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# A New Fossil Bat (Chiroptera: Phyllostomidae) from a Quaternary Cave Deposit in Cuba

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**ABSTRACT.—A new species of phyllostomid bat (Stenodermatinae: Stenodermatini) is described from a well preserved skull and two mandibular rami from a late Pleistocene cave deposit (derived from barn owl predation, Aves: *Tyto*) in Cueva El Abrón, Pinar del Río, western Cuba. This new taxon is the second fossil species described in the genus *Phyllops*, and it shares some features with extinct *P. vetus*, also from Cuba. The fossil record supports that Cuba was an important center of radiation of the subtribe Stenodermatina during the Quaternary. The extant species, *Phyllops falcatus*, seems a recent arrival to Cuba from Hispaniola, after the declination and extinction of the Cuban endemic "short-faced bats" at the end of the Pleistocene and early Holocene.**

## INTRODUCTION

The Chiroptera of the West Indies include a distinctive small group of bats, traditionally called "short-faced bats," which are members of the subtribe Stenodermatina (Wetterer et al. 2000). Four genera are endemic to the subregion (Miller 1907; Baker and Genoways 1978; Morgan 2001): *Ardops* Miller, confined to the Lesser Antilles; *Ariteus* Gray, from Jamaica; *Phyllops* Peters, from Cuba, Hispaniola (Haiti and Dominican Republic), and the Cayman Islands; and *Stenoderma* Geoffroy, from Puerto Rico and the Virgin Islands. The genus *Phyllops* contains an extant species with two subspecies: *P. falcatus falcatus* (Gray), from Cuba, Grand Cayman, and Cayman Brac, and *P. f. haitiensis* (Allen) from Hispaniola. *Phyllops vetus* Anthony, from Cuba and Isla de la Juventud (Silva 1979), is the only extinct species described in this subtribe for the West Indies.

We describe another extinct species of the genus *Phyllops* in Cuba. The material was found in a cave deposit at Cueva El Abrón, Pinar del Río Province (Fig. 1), by members of the Departamento de Paleogeografía y Paleobiología, Museo Nacional de Historia Natural de Cuba, La Habana. The deposit formed by the accumulation of barn owls (Aves: *Tyto*) pellets, but in contrast with other deposits of the same type known from Cuba (Woloszyn and Silva 1974), this one is well preserved and stratified, containing millions of bones of extinct and extant small vertebrates (see Discussion). The fauna is still under study, but we considered describing the new bat, as it supplies new evidence about the evolution of the "short-faced bats" in the West Indies.

## MATERIALS AND METHODS

Comparisons with osteological material from the West Indies were conducted at the National Museum of Natural History, Smithsonian Institution (USNM), and included the following taxa: *Stenoderma rufum* Desmarest (2), *Ariteus flavescens* (Gray) (11), *Ardops nichollsi* (Thomas) (10), and *Phyllops falcatus* (Gray) (23). We follow Jones and Carter (1976), Klingener et al. (1978), Koopman (1989) and Morgan (1994) and consider *Phyllops haitiensis* as a subspecies of *P. falcatus*. Specimens of *Phyllops falcatus falcatus* and *P. vetus*, at the Instituto de Ecología y Sistemática, La Habana (CZACC, formally Colecciones del Instituto de Zoología, Academia de Ciencias de Cuba) and Museo Nacional de Historia Natural de

