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Cover: *Platyrrhinus lineatus* - Photo by Marco A.R. Mello - Casa dos Morcegos
(<http://www.casadosmorcegos.org/indexpt.htm>)

NOTES ON BIOGEOGRAPHY OF CUBAN BATS

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Abstract. Biogeography of Cuban bats have been received a general attention and little particular analyses of internal events referred to the origins, diversification, and extinction of Cuban bats have been made. On the basis of recent discoveries of two fossils and one extant species, and other recent publications, we approach to the historical biogeography of the Cuban microchiropteran fauna in an attempt of reconciling the hypothesis of dispersal and vicariance, recognizing that in some cases taxon-specific hypotheses are required. Special attention has been paid to the relationship between the bat fauna of Isla de Cuba and Isla de Pinos.

Keywords: Cuba, historical biogeography, Microchiroptera

INTRODUCTION

The Cuban archipelago has the most diverse chiropteran fauna in the Antilles. This fauna comprises 35 species, including 27 living species, 6 extinct species, and 2 extirpated species. One of the living species (*Natalus major*) was recently discovered in western Cuba (Tejedor et al. 2004), and two of the extinct species are new records, one of them comprising a new genus (Suárez & Díaz-Franco 2003, Mancina & García-Rivera 2005). Living populations of the extirpated species are actually found in Mexico, Central and South America.

The study of the causes of such Cuban richness of bats usually has taken place into a wider context (e. g., Morgan 2001), with no analysis of the internal events that occurred in Isla the Cuba and Isla the Pinos, the two principal islands of the archipelago. Being Cuba the biggest archipelago of the Antilles, and having a geological history closely related to that of Bahamas, the rest of the Greater Antilles, and (Dávalos 2004) Jamaica, it is important to understand when and where Cuban bats evolved, what was its origin, what is its present distribution and how was modelled the Cuban present-day bat fauna through the Cenozoic.

The present work is an approach to these questions on the basis of historical biogeography, taking in account new and valuable explanations from recent studies.

Zoogeographical, Taxonomical and Ecological Contexts

The Cuban archipelago is located in the Antillean Subregion (in the sense of Genoways *et al.* 1998) within the Neotropic. It is formed by Isla de Cuba (which is the major island of all the Antilles), Isla de Pinos, and

more than 4000 islets and keys. Isla de Pinos is placed on the continental shelf of Cuba, and both islands are separated by water less than 12 m in depth. In the text, terms like Antilles or Caribbean must be considered synonyms of Antillean Subregion. The gentile Cuban is referred to the whole archipelago.

In taxonomy we follow Koopman (1993) for most of the *taxa*, and Morgan & Czaplewski (2003) for Natalidae. *Brachyphylla*, *Erophylla* and *Phyllonycteris* have been grouped in the subfamily Brachyphyllinae, following the early statements of Silva Taboada & Pine (1969).

The guild structure, and roost behaviour of living and extinct bats in the Cuban archipelago have been established according to Schnitzler & Kalko (2001), and Silva Taboada (1979), respectively.

Possible origin of Cuban Bats

According to recent paleogeographic investigations and geological evidences, 35 millions of years ago there were appropriately conditions in the Antillean Subregion for potential colonizers to invade (Iturralde-Vinent & MacPhee 1999). The morphological differentiation between Antillean bats and its continental ancestors makes improbable an earlier period for most of the insular fauna (Silva Taboada 1979). Thus, the fauna of Cuban bats has acquired its present composition (Table 1) through a series of processes and phenomena for the last 40 million years.

Analyzing biogeographical hypotheses concerning the origin, distribution, and diversity of the Caribbean fauna, a question usually arises. Which hypothesis, vicariance or aerial dispersal over water, could explain

Table 1. Distribution, endemism, guild structure, and roost behaviour of living (X) and extinct (O) bats in the Cuban archipelago. Information about other islands of the Antillean Subregion, and about continent is provided for comparison. Families and subfamilies appear in a systematic order, and species appeared in alphabetical order. Guilds of extinct species are inferred from living species of the genus or from the superior taxonomic category. (**): living taxon endemic of (or fossil records of the taxon only found in) the Cuban archipelago, (*): endemic of the Antillean Subregion. CUB: Cuban archipelago, JAM: Jamaica, ESP: Hispaniola, PR: Puerto Rico, MEX: Mexico. Roost behaviour: SC: specialized cave-dweller, FC: facultative cave-dweller, Three-dweller, G: generalist. Guild structure: AI-US: aerial insectivore in uncluttered space, AI-BS: aerial insectivore in background-cluttered space, AI-HS: aerial insectivore in highly cluttered space, GI-HS: gleaner insectivore in highly cluttered space, P-BS: piscivore in background-cluttered space, F-HS: frugivore in highly cluttered space, PN-HS: polinivore (-nectarivore) in highly cluttered space, S-HS: sanguivore in highly cluttered space. The symbol ‡ in the column of the Cuban archipelago (CUB) means that the species is shared by both Isla de Cuba and Isla the Pinos, and the symbol † means that the species was once shared by the two islands but that has been extirpated from Isla the Pinos.

