

Reconstructing the paleoenvironment of Loltún Cave, Yucatán, Mexico, with Pleistocene amphibians and reptiles and their paleobiogeographic implications

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ABSTRACT

Loltún cave in Yucatán peninsula is an important fossil site. The cave preserves Pleistocene fauna and lithic tools, and it is among the few sites with amphibian and reptile fossils of the Mexican Pleistocene. We used the fossil amphibians and reptiles community to reconstruct the paleoclimate and paleoenvironment of Loltún cave in the Late Pleistocene. The Pleistocene amphibian and reptiles community in Loltún cave consists of one frog, three lizards, five snakes and one turtle. Applying the Habitat Weighting method to the fossil herpetofaunal assemblage, we inferred a vegetation mosaic non-analog with the present one, comprising evergreen seasonal forest, tropical deciduous forest and scrub forest, in contrast to the tropical semi-deciduous forest found nowadays around Loltún cave. Using the Mutual Climatic Range (MCR) method we inferred a mean annual temperature of 25.33 °C and a mean annual precipitation of 1183.74 mm; the temperature was 1.47 °C lower and the MAP was 85.14 mm higher than the present climate condition.

Is the first time that a paleoclimatic reconstruction using amphibians and reptiles in a tropical region is made using the MCR method. Our results are in concordance with other paleoclimatic inferences using fossil pollen as a proxy, extending the use of the MCR method to different climatic regions. We found a range shift of the iguanid *Ctenosaura* subgenus *Loganosaura* during the Late Pleistocene, of 446.4 km north of the present distribution, surely given by the climatic and vegetation structure changes in the past.

Key words: Paleoclimate; paleoenvironment; amphibians; reptiles; Pleistocene; Yucatán peninsula.

RESUMEN

En la península de Yucatán, la gruta de Loltún es un sitio importante por la presencia de fauna pleistocénica junto con herramientas líticas. Este es uno de los pocos sitios con fósiles de anfibios y reptiles del Pleistoceno en el sur de México. Se utilizó la comunidad fósil de anfibios

y reptiles para reconstruir el paleoambiente y paleoclima de la gruta de Loltún para el Pleistoceno Tardío, debido a que la herpetofauna presenta características importantes para la reconstrucción de ambientes pasados. La comunidad de anfibios y reptiles del Pleistoceno Tardío de la gruta de Loltún consiste en un anuro, tres saurios, cinco serpientes y una tortuga. Por medio de la aplicación del método de Ponderación de Hábitat para la comunidad herpetofaunística fósil, se pudo inferir que existió un mosaico de vegetación, no análogo con el presente, constituido de selva perennifolia, bosque tropical caducifolio y matorral xerófito, en contraposición al bosque tropical subcaducifolio presente en la actualidad. También, se infirió una temperatura promedio anual de 25.33 °C y una precipitación promedio anual de 1,183.74 mm, siendo 1.47 °C inferior y 85.14 mm superior a las condiciones climáticas actuales; para estas estimaciones se usó el método de Intervalo Climático Mutuo (ICM). Es la primera vez que se realiza una reconstrucción paleoclimática utilizando el método de ICM con anfibios y reptiles en una región tropical. Nuestros resultados concuerdan con las inferencias paleoclimáticas realizadas con polen fósil, extendiendo el uso del método ICM a diferentes regiones climáticas. Se infiere un cambio en la distribución de *Ctenosaura* subgénero *Loganosaura* durante el Pleistoceno, 446.4 km más al norte de su distribución actual, lo cual seguramente fue producido por los cambios en la estructura de la vegetación y los cambios climáticos.

Palabras clave: Paleoclima; paleoambiente; anfibios; reptiles; Pleistoceno; península de Yucatán.

INTRODUCTION

The first study of amphibians and reptiles from the Pleistocene in Mexico was performed by Langebartel (1953) in many sites of the Yucatán peninsula. Langebartel (1953) reported six taxa of anurans, lizards and snakes and described two extinct species, an iguanid (*Ctenosaura premaxillaris*) and a xantusiid (*Lepidophyma arizeloglyphus*). Both species are still valid (Reynoso, 2006; Chávez-Galván et al., 2013). Other herpetofaunal studies of the Pleistocene in southern Mexico include the description of *Trachemys* in Tabasco, *Trachemys*

scripta, *Kinosternon scorpioides* and *Staurotypus* sp. in Chiapas (Luna-Espinoza and Carbot-Chanona, 2009), *Kinosternon hirtipes/integrum* and *Gopherus* sp. in Oaxaca (Cruz *et al.*, 2009) and *Claudius angustatus* and *Crocodylus* sp. in Veracruz (Peña-Serrano *et al.*, 2004).

One of the most intensively studied sites in the Yucatán peninsula is Loltún cave. The only sites in Mexico that have been systematically excavated with controlled stratigraphy are Loltún cave and San Josecito cave, Nuevo León (Arroyo-Cabrales and Polaco, 2003). Since the last years of the 1980 decade, the archaeological and paleontological significance of Loltún cave was emphasized by the discovery of Pleistocene fauna and lithic tools (Arroyo-Cabrales and Álvarez, 2003). It is one of the few sites in southern Mexico that has Pleistocene fossil amphibians and reptiles. The paleontological studies of Loltún cave have focused on mammals (Hatt, 1953; Álvarez and Polaco, 1972; Mercer, 1975; Cope, 1896; Álvarez and Arroyo-Cabrales, 1990; Arroyo-Cabrales and Álvarez, 1990, 2003), pollen (Xelhuantzi-López, 1986; Montúfar, 1987), mollusks (Álvarez and Polaco, 1972), birds (Fisher, 1953) and amphibians and reptiles (Langebartel, 1953).

Amphibians and reptiles can be good paleoecological proxies because they are ecologically, ethologically and physiologically restricted to microhabitats and specific environments, and many species have restricted geographic intervals and are territorial (Vitt and Caldwell, 2014). These animals are specialized to certain climatic conditions allowing the reconstruction of environments from past climates (Holman, 1995; Blain *et al.*, 2008, 2009, 2010, 2011, 2012, 2013, 2014, 2015, 2016). In this study, fossil amphibian and reptile remains from

Loltún cave were analyzed in order to infer 1) the site paleoenvironment and paleoclimate and 2) the changes in the amphibian and reptile communities during the Late Pleistocene in the Yucatán peninsula.

Loltún cave

Loltún cave is located in the southwest portion of the state of Yucatán (México), about 110 km south of Mérida and 7 km southwest from Oxcutzab, at an elevation of 40 m a.s.l. Its geographic coordinates are 20°15'14.35"N and 89°27'20.82"W (Figure 1). The site is located on the foothills of the sierra de Ticul, in a karst region with several types of solution features exposed in Miocene rocks (Arroyo-Cabrales and Álvarez, 2003). Loltún cave is an east-west-oriented series of tunnels and chambers. It has nine chambers of which Loltún and Nahkab are used as the beginning of a tourist route. The excavations from which the fossil material for this study was obtained were made in the Huechil chamber (*Huech* means armadillo in maya language) (Arroyo-Cabrales and Álvarez, 1990).

The excavations were carried out using a metric grid and controlled stratigraphy during four seasons between 1977 and 1981. The levels or layers of the sequence can be divided into three main groups (Figure 2) (Schmidt, 1988; Arroyo-Cabrales and Álvarez, 2003):

Group 1. Levels I to VII are from the Ceramic Stage, but extinct animal remains are found in the bottom of level VII.

Group 2. Level VIII is from the Pre-Ceramic Stage; it includes some lithic elements and extinct fauna.

Group 3. Levels IX to XVI are Pleistocene in age, without any

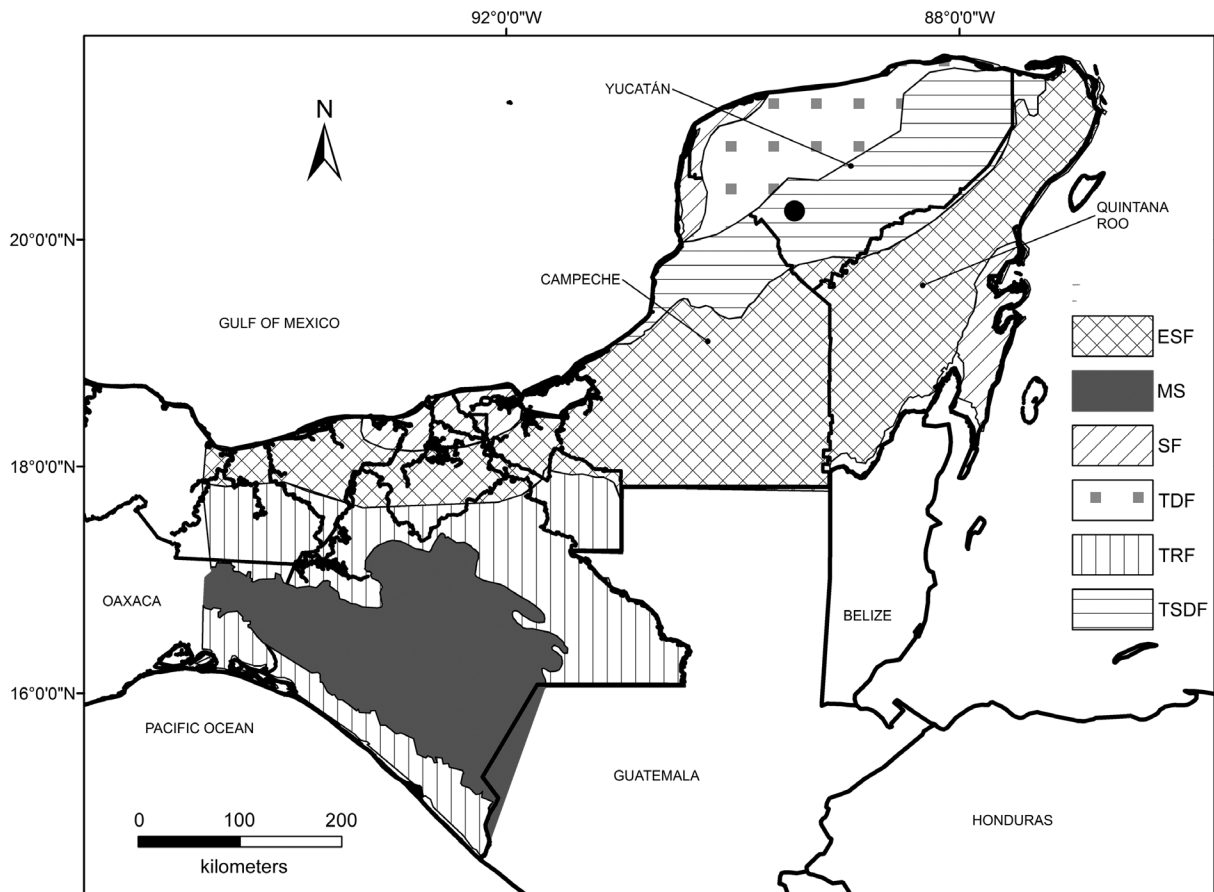


Figure 1. Loltún cave in Yucatán (black point). Habitat types found in the Yucatán peninsula and north Central America: tropical rainforest (TRF), evergreen seasonal forest (ESF), tropical semi-deciduous forest (TSDF), tropical deciduous forest (TDF), scrub forest (SF) and montane systems (MS). Modified map from Correa-Metrio *et al.* (2011).