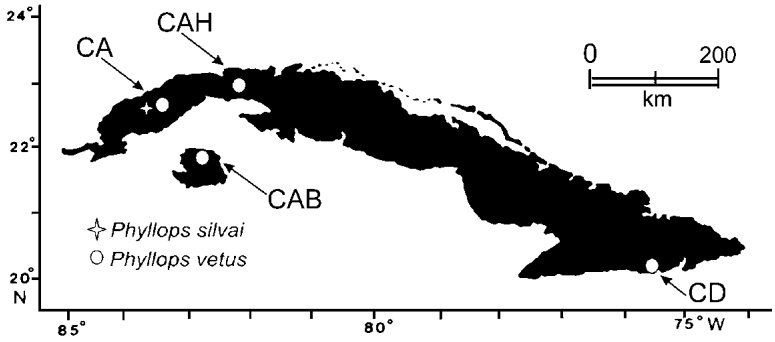


FIG. 1. The fossil record of extinct species of the genus *Phyllops* in Cuba. From left to right: CA = Cueva El Abrón, Pinar del Río; CAB = Cueva del Abuelo, Isla de La Juventud; CAH = Cueva del Ahorcado, La Habana; CD = Cuevas de Daiquirí, Santiago de Cuba.

Cuba, La Habana (MNHNCu), in Table 1 are: *Phyllops f. falcatus* (skulls and their respective mandibles), CZACC 1.2405-12, 1.2415-18, 1.2422, 1.2425-26; skulls, CZACC 1.5549, MNHNCu 76.4623-27; mandibles, MNHNCu 76.4628-37; *Phyllops vetus*, skulls, CZACC 1.5548, 1.5551-54, MNHNCu 76.4638-47; mandibles, CZACC 1.5555-56, MNHNCu 76.4648-50. We also examined a specimen (skull and mandible CZACC 1.5540) which is going to be the holotype for a new fossil taxon of the subtribe Stenodermatina (Mancina and García unpublished manuscript), also from Cuba. Osteological terminology is mainly that proposed by DeBlase and Martin (1981). Measurements were taken with a vernier caliper to the nearest 0.1 mm, following Silva (1979) and/or Owen (1987). Molar measurements were taken with linear scale ocular micrometer coupled to a stereoscope.

TABLE 1. Cranial and mandibular measurements (mm) of *Phyllops silvai,* new species, *P. falcatus,* and *P. vetus.* Mean, standard deviation, observed range (in parentheses), and sample size are given for each measurement.

| Character | *Phyllops silvai* | *Phyllops falcatus* | *Phyllops vetus* |
|---|---|---|---|
| Skull length | 21.5 | 20.6 ± 0.54 (19.6-21.4) 18 | 19.2 ± 0.27 (18.9-19.5) 4 |
| Rostral length | 6.0 | 5.0 ± 0.24 (4.4-5.4) 20 | 4.9 ± 0.23 (4.4-5.2) 14 |
| Rostral index (rostral length/skull length × 100) | 28.0 | (22.3-25.4) 17 | (26.2-26.5) 2 |
| Greatest nares width | 2.8 | 2.5 ± 0.18 (2.2-2.9) 20 | 2.3 ± 0.20 (2.1-2.8) 13 |
| Greatest nares height | 3.1 | 2.0 ± 0.16 (1.7-2.3) 21 | 1.9 ± 0.18 (1.6-2.2) 15 |
| Antorbital width | 5.4 | 5.6 ± 0.24 (5.3-6.1) 21 | 5.1 ± 0.16 (4.9-5.5) 15 |
| Postorbital width | 6.0 | 5.6 ± 0.19 (5.1-5.8) 21 | 5.1 ± 0.11 (4.9-5.3) 12 |
| Braincase width | 10.5 | 10.2 ± 0.31 (9.6-11.0) 19 | 10.0 ± 0.06 (10.0-10.1) 3 |
| Mastoid width | 11.9 | 12.2 ± 0.44 (11.4-13.0) 18 | 11.2 ± 0 (11.2) 3 |
| Greatest width of foramen magnum | 3.8 | 4.0 ± 0.21 (3.6-4.5 ) 17 | 3.7 ± 0.10 (3.6-3.8) 3 |
| Greatest antero-posterior length at crown of M1 | 4.3 | 3.5 ± 0.24 (3.2-3.9) 19 | 3.0 ± 0.10 (2.8-3.1) 8 |
| Palatal emargination width at level of M2 | 1.5 | 1.0 ± 0.15 (0.6-1.4) 20 | 1.1 ± 0.11 (1.0-1.4) 14 |
| Mental length | 10.4 | 10.2 ± 0.29 (9.7-10.7) 25 | 9.6 ± 0.33 (9.3-10.1) 5 |
| Angular process length | 10.3 | 10.3 ± 0.33 (9.6-10.9) 24 | 9.6 ± 0.36 (9.3-10.1) 5 |
| Dentary thickness | 2.1 ± 0 (2.1) 2 | 2.1 ± 0.12 (1.8-2.3) 25 | 2.0 ± 0.14 (1.8-2.1) 4 |
| Coronoid height | 6.0 ± 0.07 (5.9-6.0) 2 | 6.0 ± 0.24 (5.5-6.6) 25 | 5.6 ± 0.27 (5.2-5.9) 5 |

