

UNIVERSIDADE DE SÃO PAULO
MUSEU DE ZOOLOGIA

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**Systematics of Quaternary Squamata
from Cuba**

**Sistemática dos Squamata Quaternários
de Cuba**

Corrected version

Dissertation presented to the
PostGraduate Program of the
Museu de Zoologia da
Universidade de São Paulo to
obtain the degree of Master of
Science (Systematics, Animal
Taxonomy and Biodiversity)

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São Paulo
2019

Resumo

Aranda E. (2019). Sistemática dos Squama do Quaternário de Cuba. (Dissertação de Mestrado). Museu de Zoologia, Universidade de São Paulo, São Paulo.

A paleontologia de répteis no Caribe é um tema de grande interesse para entender como a fauna atual da área foi constituída a partir da colonização e extinção dos seus grupos. O maior número de fósseis pertence a Squamata, que vá desde o Eoceno até nossos dias. O registro abrange todas as ilhas das Grandes Antilhas, a maioria das Pequenas Antilhas e as Bahamas. Cuba, a maior ilha das Antilhas, tem um registro fóssil de Squamata relativamente escasso, com 11 espécies conhecidas de 10 localidades, distribuídas no oeste e centro do país. No entanto, existem muitos outros fósseis depositados em coleções biológicas sem identificação que poderiam esclarecer melhor a história de sua fauna de répteis. Um total de 328 fósseis de três coleções paleontológicas foi selecionado para sua análise, a busca de características osteológicas diagnosticas do menor nível taxonômico possível, e compará-los com outros fósseis e espécies recentes. No presente trabalho, o registro fóssil de Squamata é aumentado, tanto em número de espécies quanto em número de localidades. O registro é estendido a praticamente todo o território cubano. Restos fósseis pertencentes a espécies relatadas anteriormente são confirmados, como *Leiocephalus cubensis*, *L. carinatus*, *Tarentola americana*, *Chilabothrus angulifer* e *Cubophis cantherigerus*. Fósseis de *Amphisbaena*, *Pholidoscelis auberi* e *Leiocephalus macropus* são descritos pela primeira vez. Além de outros fósseis pertencentes aos gêneros *Tarentola*, *Leiocephalus* e *Chilabothrus*, mas diferentes das espécies que atualmente habitam o arquipélago. Esses resultados mostram que o registro fóssil de Squamata em Cuba é mais amplo do que era considerado anteriormente, apesar de ser composto de fósseis muito frágeis e pequenos, com pouco potencial para a fossilização. Para a paleontologia de Squamata, a descrição de novos táxons e registro de novas localidades em Cuba, são os primeiros passos para estudos mais integradores sobre diversidade biológica, evolução, biogeografia, paleoambiente entre outros que contribuam ao entendimento da fauna na região do Caribe.

Palavras-chave: Antilhas. Neógeno. Lagartos. Serpentes. Fóssil.

Abstract

Aranda E. (2019). Systematics of Quaternary Squamata from Cuba. (Master dissertation).
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The paleontology of reptiles in the Caribbean is a topic of great interest to understand how the current fauna of the area was constituted from colonization and extinction of their groups. The largest number of fossils belongs to Squamata, ranging from the Eocene to our days. The registry covers all the islands of the Greater Antilles, most of the Lesser Antilles, and of the Bahamas. Cuba, the largest island of the Antilles, has a relatively sparse Squamata fossil record, with 11 known species from 10 locations, distributed in the West and Center of the Country. However, there are many other fossils deposited in biological collections without identification that could better clarify the history of their reptile fauna. A total of 328 fossils from three paleontological collections were selected for their analysis, searching osteological characteristics that would serve to diagnose them at the lowest possible taxonomic level, and compare them with other fossils and recent species. In the present work, the Squamata fossil record is increased, both in the number of species and in the number of localities. The registry is extended to practically all of the Cuban territory. Fossil remains belonging to previously reported species are confirmed, such as *Leiocephalus cubensis*, *L. carinatus*, *Tarentola americana*, *Chilabothrus angulifer*, and *Cubophis cantherigerus*. Fossils of *Amphisbaena*, *Pholidoscelis auberi*, and *Leiocephalus macropus* are described for the first time. Besides, other fossils belonging to the genera *Tarentola*, *Leiocephalus*, and *Chilabothrus* but different from the species that currently inhabit the archipelago, are described. These results show that the Squamata fossil record in Cuba is broader than what was previously considered, despite being composed of very fragile and small fossils with little potential for fossilization. For the paleontology of Squamata the description of new taxa and record of new localities in Cuba, are the first steps for more integrating studies on biological diversity, evolution, biogeography, paleoenvironment among others that contribute to the understanding of the fauna in the Caribbean region.