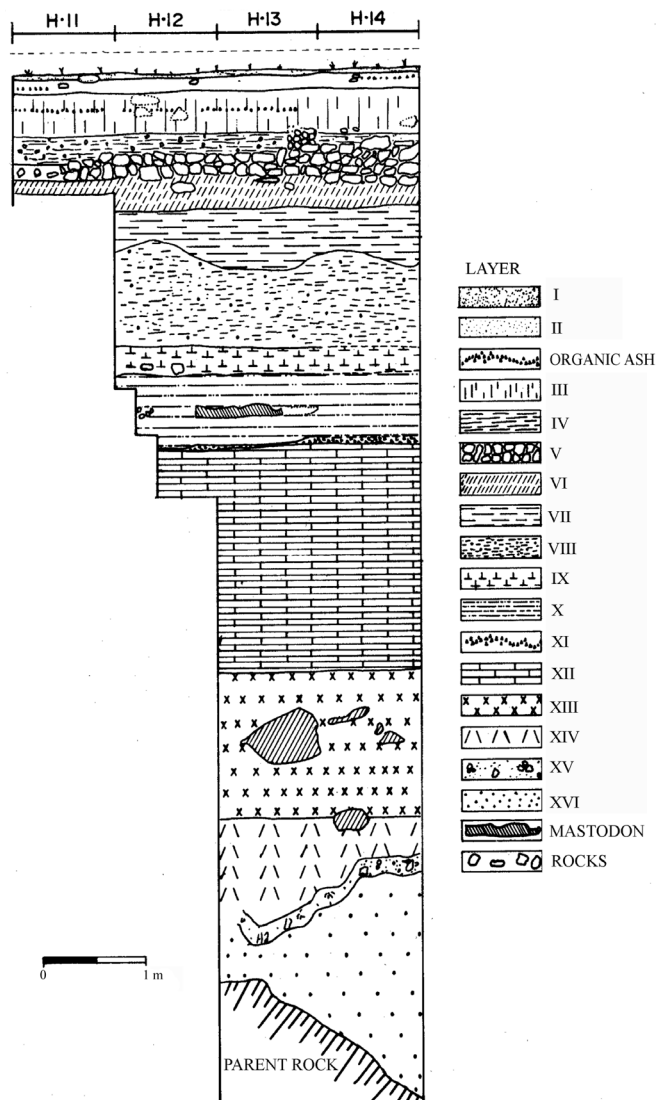


Figure 2. Stratigraphy (redrawn from Álvarez and Polaco, 1972) of El Toro Unit, Loltún cave, Yucatán peninsula. H 11-14, excavation boxes. Layer I, dark brown sediment; Layer II, light brown sediment; Layer III, dark brown sediment; Layer IV, dark brown sediment with rocks; Layer V, bed rocks; Layer VI, dark red sediment; Layer VII, red sediment; Layer VIII, light red sediment; Layer IX, dark red sediment; Layer X, light red sediment; Layer XI, volcanic ash (Rosseau tephra); Layer XII, red sediment; Layer XIII, compacted dark red sediment; Layer XIV, dark red sediment; Layer XV, compacted dark red sediment; Layer XVI, yellow red clay.

cultural material. Volcanic ash correlated to the Rosseau tephra was dated as 28,400 yrs BP by radiocarbon method (uncalibrated, Rampino *et al.*, 1979) and 32782 ± 296 cal yrs BP (Danzeglocke, 2007), and occurs in level XI.

MATERIALS AND METHODS

Fossil remains

The amphibian and reptile fossils studied were found in Loltún cave in the sequences reported as Group 3 which comprises levels XII to XVI, which are older than 32782 ± 296 cal yrs BP (Rampino *et al.*, 1979; Arroyo-Cabrales and Álvarez, 2003). The fossil remains were compared to reference osteological material from the Laboratorio

de Arqueozoología “M. en C. Ticúl Álvarez Solórzano”, Instituto Nacional de Antropología e Historia (DP) and the Colección Nacional de Anfibios y Reptiles, Universidad Nacional Autónoma de México (CNAR). The bones were identified using the criteria given by Holman (2003) for anurans, Auffenberg (1963), LaDuke (1991) and Holman (2000) for snake vertebrae and their regionalization, Evans (2008) for lizards and Preston (1979) for turtles. The remains were labeled as LC (Loltún cave), number of excavation and the level in roman numbers from which the material was obtained.

Paleoenvironmental reconstruction

In order to reconstruct the paleoenvironment, we used the Habitat Weighting Method with six different types of habitats found in the Yucatán peninsula and northern Central America: tropical rainforest (TRF), evergreen seasonal forest (ESF), tropical semi-deciduous forest (TSDF), tropical deciduous forest (TDF), scrub forest (SF) and montane systems (MS), described by Correa-Metrio *et al.* (2011) (Figure 1). This method consists in establishing, first, the present-day habitat distribution of each amphibian and reptile taxon. Each species receives a score for each habitat type proportional to habitat preference; the sum of scores for all habitat types for each species is 1 (Blain *et al.*, 2008). The reconstruction of the paleoenvironment at the study site during the Late Pleistocene was determined by summing the scores of each habitat type for all species. The habitat type with the highest score is interpreted as the predominant habitat type.

Paleoclimatic reconstruction

The Mutual Climatic Range (MCR) method was used to reconstruct the Late Pleistocene paleoclimate around Loltún cave. This method consists in calculating the potential paleoclimatic conditions by identifying the geographic region where all the species in the locality or in a stratigraphical level currently live (Blain *et al.*, 2009). It is assumed that the overlapping areas of the current distribution of each taxon occurring in the locality contain the climatic conditions that were present in the past; in other words, the climatic conditions that were present in the locality where the fossil community was found, are represented by the overlapping of the current distributions.

For each fossil taxon a species distribution model (SDM) was constructed. To accomplish this, locality data from natural history collections such as Sistema Nacional de Información sobre la Biodiversidad (CONABIO, www.conabio.org.mx), the Global Biodiversity Information Facility (GBIF, www.gbif.org), data reported in literature (Lee, 1996, 2000; Campbell, 1999; Köhler, 2003, 2010) and the Colección Nacional de Anfibios y Reptiles (CNAR), Instituto de Biología, Universidad Nacional Autónoma de México, were used.

The SDMs were constructed using the MaxEnt v3.3 software (Phillips *et al.*, 2006), which allows the use of SDMs for exploring and predicting the taxon's distribution even when using a small sample size (Wiszn *et al.*, 2008). For each species, ten distinct models were generated using the *bootstrap* sampling and each model was validated with 30% of the original records. To evaluate the model, the area under the curve (AUC) generated with the ROC technique (Receiver Operating Characteristic) was used. The potential distribution was obtained by reclassifying with the *10 percentile training presence* from the average of the ten models made for each species. As a result, a binary map was created showing the optimal climatic conditions (1 = optimal, 0 = not optimal) for each of the living taxa that represent the fossil amphibian and reptiles found in Loltún cave, Yucatán.

The values of mean annual temperature (MAT) and mean annual precipitation (MAP) for the Late Pleistocene in Loltún cave obtained with the mutual climatic range method were compared with Oxxutzab, Yucatán, the closest weather station to the Loltún cave (smn.cna.gob.mx).

RESULTS

From the fossil remains found in the Loltún cave, we were able to identify one amphibian (*Rhinella marina*), and two lizards (*Ctenosaura defensor* and *C. similis*). We also found fossils from one lizard that belongs to *Ctenosaura* subgenus *Loganosaura*; five snakes from the genera *Boa*, *Coluber*, *Drymarchon*, *Lampropeltis* and *Leptophis*, and a turtle from genus *Trachemys*.

Systematic paleontology

Class Amphibia Blainville, 1816
Order Anura Fischer von Waldheim, 1813
Family Bufonidae Gray, 1825
Genus *Rhinella* Fitzinger, 1826

Rhinella marina Linnaeus, 1758

Figure 3

Rana marina Linnaeus, 1758, Systema Naturae, Ed. 10, 1:211.
Bufo marinus Schneider, 1799, Historia Amphibiorum Naturalis: 219.
Chaunus marinus Frost *et al.*, 2006, Bulletin of the American Museum of Natural History, 297:364.
Rhinella marina Pramuk *et al.*, 2008, Herpetologica, 63:211.

Description. The radio-ulna (LC 360-XII) is slightly constricted. It

has a large quadrangular radio-ulnar foramen. Its Y element's process is in form of a spine. The separation between the radial process and the ulnar process is weak. The radial process is conserved up to the middle of the ulnar part. In dorsal view, the trochanter diverges at an angle of 90°. It has an ulnar keel. In lateral view, the anterior radio-ulna edge is slightly angled.

The seventh vertebra (LC 360-XII) has an oval cotyle with dorsal edges in a U-like form. The neural spine is thin and short. The separation between the prezygapophyseal articular facets is less than their width. The postzygapophyseal keel merges from the posterior neural spine. The neural arch is depressed and concave.

The astragalus (LC 359-XII) has a distal canal, a smooth torsion of the element, and a robust form. The distal epiphyses has a triangular cross-section.

Material. Left radio-ulna (LC 360-XII), a seventh vertebra (LC 360-XII) and a left astragalus (LC 359-XII).