## SYSTEMATICS

Order Chiroptera
Family Phyllostomidae
Subfamily Stenodermatinae
Tribe Stenodermatini
Subtribe Stenodermatina
Genus *Phyllops* Peters 1865

Among the Antillean genera of the subtribe Stenodermatina (*Ardops*, *Ariteus*, *Phyllops*, *Stenoderma*, and gen. et sp. nov. Mancina and García unpublished manuscript), the fossils studied are asigned to *Phyllops* because they show the following character combination: incisive foramina close to roots of incisors (separate from roots of incisors by a wide space in *Stenoderma*); M1 and M2 with hypocone much lower than protocone, m1 with well developed metaconid connected with ridge on inner side of protoconid (M1 and M2 with hypocone higher than, and similar in size to, protocone, and metaconid absent in m1 in *Ardops*); M3 present (evidenced by the alveoli) (absent in *Ariteus*); anterior end of palatal emargination at level with M1 (at level with M3 in gen. et sp. nov., Mancina and García unpublished manuscript).

### *Phyllops silvai*, new species
(Figs. 2 and 3)

*Holotype.*—Partial skull (MNHNCu 76.4620), lacking left zygomatic arch and small fragments of the braincase; left M1, M2, and right M2 present. Collected by William Suárez and Stephen Díaz-Franco on 21 March 2000.

*Type locality.*—Cueva El Abrón, western tip of Sierra de La Güira (ca. 22°40′N, 83°28′W; X-247, Y-317; on the 1:50 000 series map, Herradura 3583-IV, Instituto Cubano de Geodesia y Cartografía, 1982), Municipality of Los Palacios, Pinar del Río Province, Cuba.

*Chronology.*—Quaternary, late Pleistocene. Radiometric date ($^{14}$C) from a sample of long bones of the extinct barn owl *Tyto noeli* Arredondo, directly associated with the type material at level VII of the fossil deposit, gave an age of 17,406 ± 161 rcybp. Calibration (95% confidence interval) of the same sample gave ages from 20,050 to 21,474 ybp.