Key words: Antilles. Neogene. Lizard. Snake. Fossil.

1 Introduction

The Antilles are recognized as an exceptional biogeographic scenario (Losos & Ricklefs, 2010), by the extinction, colonization and adaptive radiations experienced by some of their zoological groups (Hedges, 1989; Pregill & Olson, 1981; Silva, Duque, & Díaz-Franco, 2007). From 40 million years ago there are permanent islands in the Antillean region (Iturralde-Vinent, 2005), and since then the evolutionary history of the lineages has begun (Silva et al., 2007). The main hypotheses for the arrival of terrestrial fauna are: (1) the formation of Gaarlandia during the Eocene-Oligocene transition, a chain of islands that functioned as a filter for the passage of species (Iturralde-Vinent, 2006); and (2) oceanic dispersion by rafting or intense meteorological phenomena (Buskirk, 1985; Hedges, 2001). However, there are some faunal examples for the Gaarlandia existence (Alonso, Crawford, & Bermingham, 2012), until now, no geologic data demonstrated the existence of a continuing land between the Birds Arc and the Lesser Antilles (Ali, 2012).

Squamata reptiles may have used either of these two routes to colonize the Antilles and irradiate. Molecular data accord with geological data, sustaining a Cenozoic arrival to the Antilles for all Squamata groups (Gamble et al., 2011; Hedges, 1996), except for the endemic Cuban genus *Cricosaura*. This last genus is a very ancient relic, possibly from the Upper Cretaceous, although controversial because so far no fossil remains were found on any of the islands (Gauthier, Kearney, Maisano, Rieppel, & Behlke, 2012; Savage, 1964). The genera *Cyclura* and *Leiocephalus* probably arrived during mid-Cenozoic, while the other genera of Squamata colonized the region more recently (Hedges, 2006).

The record of Squamata fossils has very good studies in some islands like Hispaniola, Puerto Rico, Antigua, Guadalupe Islands, and some of the Bahamas Bank (Bochaton et al., 2015; Etheridge, 1965; Pregill, 1981; Pregill, Steadman, Olson, & Grady, 1988; Pregill, Steadman, & Watters, 1994; Steadman et al., 2015). Other islands of the Antilles are still much less studied, or not studied at all, concerning their paleofauna of Squamata. Oldest fossils are from the Miocene of the Dominican Republic amber (Daza & Bauer, 2012; Queiroz, Chu, & Losos, 1998)

and from a Puerto Rican lignithic clayey (MacPhee & Wyss, 1990). These fossils give us some understanding about times and forms of colonization in the Antillean territories.

In the Antilles, Cuba is the largest island, with an approximate area of 110 km² and a maximum elevation of 1974 m.s.l (National Office of Statistic and Information, 2017). The autochthonous fauna of Cuban lizards are grouped into eight families, nine genera, and 99 species (Rodríguez-Schettino et al., 2013; Uetz, Freed, & Hošek, 2018). The two most diverse families are Dactyloidae with 64 species, all belonging to the genus *Anolis* (95.3% of endemism) and Sphaerodactylidae (22 species, 86.3% of endemism), composed of the genera *Sphaerodactylus*, and *Aristelliger*. Snakes are grouped into four families, nine genera, and 42 species. The most diverse families are Tropicodidae (16 species, all endemic) and Typhlopidae (12 endemic species and 1 introduced). While amphisbaenians are grouped into two families, Amphisbaenidae with three species of the genus *Amphisbaena*, and Cadeidae, with two species of the genus *Cadea* (Rodríguez-Schettino et al., 2013; Uetz et al., 2018). This last family is endemic.

