of habitat types in Colombia in general, where over150 species of bats are known (**Cuervo** et al., 1986; **Muñoz**, 1995). But it is also true to a lesser extent even locally in the disturbed tropical dry forest-thorn shrubland (the "desierto" de La Tatacoa, in which the badlands and exposures yielding the La Venta fauna occur) of the Neiva Basin, where 23 living species of bats were netted (**Santos** et al., 1995; **Ruiz** et al., 2000). In contrast, the fossil record of bats is extremely poor in the Neotropics (as it is in many parts of the world).

Eleven species of fossil bats were previously reported in the La Venta fauna by **Czaplewski** (1997). With this report we add three more taxa to the La Venta bat list (Table 2), and provide new names to two species for which the sample of specimens was improved by additional screenwashing. One of the additional taxa is a second kind of emballonurid, unidentified but not representing the previously recorded *Diclidurus* sp. Another is a fourth kind of molossid, also unidentified but not representing the previously reported *Eumops* sp., *Mormopterus colombiensis*, and *Potamops mascahehenes*. Finally, a probable vespertilionid is the first of its family listed for the fauna. These fourteen species probably represent only a portion of the chiropteran species in the paleofauna. Due to the rarity of bat fossils yielded even by screenwashing large amounts of rock matrix, much additional collecting will be necessary to fill in the remaining unknown fraction of the La Venta bat community.

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Appendix 1.

List of the 48 characters and character states used in the phylogenetic analysis of selected Phyllostominae including the two species of *Notonycteris* (Fig. 3).

1. Mandibular symphysis: (0) unfused; (1) fused.
2. Mandibular symphysis with posteroventral projection: (0) absent; (1) weak to moderate; (2) strong.
3. p3 size and position in toothrow: (0) normal; (1) reduced in size and displaced labially from toothrow; (2) p3 absent; (3) p3 with tall, laterally compressed curving blade; (4) reduced in size but not displaced from toothrow.
4. p3 roots: (0) one root; (1) two roots obliquely positioned in jaw; (2) two roots in line with toothrow.
5. Lower teeth cingula: (0) normal; (1) greatly reduced.
6. Lower premolars crown shape: (0) not expanded downward on inside and outside faces; (1) expanded.
7. m1 paraconid position: (0) falls on a line drawn through the entoconid and metaconid; (1) falls labial of this line; (2) falls lingual of this line.
8. m1 talonid: (0) wider than trigonid; (1) reduced, narrower than trigonid.
9. m2 talonid width: (0) wider than trigonid; (1) narrower than trigonid; (2) subequal to trigonid width.
10. m1 hypoconulid size: (0) normal; (1) reduced.
11. m1 talonid crests (cristid obliqua and postcristid) when unworn: (0) without adjacent depressions in talonid basin or carnassial-like notches; (1) with talonid basin near hypoconid having two shallow depressions, one adjacent to cristid obliqua and adjacent to postcristid; (2) cristid obliqua and postcristid with carnassial-like notches.
12. p2 size: (0) normal; (1) reduced.
13. m1 trigonid valley: (0) present, normal; (1) absent or much reduced (protoconid positioned about on midline of tooth and paracristid reduced).
14. m1 labial cingulum: (0) normal; (1) with strong cingular cuspid anterior to protoconid; (2) rises on base of very short protoconid with sharp notch in paracristid.
15. m1 distal metacristid: (0) absent; (1) present and separated by notch from entocristid.
16. m1 lingual wall of tooth between entoconid and metaconid in occlusal view: (0) concave; (1) vertical; (2) convex.
17. m1 small cuspulid at lingual end of cristid obliqua adjacent to metaconid: (0) absent; (1) present.
18. m1 size relative to m2: (0) subequal; (1) reduced in size, smaller than m2; (2) larger than m2.
19. M1 parastylar area: (0) with hooked parastyle and without posterolabially directed ridge; (1) with distinct, posteriorly directed short ridge; (2) with preparacrista curving posteriorly and not connected to the parastyle; (3) with long ectocingulum spanning the anterior “vee” of the ectoloph.
20. M1 and M2 preprotocrista: (0) broad from protocone all the way to parastyle; (1) weak (thin) along anterior wall of paracone; (2) absent along anterior wall of paracone.
21. M1 and M2 postprotocrista configuration: (0) extends nearly straight posteriad and stops (drops off without reaching any other feature of the tooth; (1) extends to, or nearly to, metacone; (2) drops off, but via a rounded ridge extends to hypocone; (3) curves strongly lingually as a sharp crest to join hypoconal crest; (4) extends posteriad with a slight swerve to connect to weak hypoconal crest.
22. M1 and M2 lingual margin in occlusal view: (0) with shallow or no indentation between base of protocone and talon (hypocone); (1) with deep indentation.
23. Upper canine lingual cingulum: (0) entire; (1) bilobed.
24. M1 metastyle: (0) simple and straight (in line with postmetacrista) or slightly curved; (1) hooked.
25. P4 lingual cingular cusp: (0) absent; (1) weak; (2) strong.
26. P4 configuration: (0) with small cingular cusp positioned anterior to the main cusp; (1) with broad lobe positioned anterolingual to the main cusp; (2) with small cingular cusp positioned posterolingual to the main cusp; (3) cingular cusp absent; (4) P4 expanded and shieldlike with central groove.
27. M1 and M2 lingual cingulum: (0) absent; (1) weak and limited to posterior side of base of protocone; (2) weak and connected to hypoconal crest/talon cingulum; (3) weak and interrupted around the base of the protocone but present anterior to protocone; (4) complete all the way from parastyle through lingual base and talon to metastyle.
28. M1 and M2 protocone position: (0) relatively far from paracone and metacone; (1) close to paracone and metacone, the preprotocrista and postprotocrista shortened.
29. M1 and M2 mesostyle: (0) single; (1) doubled, with a small notch between the swollen end of the postparacrista and the end of the premetacrista.
30. P4 lingual portion: (0) broadly rounded and including a large talon basin; (1) bilobed with anterolingual flat shelf and posterolingual small basined talon; (2) transversely elongated with rounded lingual border and talon basin; (3) not bilobed, with small talon; (4) broad and flattened with longitudinal central basin.
31. M3 ectoloph: (0) with 4 commissures; (1) 3 ½ commissures; (2) 3 commissures; (3) 2 commissures.
32. M1 and M2 hypocone configuration: (0) hypocone absent or formed as an indistinct low rise on the postprotocrista; (1) hypocone represented by a low rise on the anterolingual corner of the talon, continuous with the talon cingulum; (2) hypocone tall and cuspate on the anterolingual corner of the talon, aligned with but not distinctly connected with postprotocrista nor talon cingulum; (3) hypocone low and cuspate and situated internally