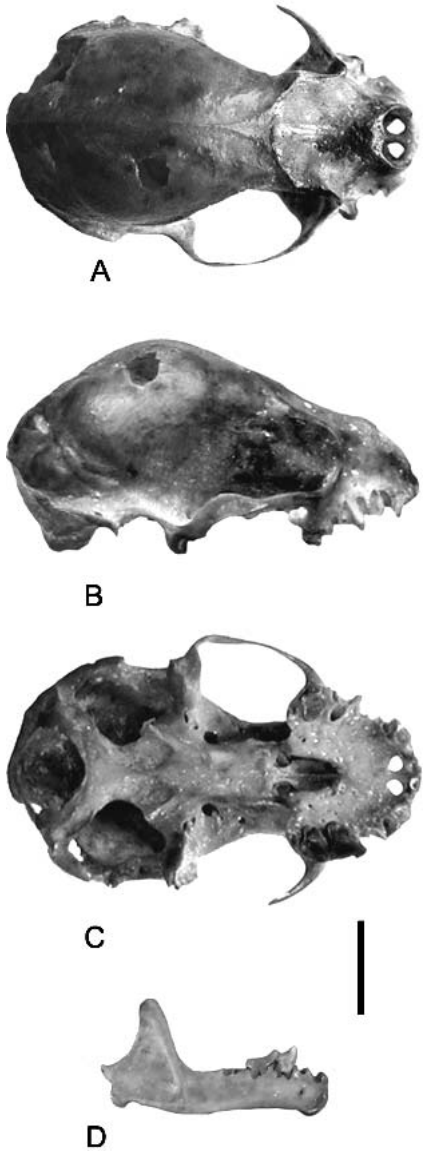


FIG. 2. Holotype skull (MNHNCu 76.4620) and paratype mandible (MNHNCu 76.4621) of *Phyllops silvai*, new species. Skull in dorsal (A), lateral (B), and ventral (C) views. Mandible (image reversed) in lateral (D) view. Scale = 5 mm.

*Paratypes (topotypes).*—Mandible without right ramus, p2 and m1 present (MNHNCu 76.4621); mandible without teeth and right ramus (MNHNCu 76.4622). Collected by William Suárez, Stephen Díaz-Franco, and

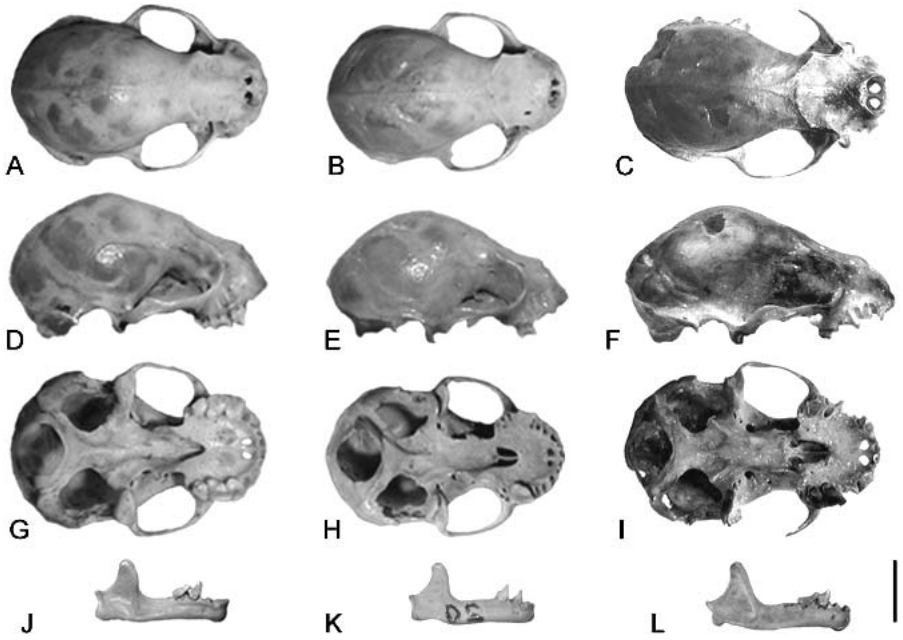


FIG. 3. Comparison of skulls in species of the genus *Phyllops*, in dorsal, lateral, and ventral views (from top to bottom). Mandible in lateral view. *Phyllops falcatus* (A, D, G, J); *P. vetus* (B, E, H, K); *P. silvai*, new species (C, F, I, L). Scale = 5 mm.

Carlos Javier Bringas, on 15-20 October 2001.

*Distribution.*—Cuba, known only from the type locality.

*Status.*—Extinct species.

*Diagnosis.*—Differs from *Phyllops falcatus* and *P. vetus* by the longer skull, wider postorbital width and long facial region; rostrum larger and upturned with nares dorsally directed, higher than wide; palatal emargination wider; anterior contact between perpendicular portions of the palatine and vomer, located beyond level of M3; vomer greatly exposed in ventral view.

*Etymology.*—After Professor Gilberto Silva Taboada, for his contribution to the knowledge of Cuban bats.