| Taxon | Greater Antilles | | | | Bahamas | LesserAntilles | Continent | | | | Roost | Guild |
|---------------------------------|------------------|-----|-----|----|---------|----------------|-----------|----|-----|----|-------|-------|
| | CUB | JAM | ESP | PR | | | SA | CA | MEX | NA | | |
| Noctilionidae | | | | | | | | | | | | |
| <i>Noctilio leporinus</i> | X ‡ | X | X | X | X | X | X | X | X | – | G | P-BS |
| Mormoopidae | | | | | | | | | | | | |
| <i>Mormoops blainvillii</i> * | X | X | X | X | O | O | – | – | – | – | SC | AI-BS |
| <i>M. magna</i> ** | O | – | – | – | – | – | – | – | – | – | SC | AI-BS |
| <i>M. megalophylla</i> | O | – | O | – | O | – | X | X | X | O | SC | AI-BS |
| <i>Pteronotus macleayi</i> * | X ‡ | X | – | – | O | – | – | – | – | – | SC | AI-BS |
| <i>P. parnelli</i> | X † | X | X | X | O | O | X | X | X | – | SC | AI-HS |
| <i>P. pristinus</i> ** | O | – | – | – | – | – | – | – | – | – | SC | AI-BS |
| <i>P. quadridens</i> * | X | X | X | X | – | – | – | – | – | – | SC | AI-BS |
| Phyllostomidae | | | | | | | | | | | | |
| Phyllostominae | | | | | | | | | | | | |
| <i>Macrotus waterhousei</i> | X ‡ | X | X | – | X | O | – | X | X | – | G | GI-HS |
| Brachyphyllinae * | | | | | | | | | | | | |
| <i>Brachyphylla nana</i> * | X ‡ | O | X | – | X | – | – | – | – | – | SC | PN-HS |
| <i>Erophylla sezekorni</i> * | X ‡ | X | – | – | X | – | – | – | – | – | SC | PN-HS |
| <i>Phyllonycteris poeyi</i> * | X ‡ | – | X | – | – | – | – | – | – | – | SC | PN-HS |
| Glossophaginae | | | | | | | | | | | | |
| <i>Monophyllus redmani</i> * | X ‡ | X | X | X | X | – | – | – | – | – | SC | PN-HS |
| Stenodermatinae | | | | | | | | | | | | |
| <i>Artibeus anthonyi</i> ** | O | – | – | – | – | – | – | – | – | – | G | F-HS |
| <i>A. jamaicensis</i> | X ‡ | X | X | X | X | X | X | X | X | X | G | F-HS |
| <i>Cubanycotis silvai</i> ** | O | – | – | – | – | – | – | – | – | – | T | F-HS |
| <i>Phyllops falcatum</i> * | X † | – | X | – | – | – | – | – | – | – | T | F-HS |
| <i>P. silvai</i> ** | O | – | – | – | – | – | – | – | – | – | T | F-HS |
| <i>P. vetus</i> ** | O ‡ | – | – | – | – | – | – | – | – | – | T | F-HS |
| Desmodontinae | | | | | | | | | | | | |
| <i>Desmodus rotundus</i> | O | – | – | – | – | – | X | X | X | – | G | S-HS |
| Natalidae | | | | | | | | | | | | |
| <i>Chilonatalus micropus</i> * | X ‡ | X | X | – | – | – | – | – | – | – | SC | AI-BS |
| <i>Natalus major</i> * | X † | X | X | – | – | – | – | – | – | – | SC | AI-BS |
| <i>Nyctiellus lepidus</i> * | X ‡ | – | – | – | X | – | – | – | – | – | SC | AI-BS |
| Vespertilionidae | | | | | | | | | | | | |
| <i>Antrozous pallidus</i> | X | – | – | – | – | – | – | – | X | X | G | GI-HS |
| <i>Eptesicus fuscus</i> | X ‡ | X | X | X | X | X | X | X | X | X | G | AI-BS |
| <i>Lasiurus borealis</i> | X | X | X | X | X | – | X | X | X | X | G | AI-US |
| <i>L. intermedius</i> | X ‡ | – | – | – | – | – | – | X | X | X | T | AI-US |
| <i>Nycticeius humeralis</i> | X | – | – | – | – | – | – | – | X | X | G | AI-BS |
| Molossidae | | | | | | | | | | | | |
| <i>Eumops glaucinus</i> | X | X | – | – | – | – | X | X | X | X | G | AI-US |
| <i>E. perotis</i> | X | – | – | – | – | – | X | X | X | X | G | AI-US |
| <i>Molossus molossus</i> | X ‡ | X | X | X | – | X | X | X | X | – | G | AI-US |
| <i>Mormopterus minutus</i> ** | X | – | – | – | – | – | – | – | – | – | G | AI-US |
| <i>Nyctinomops laticaudatus</i> | X | – | – | – | – | – | X | X | X | – | G | AI-US |
| <i>N. macrotis</i> | X | X | X | – | – | – | X | X | X | X | G | AI-US |
| <i>Tadarida brasiliensis</i> | X ‡ | X | X | X | X | X | X | X | X | X | FC | AI-US |