Continuación Appendix 1.

on talon, its ridge not connected to talon cingulum; (4) hypocone well developed and cristate on the anterolingual corner of the talon, and connected by crests or ridges with postprotocrista and talon cingulum; (5) hypocone low or absent on anterolingual corner of talon, connected to a strongly lingually-curving postprotocrista, and also continuous with the talon cingulum.

33. p2 in lateral profile: (0) tall and pointed; (1) a rounded or elongated curving blade; (2) p2 reduced in size.
34. p4 posterolabial crest: (0) absent; (1) present and separated by a concavity from the posterolingual crest.
35. M1 relative lengths of commissures: (0) all four commissures subequal (preparacrista and postmetacrista about same length as postparacrista and premetacrista); (1) first commissure short and fourth commissure long (preparacrista short and postmetacrista elongated).
36. Humerus greater tuberosity height: (0) taller than lesser tuberosity; (1) shorter than lesser tuberosity; (2) equal to lesser tuberosity height.
37. Radius flexor fossa for insertion of M. biceps: (0) an open, triangular area bounded by bony ridges; (1) a deep narrow groove.
38. Femur proximal end of shaft with long longitudinal flangelike third trochanter: (0) absent; (1) weak; (2) strong.
39. Femur distal end spline: (0) absent; (1) present.
40. Femur greater and lesser trochanters size: (0) normal; (1) reduced.
41. Femur head central fovea: (0) small; (1) large.
42. Femur head shape: (0) spheroidal; (1) cylindrical.
43. Femur with flangelike longitudinal spline distal to head (separate from third trochanter): (0) absent; (1) weak; (2) strong.
44. Femur proximal portion of shaft: (0) straight; (1) bent medially toward greater trochanter.
45. M1 and M2 mesostyle position: (0) falls on a line drawn between the parastyle and metastyle; (1) indented lingually, situated well lingual to a line through the parastyle and metastyle.
46. M1 and M2 W-shaped ectoloph "vees": (0) normal to midline of cranium (if you draw lines that bisect the angles between the preparacrista-postparacrista and between the premetacrista-postmetacrista, the lines will be approximately at right angles to the midline axis of the skull); (1) crests obliquely oriented (lines bisecting the vees of the ectoloph will be oblique to the midline of the skull).
47. m1 and m2 crown height and robustness: (0) relatively low-crowned with robust crests; (1) relatively high-crowned with slender crests.
48. m1 and m2 talonid anteroposterior length relative to trigonid length: (0) normal, talonid about as long as trigonid; (1) reduced, talonid shorter than trigonid.

Appendix 2.

Data matrix used in the phylogenetic analysis of selected Phyllostominae including the two species of *Notonycteris* (Fig. 3). Numbers following each species name denote character states given in Appendix 1. A question mark indicates that no data are available for a particular character.

	Character
	111111111122222222223333333333444444444
Taxon	123456789012345678901234567890123456789012345678
Macrotus waterhousii	010200100120100101210010000103310010021000110000
Lophostoma silvicola	0010011001201002001200102101113200120200?1010000
Phylloderma stenops	1010011001200001001001000300033110100100?0100000
Phyllostomus hastatus	003-00000110000200120100131100320112010000110000
Trachops cirrhosus	012000000100100101120010030101310112021001210111
Chrotopterus auritus	012001101000100201221010010101300010020000211011
Vampyrum spectrum	0101111010001002010211100101013010110210?0201011
Notonycteris magdalenensis	????0?10201?100201?210?0??010??1???202?0112?1000
Notonycteris sucharadeus	????0?1020??100201????????????????????????????00

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