*Description and comparisons.*—Cranium elongate, larger in some measurements than that of *Phyllops falcatus*, much larger than that of *P. vetus* (Table 1), but with a relatively small braincase and large facial region (large and high braincase, short facial region in *Phyllops falcatus* and *P. vetus*). Sagittal crest as in these species. Rostrum large and upturned, nares dorsally directed and higher than wide (rostrum shorter and not upturned, nares not dorsally directed in *P. falcatus*, intermediate in these characters in *P. vetus*; nares wider than high in both *P. falcatus* and *P. vetus*); incisive foramina relatively large (relatively small foramina in *P. falcatus*; similar in *P. vetus*); palate slender and constricted laterally (shorter, not constricted laterally, being wider in *P. falcatus*; intermediate in *P. vetus*); long and wide U-shaped palatal emargination with straight sides (small and thin V-shaped, sides not straight, converging rostrally in *P. falcatus*; long but not wide, also U-shaped with straight sides in *P. vetus*; in this respect *Phyllops silvai* recalls other genera of the subtribe, particularly *Ardops*); anterior contact between perpendicular portions of palatine and vomer located at level with back of M3; vomer greatly exposed in ventral view (located rostrally beyond level of M3, vomer less exposed in *P. vetus*; located rostrally even further from level of M3, and vomer poorly visible in *P. falcatus*); thin and long interpterygoid space, with parallel,

and poorly developed pterygoid processes (wider and shorter interpterygoid space, better developed and divergent pterygoid processes in *P. falcatus*; intermediate in characters in *P. vetus*); basisphenoid plate narrow, with very close and deep basisphenoid pits (wide plate, with separate and shallow basisphenoid pits in *P. falcatus*; intermediate, with similar pits in *P. vetus*); foramen magnum relatively small, with caudal orientation (similar in *P. falcatus*; relatively larger, more ventrally placed in *P. vetus*). Mandible similar in size to that of *P. falcatus*, and larger than that of *P. vetus*, with coronoid process thin, its anterior edge forming an open angle of much more than 90° with the perpendicular axis of the ramus (wider, close to 90° in *P. falcatus*; relatively wider and high, close to, or little more than 90° in *P. vetus*); alveoli of incisors with marked rostral inclination (more vertical or dorsal placement of alveoli of incisors in *P. falcatus*; similar inclination in *P. vetus*); m1 relatively large (relatively smaller in *P. falcatus* and *P. vetus*); coronoid process projected laterally (less projected in *P. falcatus*; similar in *P. vetus*); masseteric pit deep and expanded (shallow to deep, more restricted in *P. falcatus* and *P. vetus*).

*Measurements (mm).*—see Table 1.

*Remarks.*—Cueva El Abrón is a half-moon shape cavity no longer than 21 m with a very high ceiling, where clastic material (roof-fall) is abundant on the surface. The diagenetic environment of the cavity has favored the accumulation of well preserved terrestrial vertebrate remains. Its structure has not been remarkably modified. All levels must be considered allocthonous fossil associations. The excavated site is more than 2 m in depth, with eight layers. Most of them colored with (from the top) blackish, grayish, brownish, yellowish, and reddish hues, sometimes without well-defined limits. Fossils are highly mineralized and colored, the latter depending on the bed's color. From the surface to 0.25 m, the site is rich in vertebrate remains, followed by somewhat deeper layers (0.70-0.90 m, 1.00-1.60 m). The faunal composition is mainly amphibians, small reptiles, land birds, and micro-mammals resulting from barn owl (*Tyto* spp.) predation in different periods. Introduced taxa occurred only near the surface (e.g., *Rattus rattus* [Linnaeus]), resulting from the activity of the modern barn owl *Tyto alba* (Scopoli). Fossils of *Phyllops silvai* were recovered at layer VII (1.00 to 1.60 m depth, brownish-yellow in color), in association with bones of other bats such as: *Artibeus anthonyi* Woloszyn and Silva, *Antrozous pallidus* (Le Conte), *Brachyphylla nana* Miller, and *Macrotus waterhousei* Gray. The abundance of the remains of the extinct barn owl *Tyto noeli* (bones of adults and juveniles) and the complete absence of specimens of *T. alba* in this layer indicate that the former was the main predator responsible for the formation of this layer during late Wisconsian (one wing element of another small, undescribed species of *Tyto* is also present; Olson and Suárez unpublished data).