Discussion. The size of the material can only be compared to big anurans of the country like *Rhinella marina* (DP 732), *Lithobates catesbeianus* (DP 5086) and *Lithobates megapoda* (CNAR 15686). The radio-ulna is referred to *Rhinella marina* because they share the following characteristics: a smooth constriction, a quadrangular radio-ulnar foramen, spine-like Y process, a short distance between the radial and ulnar process, a trochanter deviation of 90°, and a slightly angled anterior edge (Table 1). The seventh vertebra is referred to *R. marina* because of the presence of an oval cotyle with dorsal edges in U-like form and a thin and short neural spine. The separation between the

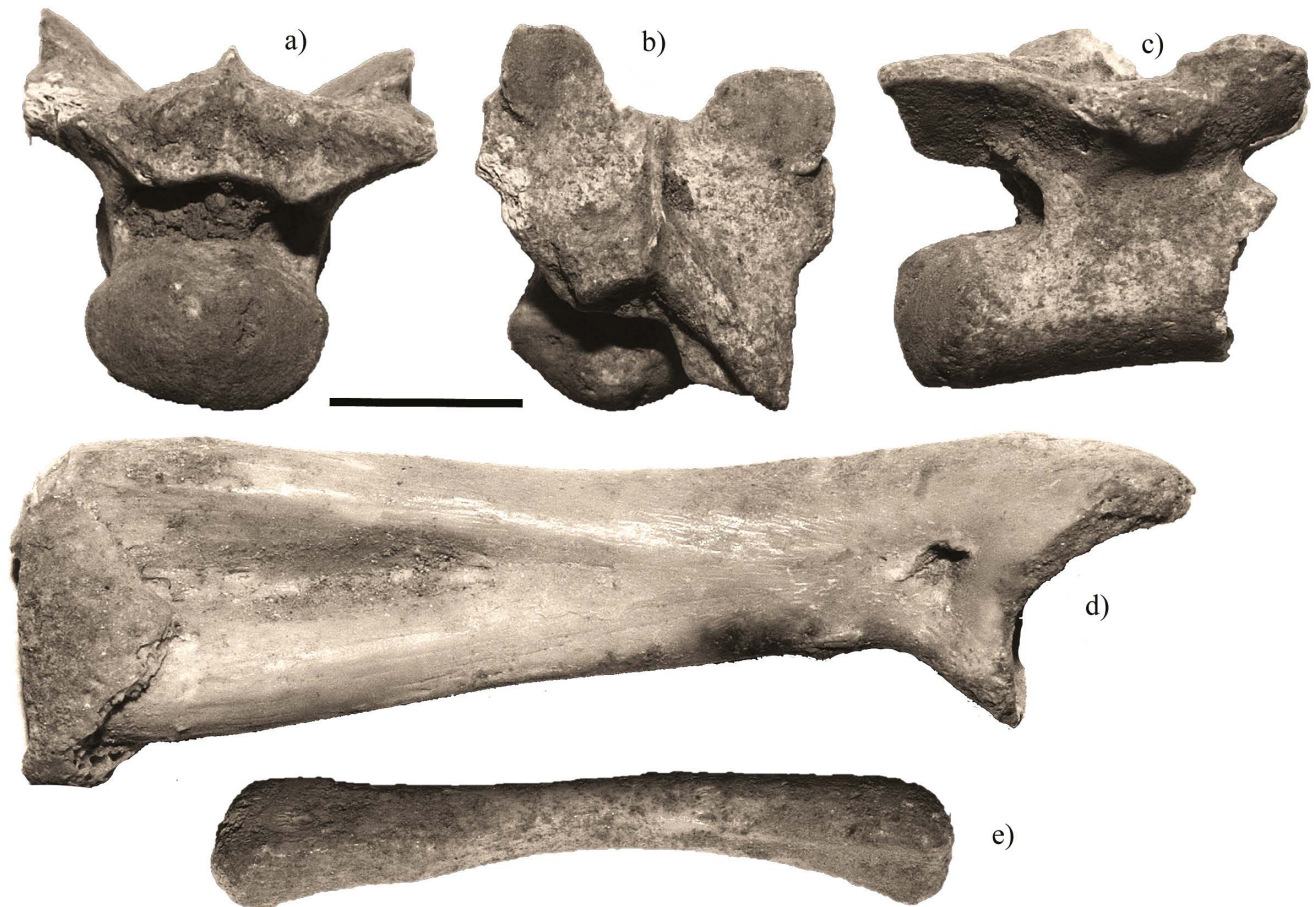


Figure 3. *Rhinella marina* fossil remains found in Loltún cave. Seventh trunk vertebra in posterior view (a), dorsal view (b) and lateral view (c). Left radio-ulna (d). Left astragalus (e). Scale bar = 5 mm.

Table 1. Comparison of radio-ulna between *Rhinella*, *Lithobates* and fossil material (LC 360-XII).

Feature	Genus		
	Fossil	<i>Rhinella</i>	<i>Lithobates</i>
Bone constriction	Unremarkable	Smooth	Strong
Ulnar and radial width	Equal	Slightly narrow the anterior part	Narrow in the anterior part
Radio-ulnar foramen	Large and quadrangular	Small and quadrangular	Small and elongated
Y process	Like spine	Like spine	Underdeveloped
Distance between the radial and ulnar process	Close	Close	Broad
Trochanter deviation	90°	90°	Less than 90°
Anterior edge	Slightly angled	Slightly angled	Strongly angled

prezygapophyseal articular facets is short and a postzygapophyseal keel merges from the posterior neural spine (Table 2). The material described above is morphologically congruent with the osteological characters of *Rhinella marina*.

Class Reptilia Laurenti, 1768
 Order Squamata Oppel, 1811
 Family Iguanidae Oppel, 1811
 Genus *Ctenosaura* Wiegmann, 1828

***Ctenosaura defensor* Cope, 1866**
 Figure 4

Cachryx defensor Cope, 1866, Proceedings of the Academy of Natural Sciences of Philadelphia, 18:124.

Ctenosaura defensor Günther, 1890, Biologica Centrali-Americana, Reptilia and Batrachia: 58.

Enyaliosaurus defensor Smith and Taylor, 1950, Bulletin of the United States National Museum, 199:77.

Ctenosaura (Enyaliosaurus) defensor Köhler et al., 2000, Amphibia-Reptilia, 21:188.

Description. The left dentary (LC 374-XIII) is small (19.8 mm). It has a closed Meckelian canal without sutures. This element shows 18 tooth positions, 14 of which preserve complete teeth. The teeth are pentacuspoid.

Material. A left dentary (LC 374-XIII).

Discussion. The material here described can be confidently referred to *Ctenosaura defensor* on the basis of the characters discussed by de

Queiroz (1987). A relevant character is the closed Meckelian canal without sutures present in all iguanids (Figure 4a). The identification is straightforward excluding the genus *Dipsosaurus* and some species of *Ctenosaura* (*C. acanthura*, *C. clarki*, *C. hemilopha*, *C. palearis*, *C. pectinata* and *C. similis*) because the teeth in these taxa have a maximum of four cusps. The presence of pentacuspoid teeth is characteristic of *Ctenosaura defensor* and *Cyclura pinguis* excluding other polycuspoid genus *Cyclura*, *Sauromalus* and *Iguana*) with six or more cusps. However, *C. pinguis* is excluded because it has a bigger dentary than *C. defensor*. The size of the latter is more consistent with the fossil remains.

***Ctenosaura similis* Gray, 1831**
 Figure 4

Iguana (Ctenosaura) similis Gray, 1831 in Griffith and Pidgeon (eds.), The animal kingdom arranged in conformity with its organization by the Baron Cuvier with additional descriptions of all species higher named, and of many before noticed, 38 p.

Ctenosaura similis Bailey, 1929, Proceedings of the United States National Museum, 73:32.

Ctenosaura (Ctenosaura) similis Köhler et al., 2000, Amphibia-Reptilia, 21:187.

Material. A posterior fragment of the left maxilla (LC 367-XII-XIII), first and second sacral vertebrae (LC 367-XII-XIII, LC 360-XII), two cervical vertebrae (LC 361-XII), six trunk vertebrae (LC 357-XIII, 359-XII, 361-XII, 367-XII-XIII) and six caudal vertebrae (LC 357-XIII, 359-XII, 361-XII, 362-XII, 367-XII-XIII).

Discussion. The fossils were compared with recent osteological material of *Ctenosaura similis* and *C. pectinata*, without finding important differences in the maxilla or the trunk vertebrae. The fossil material is referred to *C. similis* because they share the following characteristics: the sacral vertebra have a neural spine that overhangs dorsally, in the first sacral vertebra, the distal part of the pleurapophysis is large and flat and the condyle of the second sacral vertebra is dorsoventrally large. These characteristics differ from *C. pectinata*.

Genus *Ctenosaura* Wiegmann, 1828
Subgenus *Loganosaura* Köhler et al., 2000
 Figure 4

Ctenosaura Stejneger, 1901, Proceedings of the United States National Museum, 23:467.

Enyaliosaurus Cochran, 1961, United States National Museum Bulletin, 1961:105.

Ctenosaura subgenus *Loganosaura* Köhler et al., 2000, Amphibia-Reptilia, 21:187.

Type species. *Ctenosaura bakeri* Stejneger, 1901.

Table 2. Comparison of the seventh vertebra between *Rhinella*, *Lithobates* and fossil material (LC 360-XII).

Feature	Genus		
	Fossil	<i>Rhinella</i>	<i>Lithobates</i>
Cotyle	Oval with dorsal edges U-like form	Oval with dorsal edges U-like form	Oval with convex dorsal edges
Neural spine	Thin and short	Thin and short	Thick and tall
Separation between prezygapophyseal articular facets	Short	Short	Wide
Postzygapophyseal keel	Merges from the posterior segment of neural spine	Merges from the posterior segment of neural spine	Merges from the anterior segment of neural spine

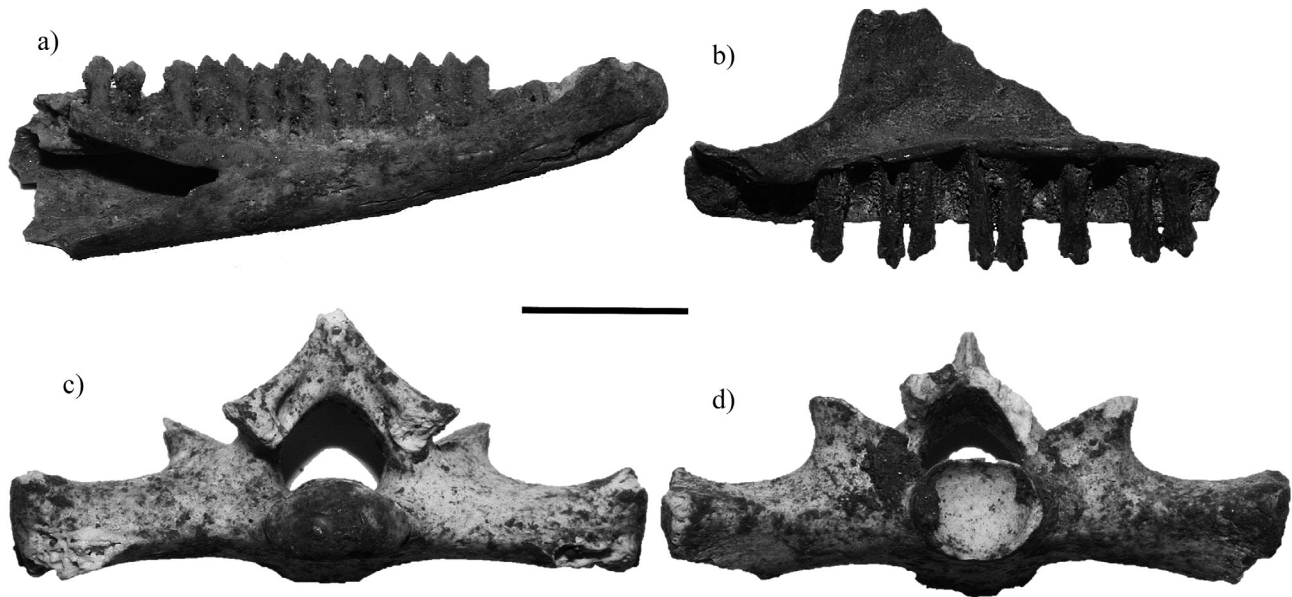


Figure 4. Fossil iguanid remains found in Loltún cave. *Ctenosaura defensor* left dentary (a). *Ctenosaura* subgenus *Loganiosaura* right maxilla (b). *Ctenosaura similis* sacral vertebra in posterior (c) and anterior view (d). Scale bar = 5 mm.