Figure 1. Caribbean Sea with Great Antilles (Cuba, Jamaica, Hispaniola [Haiti and Dominican Republic] and Puerto Rico, The Bahamas, Lesser Antilles, and the continents (North America, Central America and South America)

the Cuban bat fauna? Three routes of dispersal and a vicariant model have been proposed. The routes of dispersal proposed by Rodríguez-Durán & Kunz (2001) include a northern route from Florida to Cuba directly or through Bahamas, a western route from Central America, and a southern route from South America through the Lesser Antilles. The Gaarlandia vicariant model of Iturralde-Vinent & MacPhee (1999) could explain the relationships of brachyphyllines and stenodermatines with the continent. According to Dávalos (2004), the routes of dispersal must be clarified for families as Mormoopidae and Natalidae, and other groups of bats that not fit to the vicariant model require taxon-specific hypotheses.

Silva Taboada (1979) suggested a South American origin for *Noctilio leporinus*. The contribution of Gaarlandia to the invasion, and the period it took place remain unclear. Baker & Genoways (1978) did not exclude for this species colonization from Central America.

Five of the seven species of mormoopids present in Cuba are endemic of the Antillean Subregion (Table

1), which becomes an important centre of secondary differentiation of the family. Mormoopids arrived to Cuba from Central America (Baker & Genoways 1978, Silva Taboada 1979, Koopman 1989) in repeated dispersal events (at least twice in *Pteronotus*), which could include other Antillean islands as Jamaica (Dávalos 2004). Nevertheless, Silva Taboada (1979) proposed a single dispersal event for *Pteronotus quadridens*, *P. macleayi* and the ancestor of *P. pristinus*. Which it is clear is that *Mormoops blainvillii* and the ancestors of *M. magna*, *P. pristinus*, and *P. quadridens* should represent early invasions, probably in Middle or Superior Pliocene, according to Silva Taboada (1979). A northern origin is not discarded for the genus *Mormoops* (Koopman 1989), and this could be supported for the presence of fossil records of *M. blainvillii*, *M. megalophylla*, *P. macleayi* and *P. parnelli* in Bahamas (Simmons & Conway 2001). The southern route could also be possible for some species of the family.

The Antillean Subregion is also a center of radiation of the family Phyllostomidae, with nine endemic species from the twelve present in the Cuban

archipelago (Table 1). These endemics probably represent the earliest invasions to the Antilles. Cuba should play an important role for differentiation of Brachyphyllinae and Stenodermatinae, for which a southern origin have been proposed (Silva Taboada 1979, Koopman 1989). The southern route has been also suggested for *Monophyllus*, while *Artibeus anthonyi* has been related to *A. lituratus*, a species with a South American origin (Silva Taboada 1979, Baker & Genoways 1978). *Macrotus waterhousei*, *Artibeus jamaicensis*, and *Desmodus rotundus* probably arrived from Central America (Baker & Genoways 1978, Silva Taboada 1979, Koopman 1989). The endemic Antillean genera *Brachyphylla*, *Erophylla*, and *Phyllonycteris* seem part of a single radiation, and dispersal events from Hispaniola, Puerto Rico and Jamaica to Cuba possibly occurred (Dávalos 2004). Also it is probably that at least two invasions of stenodermatines took place. A first invasion from the continent gave rise to *Phyllops* on Hispaniola, and *Cubanycteris* (Mancina & García-Rivera 2005) on Cuba. Dispersal of *Phyllops*, from Hispaniola to the Cuban archipelago during the Pleistocene, resulted in the evolution of *P. vetus* and *P. silvai* (Suárez & Díaz-Franco 2003).