All known fossil records of Squamata are from the Pleistocene-Late Holocene age, mainly associated to cave deposits (Consuegra, 2014). So far, registered species from the western and central part of the country are *Anolis lucius*, *A. equestris*, *A. porcatus*, *A. luetogularis*, *A. chamaleonides*, *Tarentola americana*, *Leiocephalus cubensis*, *L. carinatus*, *Cyclura nubila*, *Chilabothrus angulifer*, e *Cubophis cantherigerus* (Arredondo, 1997; Arredondo & Villavicencio, 2004; Brattstrom, 1958; Jiménez, Condis, & García, 2005; Jiménez & Valdés, 1995; Koopman & Ruibal, 1955; Orihuela, 2012; Salgado, Calvache, Macphee, & Gould, 1992; Varona & Arredondo, 1979), which represents 7.5% of the extant Cuban Squamata autochthonous fauna (Torres, Rodríguez-Cabrera, & Romero, 2017).

So far, there is not a study dedicated to this fossil group. The papers in which fossil species of Squamata are reported, mention them as an associated fauna of fossil mammals and birds (Arredondo, 1997; Jiménez et al., 2005; Koopman & Ruibal, 1955; Orihuela, 2012; Varona & Arredondo, 1979), without a properly description, or images for illustration.

The lack of effort and specialists in this field limits the correct identification of the species, or in the worst of cases, leave the piece indeterminate (Pregill, 1992). So far, the method used in Cuban fossils is the empirical comparison with current species, without verify all the

characters that could help to identify the species. In addition, there is a poor representation of Cuban species in osteological collections, which can lead to erroneous assignment of a character to a species given that the range of variation for a character is deduced from only one, or a few individuals (Pregill, 1992). Therefore, studies of paleoenvironment (Arredondo & Villavicencio, 2004), biological diversity (Consuegra, 2014; Rodríguez-Schettino, 2003), and extinctions (Díaz-Franco, 2004; Pregill & Olson, 1981) are incomplete without a good understanding of Squamata paleofauna.

In this work, we propose to perform a detailed description of the Quaternary fossil remains of Squamata, based on defined osteological characters; and conduct a survey of the Cuban fossil record.

2 Conclusions

Based on the osteological descriptions and the geographical location of the records, we reached the following conclusions

- Detailed descriptions of frontal, parietal, occipital, maxillae, dentaries, articulate-surangular complexes, vertebrae, and pelvis of Cuban Squamata fossils are provided, using characters described in the scientific literature.
- Six genera and seven species were identified.
- The genera *Amphisbaena* and *Pholidoscelis* are reported by the first time in the fossil record of Cuba. *Amphisbaena* based on a vertebra of the middle of the body, and *Pholidoscelis* from frontals, parietals, maxillae, dentaries, articular-surangular complexes, and pelvis.
- The presence in the fossil record of species such as *Tarentola americana*, *Leiocephalus cubensis*, *L. carinatus*, *Chilabothrus angulifer*, and *Cubophis cantherigerus* is confirmed, with descriptions of new fossilized bones.
- New records of species not present in Cuba are described. It is necessary to compare with other Antillean and continental species to see which species they belong to.
 - From the genus *Leiocephalus*, two frontals, and a dentary that does not coincide with the living species of the genus are described.
 - From the genus *Tarentola*, two parietals and two articular-surangular complexes are described with forms different from those currently present in Cuba.
 - From the genus *Chilabothrus*, a quadrate and two compound bones are described, distinct even of known Antillean species.
- The number of reported localities with Squamata fossil remains was increased from 10 known to 19.
- The Squamata fossil record was extended to practically the whole country, by including one locality in Santiago de Cuba and another in Isla de la Juventud.
- The localities of fossil remains coincide with the current distribution of living species.

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