Description. A right maxilla. This element shows 16 tooth positions, eight of which preserved complete teeth. The teeth are tetracuspoid. The anterior part of the maxilla has a ventral straight edge.

Material. Right maxilla (LC 359-XII).

Discussion. The genus *Ctenosaura* includes three subgenera: *Enyaliosarus*, *Ctenosaura* and *Loganiosaura* (de Queiroz, 1987). The subgenus *Enyaliosarus* is composed of *Ctenosaura quinquecarinata* complex (Hasbún *et al.*, 2005) which can be excluded because the species of this group have tricuspid teeth (e.g. *C. oaxacana*) or pentacuspoid (e.g. *C. defensor*). Tetracuspoid teeth are found in the subgenera *Ctenosaura* and *Loganiosaura*, of which the subgenus *Ctenosaura* is excluded because the anterior part of the fossil maxilla is straight (Oelrich, 1956; de Queiroz, 1987). The subgenus *Loganiosaura* is composed of four species, of which de Queiroz (1987) mentions that *C. bakeri* has tricuspid teeth and *C. palearis* tetracuspoid teeth. There is no reference osteological material for the other two species, *C. melanosterna* and *C. oedirhina*, so the fossil remains were only identified at the subgenus level.

Family Boidae Gray, 1825

Genus *Boa* Linnaeus, 1758

Figure 5

Boa Linnaeus, 1758, *Systema Naturae*, Ed. 10, 1:215.

Constrictor Martin, 1958, *Miscellaneous publications*, Museum of Zoology, University of Michigan, 101:67.

Type species. *Boa constrictor* Linnaeus, 1758.

Material. Three cervical vertebrae (LC 363-XII, 372-XIII, 378-XVI), six anterior trunk vertebrae (LC 357-XIII, 370-XIII, 371-XIII) and four posterior trunk vertebrae (LC 360-XII, 362-XII, 370-XIII).

Discussion. The material can be referred to *Boa* on the basis of the character discussed, among others, by Holman (1981, 2000), Albino and Carlini (2008) and Albino (2011). The fossil vertebrae present diagnostic characters such as: robust, tall and short form; a tall neural arch and spine; small prezygapophyseal processes; diapophysis and

parapophysis are slightly distinguished; cotyles and condyles are bigger than the neural canal; a robust zygosphen and the neural arch is clearly convex. Hynková *et al.* (2009) and Card *et al.* (2016) separated *Boa constrictor* into three species *B. constrictor*, *B. imperator* and *B. sigma*. There are no osteological studies available to separate the fossil material to a specific level, so the fossil remains were only identified at the genus level.

Family Colubridae Oppel, 1811

Genus *Drymarchon* Fitzinger, 1843

Figure 5

Drymarchon Boie, 1827, *Bermerkungen über Merrem's Versuch eines Systems der Amphibien*, 1. Lieferung, Ophidier: Isis van Oken, 20, 508-566.

Coluber Boie, 1827, *Bermerkungen über Merrem's Versuch eines Systems der Amphibien*, 1. Lieferung, Ophidier: Isis van Oken, 20, 508-566.

Spilotes melanurus Duméril, Bibron and Duméril, 1854, *Erpétologie Générale ou Histoire Naturelle Complète des Reptiles*, 9, 224.

Drymarchon Stuart, 1935, *University of Michigan Museum of Zoology Miscellaneous Publications* 29: 49.

Type species. *Drymarchon corais* Boie, 1827.

Material. Seven anterior trunk vertebrae (LC 356-XII, 359-XII, 361-XII, 364-XII, 374-XIII) and two posterior trunk vertebrae (LC 360-XII, 361-XII).

Discussion. The material can be referred to *Drymarchon* on the basis of the characters discussed by Auffenberg (1963) and Holman (2000). The fossil vertebrae present relevant characters such as, evident subcentral bridges, in ventral view the centrum is subtriangular; a gladiate hemal keel; epizygapophyseal spines and in posterior and dorsal view the accessory processes overhang laterally. Molecular studies (Wüster *et al.*, 2001) separated *D. corais* into three species *D. corais*, *D. melanurus* and *D. caudomaculatus* so that new osteological studies should be performed to identify our fossil remains to a specific level.

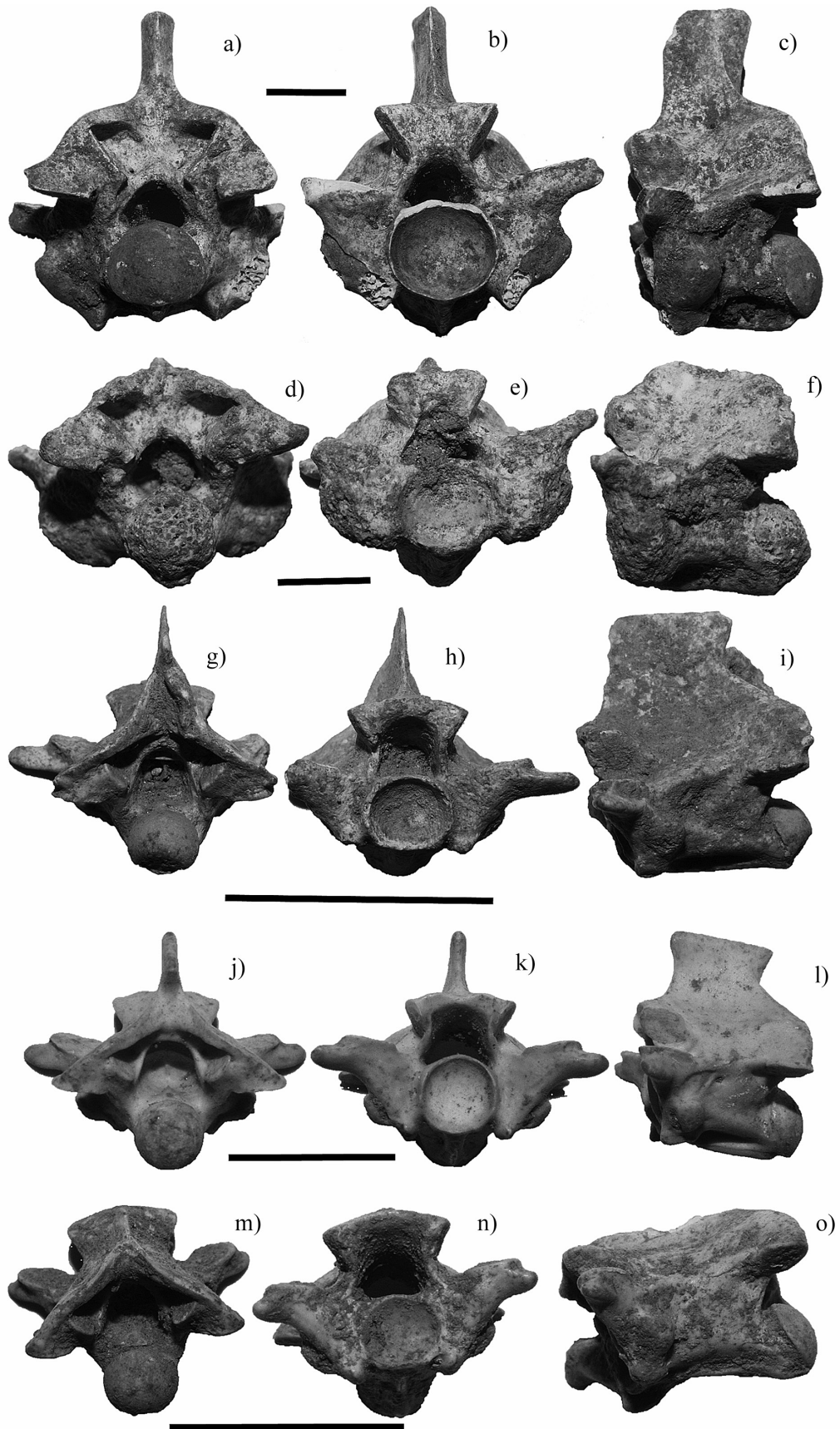


Figure 5. Fossil trunk vertebrae of the snakes found in Loltún cave. *Boa constrictor* (a,b,c), *Drymarchon melanurus* (d,e,f), *Coluber* (g,h,i), *Lampropeltis* (j, k, l), and *Leptophis* (m, n, o). Posterior view (a, d, g, j, m), anterior view (b, e, h, k, n) and lateral view (c, f, i, l, o). Scale bar = 5 mm.

Genus *Coluber* (*Masticophis*) Baird and Girard 1853

Figure 5

Leptophis Hallowell, 1852, Proceedings of the Academy of Natural Sciences of Philadelphia, 6:181.

Masticophis Baird and Girard, 1853, Catalogue of North American Reptiles in the Museum of the Smithsonian Institution, 103.

Coluber Utiger *et al.*, 2005, Russian Journal of Herpetology, 12:51.

Type species. *Coluber constrictor* Linnaeus, 1758.

Material. An anterior trunk vertebra (LC 362-XII).

Discussion. Meylan (1982), LaDuke (1991) and Holman (2000) mention that the differences between the vertebrae from *Masticophis* and *Coluber* are not clear. Molecular studies have supported the synonymy of the genus *Masticophis* with *Coluber* (Utiger *et al.*, 2005), giving a possible explanation for the osteological similarity of the vertebrae between these genera. Despite this, Auffenberg (1963), Meylan (1982) and LaDuke (1991) identify the genus *Masticophis* on the basis of the following characteristics: long vertebrae with convex neural arch; a subquadrangular neural canal with a dorsal edge smaller than the ventral one; round postzygapophyseal articular facets; long, thick and blunt accessory processes; slightly developed subcentral ridges; gladiate hemal keel and epizygapophyseal spines. The fossil remain presents all of the characteristics mentioned above allowing us identify it as the genus *Masticophis*.