In Cuba, *Phyllops falcatus* and *P. vetus* were found in association in at least three Quaternary cave deposits: two in eastern Cuba (Anthony 1917, 1919) and one in Isla de Pinos (=Isla de la Juventud) (Silva and Woloszyn 1975). Anthony (1919:640) considered remains of *P. vetus* more common and apparently older than *P. falcatus*; but Silva and Woloszyn (1975) considered the two taxa supposedly sympatric in the Holocene, and *P. falcatus* being the commonest. Koopman and Ruibal (1955), recorded only *P. falcatus* in cave deposits, but those are apparently derived from fresh, modern barn owl pellets. We have evidence of *Phyllops vetus* in a cave deposit in La Habana Province (Cueva del Ahorcado, Municipality of Caimito) which also originated from accumulation of barn owl pellets; no remains of *P. falcatus* were recovered. At the type locality, *Phyllops silvai* is known from three specimens in one of the lower and older layers (see above), while *P. vetus* comes from layer II (younger), and *P. falcatus* from the surface only. This last being fresh material, sometimes still inside complete barn owl pellets.

*Phyllops* is the only genus of "short-faced bats" shared by the two larger islands of the Greater Antilles, Cuba and Hispaniola, but it is also present in Grand Cayman and Cayman Brac (Morgan 1994). It is also the only polytypic genus of the subtribe Steno-

dermatina (*Ardops*, from the Lesser Antilles, was considered monotypic by Jones and Schwartz 1967). *Phyllops silvai* is morphologically closer to *vetus* than to *falcatus* in most of its characters (see description), especially the U-shaped palatal emargination with straight sides. Wetterer et al. (2000) considered the palatal emargination in the genus *Phyllops* as V-shaped, but this condition is present only in *falcatus* and seems variable within the genus, as occurrs in some genera of phyllostomids with long palates (see Wetterer et al. 2000:71). Some characters observed in the two Cuban fossil species of *Phyllops* probably deserve subgeneric recognition.

Possibly, more than two invasions of "short-faced bats" occurred in Cuba. We hypothesize that a first, ancestral invasion from the continental mainland (sensu Baker and Genoways 1978) gave rise to an endemic genus on the Lesser Antilles (*Ardops*) and on each of the main Greater Antillean islands: *Stenoderma* on Puerto Rico, *Phyllops* on Hispaniola, *Ariteus* on Jamaica, and n. gen. (Mancina and García, unpublished manuscript) on Cuba. A second invasion of *Phyllops*, from Hispaniola to the Cuban archipelago during the Pleistocene, resulted in the evolution of *P. vetus* and *P. silvai*. The cranial differences observed in the three extinct taxa (including the undescribed genus and species) of the Stenodermatina in Cuba, reflect their high specialization for a particular niche, which was modified subsequently as a consequence of ecological changes at the end of the Pleistocene and early Holocene (see Curtis et al. 2001). Apparently, two of these bats are part of the late Pleistocene extinction, while *Phyllops vetus* survived during part of the Holocene. Decline of these species (and the later ecological opportunities offered in the early Holocene by changes in habitats, see Curtis et al. 2001) favored another invasion of *Phyllops* from Hispaniola, in this case *P. falcatus* (see Morgan 2001 for the fossil record of the species in Hispaniola), originated the living subspecies present in Cuba. This taxon reached the Cayman Islands very recently, as remains of it have not been found in any of the cave fossil deposits excavated (Morgan 1994:442). Actually, Cuba is the only island of the West Indies with evidence of sympatric "short-faced" stenodermatines (Morgan 2001). The fossil record provides evidence that the Cuban archipelago was an important center of radiation of the subtribe Stenodermatina, and it supported four different taxa during the Quaternary. Today these arboricolous bats are a depauperate group on the island, with one nonendemic extant species.

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