Cuba has the highest diversity of Natalidae in the Neotropics in what sympatry concerns (Tejedor et al. 2004), being the three extant species endemic from the Antillean Subregion (Table 1). Genetic studies showed that Jamaican *Natalus major* belongs to a lineage basal to a Central America/Lesser Antilles *N. stramineus* clade (Arroyo-Cabrales et al. 1999), and this suggests events of dispersal within the Antilles. Silva Taboada (1979) proposed a Central American origin for the Caribbean species. Nevertheless, the Early Oligocene natalid from Florida (Morgan & Czaplewski 2003) points out to a North American origin for the ancestor of Antillean natalids, which should reach Cuba through Bahamas, and from there the species dispersed to other regions of the Antilles and to the north of South America.

The five species of vespertilionids present in Cuba (Table 1) show affinities with the temperate region of North America, though *Eptesicus fuscus* and *Lasiurus borealis* are widespread through Central and South America. The western route is the most accepted (Baker & Genoways 1978, Silva Taboada 1979). Koopman (1989) proposed a Central American origin for *Antrozous*, and a North American origin for *Nycticeius* and *Lasiurus*.

Mormopterus minutus is the only endemic species of Cuban bat. Populations of the other molossids species have not been well differentiated from populations in mainland continent. Invasions from Central America have been proposed for most of the molossids (Silva

Taboada 1979) and the ancestor of *Mormopterus minutus* (Koopman 1989). *Tadarida brasiliensis* probably arrived from North America while *Molossus molossus* possibly arrived through the southern route (Baker & Genoways 1978, Koopman 1989).

Bats of Isla de Pinos

Isla de Cuba and Isla de Pinos share half of the bat species that have been found in the Cuban archipelago. With 17 species exclusively in the former, the rest are present in the latter (Table 1). Three of the 18 shared species are extirpated from Isla de Pinos (*Pteronotus parnelli*, *Phyllops falcatum*, and *Natalus major*), and *Phyllops vetus* is the only fossil bat shared by both islands.

Bats should arrive to Isla de Pinos from Isla de Cuba, especially during low sea level stands in Pleistocene, when both islands were connected (Iturralde-Vinent 2003). Two of the six families of Cuban bats, Phyllostomidae and Natalidae, seem to have had a great success of colonization. In the case of *Phyllops vetus*, the species probably evolved in Isla de Cuba from its Hispaniolan ancestor, according to what Suárez & Díaz-Franco (2003) have proposed, and then reached Isla de Pinos, suffering extinction events in both islands.

The recent geographical segregation of Isla de Pinos from Isla de Cuba did not allowed any speciation in the former. Nevertheless, Silva (1974) reported a subspecies of *Eptesicus fuscus* (*E. f. petersoni*), which is smaller, and has a pelage and colour different from the subspecies present in Isla de Cuba (*E. f. dutertrei*). This could represent an attempt of speciation though time and conservation efforts should state the last word.

Events of Extinction

Having Cuba the richest chiropteran fauna in the Caribbean, the archipelago also suffered the largest number of extinctions (Morgan 2001). *Mormoops megalophylla*, and *Desmodus rotundus* are extirpated from the Cuban archipelago, and other six species including mormoopids and stenodermatines are extinct (Table 1). The extinctions affected particularly obligatory cave-dwelling species, but also tree-dwelling and generalist species. Post-Pleistocene climate changes and variations in cave environments are the main causes attributed to such extinctions (Morgan 2001).

If climate changes were the main cause of extinction of Cuban microchiropteran, the extinction of tree-dweller species should reach higher levels than cave-dweller bats. But from the eight Cuban bats species no longer in the archipelago, three roosted in trees, and other three species roosted in caves, which points to

the capability of dispersion of bats as another cause of extinction. Although a lot of caves were and still are available in Cuba as roosts for bats, specialized cave-dwelling species (like the extinct Cuban mormoopids) require exclusively humid and warm caves. Probably, if the dispersal ability of the extinct mormoopids was limited by physiological features, and long distances between one hot cave to another, then these species were affected by the lost of the roost sites due to stochastic events, more than other species, as have been proposed for extirpation events of *Natalus major* in the Cuban archipelago (see Tejedor et al. 2004). This could also explain the extirpation events of *Pteronotus parnelli* in Isla de Pinos, where caves are scarce.

However, the ecological information available for the extinct species is still insufficient, and this limits any speculation about causes of extinctions of Cuban bats. New evidences from geology, phylogeny, and ecology, and new fossil records and taphonomic explanations are required to clarify the origins, diversification, and extinction events that have shaped the fauna of Cuban bats.

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