Genus *Lampropeltis* Linnaeus, 1766

Figure 5

Coluber Linnaeus, 1766, Systema Naturae per regna tria nature, secundum clases, ordines, genera, species, cum characteribus differentiis, synonymis, locis: 328.

Herpetodryas Schlegel, 1843, Essay on the physiognomy of serpents: 152.

Ophibolus Baird and Girard, 1853, Catalogue of North American Reptiles in the Museum of the Smithsonian Institution, 85.

Coronella Duméril, Bibron and Duméril, 1854, Erpétologie Générale ou Histoire Naturelle Complète des Reptiles, 9:616.

Triaeniopholis Werner, 1924, Gedruckt mit Unterstützung aus dem Jerome und Margaret Stonborough-Fonds, 133:50.

Lampropeltis Pyron and Burbrink, 2009, Zootaxa, 2241:24.

Type species. *Lampropeltis getula* Linnaeus, 1766.

Material. A cervical vertebra (LC 366-XII), four anterior trunk vertebrae (LC 359-XII, 366-XII, 372-XIII) and a posterior trunk vertebra (LC 356-XII).

Discussion. Genus *Lampropeltis* is diagnosed by the following characteristics: vertebrae are wider than long; a strongly depressed neural arch; cotyle is bigger than the neural canal; moderately blunt accessory processes; slightly developed subcentral ridges; thin and gladiate hemal keel and it does not have epizygapophyseal spines (Auffenberg, 1963, Meylan, 1982; Holman, 2000). The fossil remains present all of the characteristics mentioned above allowing us identify them as genus *Lampropeltis*.

Genus *Leptophis* sp. Linnaeus, 1758

Figure 5

Coluber Linnaeus, 1758, Systema Naturae, Ed. 10, 1:225.

Leptophis Bell, 1825, Zoological Journal, London, 2:328.

Ahaetulla Gray, 1831, in Griffith and Pidgeon, The animal kingdom arranged in conformity with its organisation by the Baron Cuvier

with additional descriptions of all the species higher named, and of many before noticed, 93.

Dendrophis Schlegel, 1837, Essai sur la physionomie des serpens, 224.

Type species. *Leptophis ahaetulla* Linnaeus, 1758.

Description. Long, narrow and flattened vertebrae. In anterior view, the cotyles are laterally subrounded, slightly bigger than the neural canal; a convex zygosphenes; short accessory processes that overhang laterally. In posterior view, the neural arch is convex and slightly flattened; it has a keel between the parazygantral facet and the postzygapophyseal articular facet; circular condyle. In dorsal view, the zygosphenes is convex; rounded, subtriangular or oval prezygapophyseal articular facets; short, wide and rounded accessory processes; the neural spine is no longer than the posterior part of the neural arch. In ventral view, the anterior trunk vertebrae have a short gladiate hemal keel which is only evident in the posterior part of the centrum; the posterior trunk vertebra does not have a hemal keel. It has a long subtriangular to cylindrical centrum; the articular postzygapophyseal facets are rounded or subtriangular; weak or absent subcentral ridges. In lateral view, interzygapophyseal ridges are absent; the neural spine is long and short and the anterior edge beveled; and centrum deeply concave.

Material. Two anterior trunk vertebrae (LC 57-XIII, 359-XIII) and a posterior trunk vertebra (LC 359-XII).

Discussion. *Leptophis* Pleistocene fossil remains are here described for the first time for México (Chávez-Galván *et al.*, 2013). Osteological studies of *Leptophis* have focused on the skull (Oliver, 1948; Wilson, 1970; Souza and Lema, 1990) making this study the first one to describe *Leptophis* vertebrae. The vertebrae are characterized by a concave centrum and a hemal keel in the posterior part. We could only identify the fossil remains as *Leptophis* because only *L. mexicanus* had reference osteological material.

Order Testudines Batsch, 1788

Family Emydidae Rafinesque, 1815

Genus *Trachemys* Agassiz, 1857

Figure 6.

Trachemys Agassiz, 1857, Contributions to the Natural History of the United States of America, North American Testudinata, 252.

Callichelys Gray, 1863, Annals and Magazine of Natural History 13:181

Redamia Gray, 1870, Supplement to the Catalogue of Shield Reptiles in the Collection of the British Museum. Testudinata, 35.

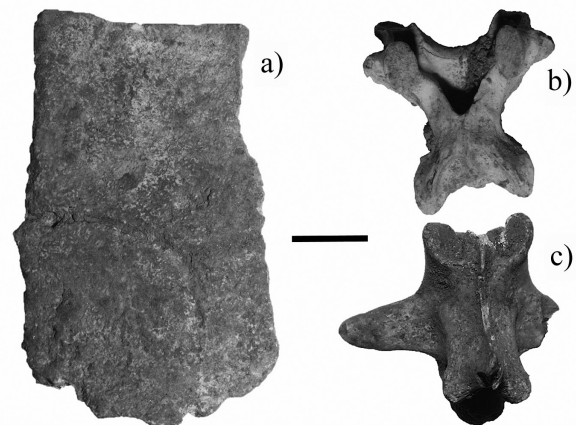


Figure 6. *Trachemys* fossil remain found in Loltún cave. Ninth peripheral bone (a), cervical vertebra (b) and caudal vertebra (c). Scale bar = 5 mm.

Type species. *Trachemys terrapen* Bonnaterra, 1789.

Description. Fragment of the ninth right peripheral bone. In exterior view, imprints of the ninth and tenth marginals scutes are present. The fifth costal can be seen in the upper part. In the visceral surface, the characteristic bulge of the last scutes with a small central foramen can be seen.

Material. Ninth right peripheral bone (LC 356-XII), two cervical vertebrae (LC 360-XII, 363-XII) and a caudal vertebra (LC 362-XII).

Discussion. The ninth right peripheral was compared with reference osteological material of *Rhinoclemmys* and *Trachemys* assigning the fossil material to *Trachemys* because it only has one mark (Souza et al., 2000). It cannot be assigned to Kinosternidae because it does not present a vermiform ornamentation (Cadena et al., 2007) nor elevated imprints of the ninth and tenth marginals (Preston, 1979). The vertebrae did not have morphological features that helped with the identification.

Pleistocene amphibians and reptiles

Amphibian and reptile remains from Loltún cave are here described finding six new taxa for this site: *Ctenosaura defensor*, *C. (Loganiosaura)* sp., *Boa* sp., *Lampropeltis*, *Leptophis* and *Trachemys* (Table 3). *Ctenosaura defensor*, *C. (Loganiosaura)* sp. and *Leptophis* are here reported for the first time for the Pleistocene in México and North America. Nowadays, *C. (Loganiosaura)* sp. is not found in the Yucatán peninsula. For the Pleistocene herpetofauna of southern México, Loltún cave is now the most studied site.

Paleoclimatic and paleoenvironmental reconstruction

The habitat types that have the highest score (1.9) obtained by the habitat weightings method are evergreen seasonal forest (ESF), tropical deciduous forest (TDF) and scrub forest (SF) (Table 4), suggesting that these habitat types were found at the study site during the Late Pleistocene. This mosaic differs from the vegetation structure of tropical semi-deciduous forest (TSDF) found today in the Loltún cave (Correa-Metrio et al., 2011) and indicates that the paleoenvironment for Loltún cave had a vegetation mosaic not analogous with the present one.

The inferred paleoclimate for the Late Pleistocene in Loltún cave indicates climate conditions proper of the north and west part of the Yucatán peninsula with ESF, TDF and SF habitat types. This shows that for the Late Pleistocene, older than 32782 ± 296 cal yrs BP, Loltún cave had a MAT of 25.33 ± 0.47 °C and an MAP of $1,183.74 \pm 143.35$ mm.

Table 3. Taxa from the Pleistocene of the Loltun Cave. ^a Current names taken from Uetz et al. (2015).

Langebartel (1953)	Current names ^a	This study
<i>Bufo ?horribilis</i>	<i>Rhinella marina</i>	<i>Rhinella marina</i>
<i>Ctenosaura ?similis</i>	<i>Ctenosaura similis</i>	<i>Ctenosaura similis</i>
<i>?Drymarchon corais</i>	<i>Drymarchon melanurus</i>	<i>Drymarchon</i> sp.
<i>Elaphe ?flavirufa</i> or <i>E. ?triaspis</i>	<i>Pseudoelephas flavirufa</i> or <i>Senticolis triaspis</i>	-
<i>Masticophis ?mentovarius</i>	<i>Coluber mentovarius</i>	<i>Coluber</i> subgenus <i>Masticophis</i>
<i>Crotalus</i> or <i>Bothrops</i>	<i>Crotalus</i> or <i>Bothrops</i>	- <i>Ctenosaura defensor</i> <i>Ctenosaura</i> subgenus <i>Loganiosaura</i> <i>Boa</i> sp. <i>Lampropeltis</i> sp. <i>Leptophis</i> sp. <i>Trachemys</i> sp.

Table 4. Habitat weighting analysis using amphibians and reptiles assemblage from Loltún cave, Yucatán. TRF, tropical rainforest; ESF, evergreen seasonal forest; TSDF, tropical semi-deciduous forest; TDF, tropical deciduous forest; SF, scrub forest; MS, montane systems.

	TRF	ESF	TSDF	TDF	SF	MS
<i>Rhinella marina</i>	0.167	0.167	0.167	0.167	0.167	0.167
<i>Ctenosaura defensor</i>		0.5		0.5		
<i>Ctenosaura similis</i>	0.2	0.2	0.2	0.2	0.2	
<i>Ctenosaura (Loganiosaura)</i>					0.5	0.5
<i>Boa</i>	0.167	0.167	0.167	0.167	0.167	0.167
<i>Coluber (Masticophis)</i>	0.167	0.167	0.167	0.167	0.167	0.167
<i>Drymarchon</i>	0.167	0.167	0.167	0.167	0.167	0.167
<i>Lampropeltis</i>	0.167	0.167	0.167	0.167	0.167	0.167
<i>Leptophis</i>	0.167	0.167	0.167	0.167	0.167	0.167
<i>Trachemys</i>	0.2	0.2	0.2	0.2	0.2	
Total	1.4	1.9	1.4	1.9	1.9	1.5

These values when compared with the values given by Oxcutzcab weather station suggest that the MAT during the Late Pleistocene was -1.47 °C lower and the MAP was 85.14 mm higher than today conditions (Table 5).

DISCUSSION

Loltún cave is an important site in southern México, where 12 taxa of Pleistocene amphibians and reptiles have been found and described (Langebartel 1953; this study). A fewer taxa have been described in other places, for example, in Tabasco, one turtle (Luna-Espinoza and Carbot-Chanona, 2009); in Chiapas, three turtles (Luna-Espinoza and Carbot-Chanona, 2009); in Oaxaca, two turtles (Cruz et al., 2009), and in Veracruz, one turtle and a crocodile (Peña-Serrano et al., 2004).

The results suggest a paleoenvironment composed of a vegetation mosaic, different of the present one, with three habitat types: evergreen seasonal forest (ESF), tropical deciduous forest (TDF), and scrub forest (SF). Vegetation communities non-analog with the present ones have been reported in Petén Itza lake, in the Yucatán peninsula (Correa-Metrio et al., 2012a, 2012b), which agree with our findings.

The paleoclimate reconstruction infers a MAT 1.47 °C lower and an MAP 85.14 mm higher than the present one. Since 65 ka BP to LGM (22 ka), Correa-Metrio et al. (2012a) suggest that the MAT decreased 1.5 °C compared with today. Periods of lower humidity occurred during the Heinrich Stadials (Correa-Metrio et al., 2012a) suggesting that the period of the fossil remains in Loltún cave is an interglacial before the LGM (Correa-Metrio et al., 2012a).

The distribution of *Ctenosaura* subgenus *Loganiosaura* suffered changes during the Pleistocene. Today, *Loganiosaura* is found in tropical rainforest areas (TRF) and montane systems (MS) (Köhler, 2003). This study shows that in the past this species could be found in Loltún cave, 446.4 km further to the north than its present distribution (Figure 7). This range shift has been found also for the skunk (*Mephitis macroura*) and the wolf (*Canis lupus*) (Arroyo-Cabrales and Álvarez, 2003) that, like *Loganiosaura*, are not found today in the Yucatán peninsula (Sosa-Escalante et al., 2014). During the Late Pleistocene, *Mephitis macroura* and *Canis lupus* were found 489.78 km and 714.94 km further northeast (García-Moreno et al., 1996; Hwang y Larivière, 2001) (Figure 7). The changes in the distribution of these species could be caused by the isotherm displacement which is calculated for the region between 179 to 250 m/yr for the 38-29 ka time interval (Correa-Metrio et al., 2013).

Table 5. Paleoclimatic reconstruction in Loltún cave, Yucatán, using Mutual Climatic Range method, and compared with Oxkutzcab, Yucatán, the closest weather station to Loltún cave. MAT, mean annual temperature; MAP, mean annual precipitation; sd, standard deviation.

	Oxkutzcab	Loltún	sd	Minimum	Maximum	Difference
MAT	26.8	25.33	±0.47	25	26	-1.47
MAP	1,098.6	1,183.74	±143.35	968	1,490	+85.14

CONCLUSIONS

The Loltún cave is now the most studied site of southern Mexico because of amphibian and reptile fossils found there. In Loltún cave, the herpetofaunal community is a good paleoenvironment and paleoclimate indicator for the Late Pleistocene and shows a decrease in the MAT, and an increase in the MAP, suggesting an interglacial period before the LGM. In the past, the habitat type was a mosaic vegetation composed of evergreen seasonal forest (ESF), tropical deciduous forest (TDF), and scrub forest (SF). The paleoenvironment for Loltún cave shows a mixture of habitat types, not found today in the area. Climate and vegetation composition changes during the Late Pleistocene could have affected the distribution of *Ctenosaura* subgenus *Loganiosaura* and of other species, such as mammals.

Implementing the MCR method, using amphibians and reptiles as paleoclimatic proxies, allowed us to compare and evaluate this method, and to find trends of past climates and how they affect different organisms. It is the first time that a paleoclimatic reconstruction using amphibians and reptiles in a tropical region is made using the MCR method. Our results are in concordance with other paleoclimatic inferences using fossil pollen as a proxy, extending the use of the MCR method to different climatic regions.

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SUPPLEMENTARY MATERIAL

Supplementary Figure S1 “Overlapping area (black area) inhab-

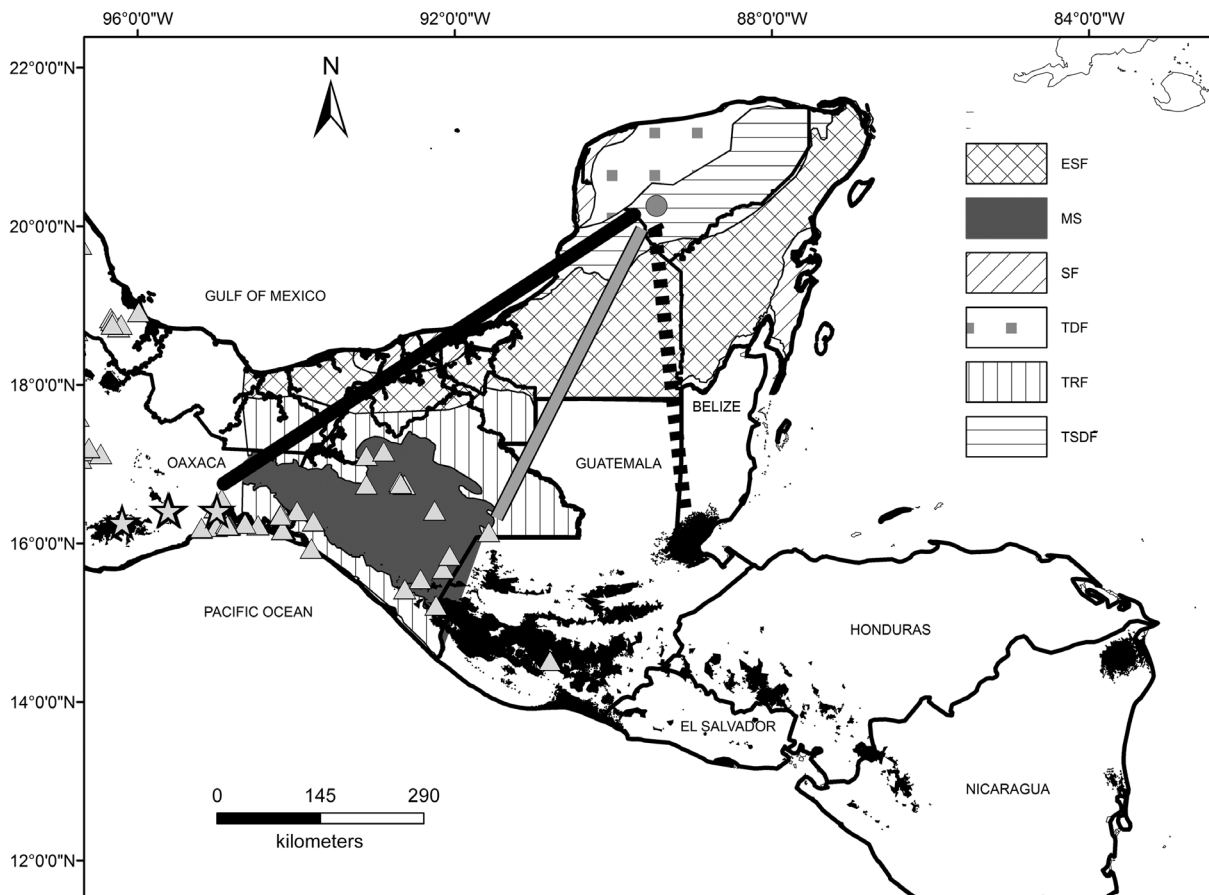


Figure 7. Present distribution of *Ctenosaura* subgenus *Loganiosaura* (black area), *Mephitis macroura* (grey triangles), historic distribution of *Canis lupus baileyi* (grey stars) and their changes in distribution during the Late Pleistocene in Loltún cave (grey point). Distance of changes are shown as dotted line for *Ctenosaura* subgenus *Loganiosaura*, gray line for *Mephitis macroura* and bold line for *Canis lupus baileyi*. Habitat types found in the Yucatán peninsula and Central America: tropical rainforest (TRF), evergreen seasonal forest (ESF), tropical semi-deciduous forest (TSDF), tropical deciduous forest (TDF), scrub forest (SF) and montane systems (MS). Modified map from Correa-Metrio *et al.* (2011).

ited by the species of amphibians and reptiles from Loltún cave” and Supplementary File 1 “Georeferenced data of the actual representatives of fossil taxa founded in Loltún cave” can be found at the journal web site <<http://rmcg.unam.mx/>>, in the table of contents of this issue.

REFERENCES

- Agassiz, L., 1857, Contributions to the Natural History of the United States of America: Boston, Little, Brown & Co., 1, 452 pp.
- Albino, A.M., 2011, Morfología vertebral de *Boa constrictor* (Serpentes: Boidae) y la validez del género Mioceno *Pseudoepicrates* Auffenberg, 1923: *Ameghiniana*, 48, 53-62.
- Albino, A.M., Carlini, A.A., 2008, First record of *Boa constrictor* (Serpentes, Boidae) in the Quaternary of South America: *Journal of Herpetology*, 42, 82-88.
- Álvarez, T., Arroyo-Cabrales, J., 1990, Variación osteométrica de *Marmosa* (Didelphidae: Marsupialia) del Reciente y el Pleistoceno de Yucatán, México, con descripción de una nueva especie: Colección Científica, Instituto Nacional de Antropología e Historia, México, 188, 333-345.
- Álvarez, T., Polaco, O.J., 1972, Restos de moluscos y mamíferos cuaternarios procedentes de las grutas de Loltún, Yucatán, México: Cuadernos de Trabajo 26, Departamento de Prehistoria, Instituto Nacional de Antropología e Historia, 41 pp.
- Arroyo-Cabrales, J., Álvarez, T., 1990, Restos óseos de murciélagos (Orden Chiroptera) procedentes de las excavaciones arqueológicas en las Grutas de Loltún, Yucatán, México: Colección Científica, Instituto Nacional de Antropología e Historia, México, 194, 1-103.
- Arroyo-Cabrales, J., Álvarez, T., 2003, A preliminary report of the late Quaternary mammal fauna from Loltún Cave, Yucatán, México, in Schubert, B.W., Mead, J.I., Graham, R.W. (eds.), Ice age cave faunas of North America: Indiana, United States of America, Indiana University Press, 262-272.
- Arroyo-Cabrales, J., Polaco, O.J., 2003, Caves and the Pleistocene vertebrate paleontology of Mexico, in Schubert, B. W., Mead, J. I., Graham, R. W. (eds.), Ice age cave faunas of North America: Indiana, United States of America, Indiana University Press, 273-292.
- Auffenberg, W., 1963, The fossil snakes of Florida: *Tulane Studies in Zoology*, 10, 131-216.
- Bailey, J. W., 1929, A revision of the lizards of the genus *Ctenosaura*: *Proceedings of the United States National Museum*, 73, 1-55.
- Baird, S. F., Girard, C., 1853, Catalogue of North American Reptiles in the Museum of the Smithsonian Institution. Part 1. Serpents: Washington, Smithsonian Institute, 172 pp.
- Batsch, A. J. G. K., 1788, Versuch einer Anleitung zur Kenntniss und Geschichte der Pflanzen, Thiere, Mineral, Erster Theil: Jena, Academischen Buchhandlung, 678 pp.
- Bell, T., 1825, Type species: *Coluber ahaetulla* Linnaeus, 1758: London, *Zoological Journal*, 2, 328.
- Blain, H-A., Bailon, S., Cuenca-Bescós, G., 2008, The Early-Middle Pleistocene palaeoenvironmental change based on the squamate reptile and amphibian proxies at the Gran Dolina site, Atapuerca, Spain: *Palaeogeography, Palaeoclimatology, Palaeoecology*, 261, 177-192.
- Blain, H-A., Bailon, S., Cuenca-Bescós, G., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2009, Long-term climate record inferred from early-middle Pleistocene amphibian and squamate reptile assemblages at the Gran Dolina Cave, Atapuerca, Spain: *Journal of Human Evolution*, 56, 55-65.
- Blain, H-A., Bailon, S., Cuenca-Bescós, G., Bannasar, M., Rofes, J., López-García, J.M., Huguet, R., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2010, Climate and environment of the earliest West European hominins inferred from the amphibian and squamate reptile assemblages: Sima del Elefante lower red unit, Atapuerca, Spain: *Quaternary Science Reviews*, 29, 3034-3044.
- Blain, H-A., López-García, J.M., Cuenca-Bescós, G., 2011, A very diverse amphibian and reptile assemblage from the late Middle Pleistocene of the Sierra de Atapuerca (Sima del Elefante, Burgos, Northwestern Spain): *Geobios*, 44, 157-172.
- Blain, H-A., Panera, J., Uribealrrea, D., Rubio-Jara, S., Pérez-González, A., 2012, Characterization of a rapid climate shift at the MIS 8/7 transition in central Spain (Valdecarros II, Autonomous Region of Madrid) by means of the herpetological assemblages: *Quaternary Science Reviews*, 47, 73-81.
- Blain, H-A., Glead-Owen, C.P., López-García, J.M., Carrión, J.S., Jennings, R., Finlayson, G., Finlayson, C., Giles-Pacheco, F., 2013, Climatic conditions for the last Neanderthals: herpetofaunal record of Gorham's Cave, Gibraltar: *Journal of Human Evolution*, 64, 289-299.
- Blain, H-A., Laplana, C., Sevilla, P., Arsuaga, J.L., Baquedano, E., Pérez-González, A., 2014, MIS 5/4 transition in a mountain environment: herpetofaunal assemblages from Cueva del Camino, central Spain: *Boreas*, 43, 107-120.
- Blain, H-A., Lozano-Fernández, I., Ollé, A., Rodríguez, J., Santonja, M., Pérez-González, A., 2015, The continental record of Marine Isotope Stage 11 (Middle Pleistocene) on the Iberian Peninsula characterized by herpetofaunal assemblages: *Journal of Quaternary Science*, 30, 667-678.
- Blain, H-A., Lozano-Fernández, I., Agustí, J., Bailon, S., Menéndez-Granda, L., Espígares-Ortiz, M.P., Ros-Montoya, S., Jiménez-Arenas, J.M., Toro-Moyano, I., Martínez-Navarro, B., Sala, R., 2016, Refraining upon the climatic background of the Early Pleistocene hominid settlement in western Europe: Barranco León and Fuente Nueva-3 (Guadix-Baza Basin, SE Spain): *Quaternary Science Reviews*, 144, 132-144.
- Blainville, H.-M.D., 1816, Prodrôme d'une nouvelle distribution systématique du regne animal: *Bulletin de la Société Philomathique de Paris*, 3, 113-124.
- Boie, F., 1827, Bemerkungen über Merrem's Versuch eines Systems der Amphibien, 1. Lieferung, Ophidier: Isis von Oken, 20, 508-566.
- Bonnaterre, P.J., 1789, Tableau encyclopédique et méthodique des trois règnes de la nature, *Erpétologie*: Paris, Pnackoucke, 71 pp.
- Cadena, E.R., Jaramillo, C.M., Paramo, M., 2007, The first late Pleistocene record of *Kinosternon* (Cryptodira: Kinosternidae) turtles for northern South America, Pubenza Locality, Colombia: *South American Journal of Herpetology*, 2, 201-205.
- Campbell, J.A., 1999, Amphibians and reptiles of Northern Guatemala, the Yucatán, and Belize: Oklahoma, United States of America, Animal Natural History Series, University of Oklahoma Press, 400 pp.
- Card, D.C., Schield, D.R., Adams, R.H., Corbin, A.B., Perry, B.W., Andrew, A.L., Pasquesi G.I.M., Smith, E.N., Jezkova, T., Boback, S.M., Booth, W., Castoe, T.A., 2016, Phylogeographic and population genetic analyses reveal multiple species of *Boa* and independent origins of insular dwarfism: *Molecular Phylogenetics and Evolution*, 102, 104-116.
- Chávez-Galván, B., Guzmán, A.F., Polaco, O.J., 2013, Sinopsis de la herpetofauna en contextos paleontológicos y arqueológicos: Colección Interdisciplinaria, Serie Sumaria, Instituto Nacional de Antropología e Historia, México, 304 pp.
- Cochran, D.M., 1961, Type specimens of reptiles and amphibians in the United States National Museum: *United States National Museum Bulletin*, 220, 1-291.
- Cope, E. D., 1866, On the species of Iguaninae: *Proceedings of the Academy of Natural Sciences of Philadelphia*, 23, 121-231.
- Cope, E. D., 1893, Notes on some snakes from tropical America lately living in the collection of the Zoological Society of Philadelphia: *Proceedings of Academy of Natural Sciences of Philadelphia*, 429-435.
- Cope, E.D., 1896, List of vertebrates obtained by Mr. H. C. Mercer in the caves of Yucatán, in Mercer, H.C. (ed.), *The Hill caves of Yucatán*: Norman, University of Oklahoma Press, 68-171.
- Correa-Metrio, A., Bush, M.B., Pérez, L., Schwalb, A., Cabrera K.R., 2011, Pollen distribution along climatic and biogeographic gradients in northern Central America: *The Holocene*, 21, 681-692.
- Correa-Metrio, A., Bush, M.B., Cabrera K.R., Sully, S., Brenner, M., Hodell, D.A., Escobar, J., Guilderson, T., 2012a, Rapid climate change and no-analog vegetation in lowland Central America during the last 66,000 years: *Quaternary Science Reviews*, 38, 63-75.
- Correa-Metrio, A., Bush, M.B., Hodell, D.A., Brenner, M., Escobar, J., Guilderson, T., 2012b, The influence of abrupt climate change on the ice-age vegetation of the Central American lowlands: *Journal of Biogeography*, 39, 497-509.
- Correa-Metrio, A., Bush, M.B., Lozano-García, S., Sosa-Nájera, S., 2013, Millennial-scale temperature change velocity in the continental Northern Neotropics: *PLoS ONE*, 8, e81958. doi:10.1371/journal.pone.0081958.
- Cruz, J.A., Arroyo-Cabrales, J., Viñas-Vallverdú, R., 2009, Tortugas fósiles del Pleistoceno tardío de Santiago Chazumba, Oaxaca: *Boletín de la Sociedad Geológica Mexicana*, 61, 225-232.

- Danzeglocke, U., 2007, Cologne Radiocarbon Calibration & Paleoclimatic Research Package, CalPal: <www.calpal-online.de>.
- de Queiroz, K., 1987, Phylogenetic systematics of the iguanine lizards: a comparative osteological study: California, United States of America, University of California Press, 203 pp.
- Duméril, A.M.C., Bibron, G., Duméril, A.H.A., 1854, *Erpétologie générale ou Histoire Naturelle complète des Reptiles*: Paris, Librairie Encyclopédique Roret, 1(1), 780 pp.
- Evans, S.E., 2008, The skull of lizards and tuatara, in Gans, C., Gaunt, A.S., Adler K. (eds.), *The Skull of Lepidosauria, Biology of Reptilia: Morphology H*, Ithaca, New York, Society for Study of Amphibians and Reptiles, 20, 1-347.
- Fisher, H.I., 1953, Fishes, in Hatt, T.R. (ed.), *Faunal and archeological researches in Yucatán caves*: Cranbrook Institute of Sciences Bulletin, 33, 1-119.
- Fischer von Waldheim, G., 1813, *Zoognosia, Tabulis Synopticus Illustrata, in Usum Praelectionum Academiae Imperialis Medico-Chirurgicae Mosquensis Edita, auctore Gotthelf Fischer*: Moscow, Typis Nicolai Segeidis Vsevolozsky, Editio Tertia, Volumen Primum, 465 pp.
- Fitzinger, L.J.F.J., 1826, *Neue Classification des Reptilien nach ihren Natürlichen Verwandtschaften nebst einer Verwandtschafts-Tafel und einem Verzeichnisse der Reptilien-Sammlung des K. K. Zoologisch Museum's zu Wien*: Vienna, Austria, J.G. Heubner, 88 pp.
- Fitzinger, L.J.F.J., 1843, *Systema Reptilium, Fasciculus Primus*: Vienna, Austria, Braumüller et Seidel, 132 pp.
- Frost, D.R., Grant, T., Faivovich, J., Bain, R.H., Haas, A., Haddad, C.F.B., de Sá, R.O., Channing, A., Wilkinson, M., Donnellan, S.C., Raxworthy, C.J., Campbell, J.A., Blotto, B.L., Moler, P.E., Drewes, R.C., Nussbaum, R.A., Lynch, J.D., Green, D.M., Wheeler, W.C., 2006, The amphibian tree of life: *Bulletin of the American Museum of Natural History*, 297, 1-130.
- García-Moreno, J., Matocq, M.D., Roy, M.S., Geffen, E., Wayne, R.K., 1996, Relationships and genetic purity of the endangered Mexican wolf based on analysis of microsatellite loci: *Conservation Biology*, 10, 376-389.
- Gray, J.E., 1825, A synopsis of the genera of reptiles and amphibian, with a description of some new species: *Annals of Philosophy, Series 2*, 10, 193-217.
- Gray, J.E., 1831, A synopsis of the species of Class Reptilia, in Griffith, E., Pidgeon, E., (eds.), *The animal kingdom arranged in conformity with its organization by the Baron Cuvier with additional descriptions of all the species hither named, and of many before noticed*: London, Whittaker, Treacher and Co., 481 pp.
- Gray, J.E., 1863, Notes on American Emydididae, and Professor Agassiz's observations on my Catalogue of them: *Annals and Magazine of Natural History* 13:176-183.
- Gray, J.E., 1870, Supplement to the Catalogue of Shield Reptiles in the Collection of the British Museum: Testudinata, 120 pp.
- Günther, A.C.L.G., 1890, *Biologica Centrali-Americana, Reptilia and Batrachia*: Taylor & Francis, London, 326 pp.
- Hallowell, E., 1852, Notice of a collection of reptiles from Kansas and Nebraska, presented to the Academy of Natural Sciences by Dr. Hammond: *Proceedings of the Academy of Natural Sciences of Philadelphia*, 6, 178-183.
- Hasbún, C.R., Gómez, A., Köhler, G., Lunt, D.H., 2005, Mitochondrial DNA phylogeography of the Mesoamerican spiny-tailed lizards (*Ctenosaura quinqueringata* complex): historical biogeography, species status and conservation: *Molecular Ecology*, 14, 3095-3107.
- Hatt, T.R., 1953, Faunal and archeological researches in Yucatán caves: *Cranbrook Institute of Sciences Bulletin*, 33, 1-119.
- Holman, J.A., 1981, A review of North American Pleistocene snakes: *Publications of the Museum, Michigan State University Paleontological Series*, 1, 263-306.
- Holman, J.A., 1995, *Pleistocene amphibians and reptiles in North America*: Oxford, Oxford University Press, 256 pp.
- Holman, J.A., 2000, *Fossil snakes of North America: Origin, evolution, distribution, paleoecology*: Indiana, United States of America, Indiana University Press, 355 pp.
- Holman, J.A., 2003, *Fossil frogs and toads of North America: Life of the past*: Indiana, United States of America, Indiana University Press, 246 pp.
- Hwang, Y.T., Larivière, S., 2001, *Mephitis macroura*: *Mammalian Species*, 686, 1-3.
- Hynková, I., Starostová, Z., Frinta, D., 2009, Mitochondrial DNA variation reveals recent evolutionary history of main *Boa constrictor* clades: *Zoological Sciences*, 26, 623-631.
- Köhler, G., 2003, *Reptiles of Central America*: Frankfurt, Germany, Herpeton Verlag Elke Kohler, 400 pp.
- Köhler, G., 2010, *Amphibians of Central America*: Frankfurt, Germany, Herpeton Verlag Elke Kohler, 380 pp.
- Köhler, G., Schroth, W., Streit, B., 2000, Systematics of the *Ctenosaura* group of lizards (Reptilia: Sauria: Iguanidae): *Amphibia-Reptilia*, 21, 177-191.
- LaDuke, T.C., 1991, The fossil snakes of Pit 91 Rancho La Brea, California: *Contributions in Science*, 424, 1-28.
- Langebartel, S.D., 1953, The reptiles and amphibians, in Hatt, T.R. (ed.), *Faunal and archeological researches in Yucatán caves*: *Cranbrook Institute of Sciences Bulletin*, 33, 91-108.
- Laurenti, J.N., 1768, *Specimen Medicum Exhibens Synopsis Reptilium Emendatum cum Experimentis Circa Venena et Antidota Reptilium Austriacorum*: Wien, Austria, Joan, Thomae nob. De Trattner, 234 pp.
- Lee, J.C., 1996, *The amphibians and reptiles of the Yucatán Peninsula*: New York, United States of America, Cornell University Press, 500 pp.
- Lee, J.C., 2000, *A field guide to the amphibians and reptiles of the Maya World: The lowlands of Mexico, Northern Guatemala, and Belize*: New York, United States of America, Comstock Publishing Associates, 416 pp.
- Linnaeus, C., 1758, *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*: Stockholm, Sweden, L. Salvii, 10th Edition, Volume 1, 328 pp.
- Linnaeus, 1766, *Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus differentiis, synonymis, locis*: Stockholm, Sweden, 12th Edition, Volume 1, L. Salvii, 328 pp.
- Luna-Espinoza, J.R., Carbot-Chanona, G., 2009, First records of Late-Pleistocene turtles from Chiapas, Mexico: *Current Research in the Pleistocene*, 26, 162-164.
- Martin, P.S., 1958, A biogeography of reptiles and amphibians in the Gomez Fariás Region, Tamaulipas, Mexico: *Miscellaneous publications, Museum of Zoology, University of Michigan*, 101, 1-102.
- Mercer, H.C., 1975, *The Hill Caves of Yucatán*: Norman, Oklahoma, University of Oklahoma Press, 183 pp.
- Meylan, P.A., 1982, The squamate reptiles of the Inglis IA fauna (Irvingtonian: Citrus County, Florida): *Bulletin of the Florida State Museum Biological Sciences*, 27, 1-85.
- Montúfar, L.A., 1987, Breves notas sobre flora, vegetación y etnobotánica de Loltún, y Labna, Yucatán: *Cuadernos de Trabajo, Departamento de Prehistoria, Instituto Nacional de Antropología e Historia*, 34, 1-34.
- Oelrich, T.M., 1956, The anatomy of the head of *Ctenosaura pectinata* (Iguanidae): *Miscellaneous Publications of the Museum of Zoology*, 94, 9-122.
- Oliver, J.A., 1948, The relationships and zoogeography of the genus *Thalerophis* Oliver: *Bulletin of the American Museum of Natural History*, 92, 157-280.
- Oppel, M., 1811, *Second memoire sur las classification des Reptiles*: *Annales du Muséum d'Histoire Naturelle, Paris*, 16, 394-418.
- Peña-Serrano, J., Lozano-Ramos, T., Aguilar, F.J., Miranda, F., 2004, Hallazgos paleontológicos recientes en la región de Córdoba-Orizaba, Veracruz, México (resumen), in IX Congreso Nacional de Paleontología: Tuxtla Gutiérrez, Chiapas, México: México, Sociedad Mexicana de Paleontología, 58.
- Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006, Maximum entropy modeling of species geographic distributions: *Ecological Modelling*, 190, 231-256.
- Pramuk, J.B., Robertson, T., Sites, J.W., Noonan, B.P., 2008, Around the world in 10 million years: biogeography of the nearly cosmopolitan true toads (Anura: Bufonidae): *Global Ecology and Biogeography*, 17, 72-83.
- Preston, R.E., 1979, Late Pleistocene cold-blooded vertebrate faunas from the midcontinental United States, I, Reptilia; Testudines, Crocodylia: *University of Michigan Museum of Paleontology, Papers on Paleontology*, 19, 1-53.
- Pyron, R.A., Burbrink, F.T., 2009, Systematics of the common kingsnake (*Lampropeltis getula*; Serpentes: Colubridae) and the burden of heritage in taxonomy: *Zootaxa*, 2241, 22-32.
- Rafinesque, C.S., 1815, *Analyse de Nature ou Tableau de l'Univers et des Corps Organisés*: Palermo, Jean Barravecchia, 223 pp.
- Rampino, M.R., Self, S., Fairbridge, R.W., 1979, Can rapid climate change cause volcanic eruptions?: *Science*, 206, 826-829.

- Reynoso, V.H., 2006, Research on fossil amphibians and reptiles in Mexico, from 1869 to early 2004 (including marine forms but excluding pterosaurs, dinosaurs, and obviously, birds), in Vega, F., Nyborg, T.G., Perrilliat, M. del C., Montellano-Ballesteros, M., Cevallos-Ferriz, S.R.S., Quiroz-Barroso, S.A. (eds.), Studies on Mexican Paleontology: Netherlands, Springer, 209-231.
- Schlegel, H., 1837, Essai sur la physionomie des serpens, partie generale et partie descriptive: Amsterdam, MH Schonekat, 606 pp.
- Schlegel, H., 1843, Essay on the physiognomy of serpents: Edinburgh, Maclachlan, Stewart & Co., 232 pp.
- Schmidt, P.J., 1988, La entrada del hombre en la Península de Yucatán, in González-Jácome, A. (comp.), Orígenes del hombre americano: México, D.F., Secretaría de Educación Pública, 25-261.
- Schneider, J.G., 1799, Historia amphibiorum naturalist et literarariae, fasciculus primus. Continens ranas, calamitas, bufones, salamandras et hydras in genera et species, descriptos notisque suis distinctos: Jena, Friederici Frommanni, 219 pp.
- Sosa-Escalante, J.E., Hernández-Betancourt, S., Pech-Canché, J.M., MacSwiney-G., M.C., Díaz-Gamboa, R., 2014, Los mamíferos del Estado de Yucatán: Revista Mexicana de Mastozoología, Nueva Época, 4, 1-41.
- Souza, A.M., Malvasio, A., Araújo Brito Lima, L., 2000, Estudo do esqueleto em *Trachemys dorbignyi* (Duméril and Bibron) (Reptilia, Testudines, Emydidae): Revista Brasileira de Zoologia, 17, 1041-1063.
- Souza, M.F.B., Lema, T., 1990, Osteología craneana de *Dryadophis bifossatus* (Raddi, 1820) (Serpentes, Colubridae): Iheringia, Série Zoologia, 70, 3-15.
- Smith, H.M., Taylor, E.H., 1950, Type localities of mexican reptiles and amphibians: University of Kansas Science Bulletin, 33, 313-380.
- Stejneger, L., 1901, On a new species of spiny-tailed iguana from Utila Island, Honduras: Proceedings of the United States National Museum, 23, 467-468.
- Stuart, L.C., 1935, A contribution to a knowledge of the herpetology of a portion of the savanna region of Central Peten, Guatemala: University of Michigan Museum of Zoology Miscellaneous Publications, 29, 1-56.
- Uetz, P., Freed, P., Hošek, 2015, The Reptile Database, accessed: <http://www.reptile-database.reptarium.cz/>, query date 28 January 2015.
- Utiger, U., Schatti, B., Helfenberger, N., 2005, The oriental colubrine genus *Coelognathus* and classification of old and new world racers and ratsnakes (Reptilia, Squamata, Colubridae, Colubrinae): Russian Journal of Herpetology, 12, 39-60.
- Vitt, L.J., Caldwell, J.P., 2014, Herpetology: an introductory biology of amphibians and reptiles: San Diego, California, Academic Press, 697 pp.
- Werner, F., 1924, Neue order wenig bekannte Schlangen aus dem Naturhistorischen Staatsmuseum in Wien: Sitzungsberichte der Akademie der Wissenschaften in Wien, abt. 1, 133, 29-56.
- Wiegmann, A.F.A., 1828, Beyträge zur Amphibienkunde: Isis von Oken, 21, 364-383.
- Wilson, L.D., 1970, A review of the *chloroticus* group of the colubrid snake genus *Drymobius*, with notes on a twin-striped form of *D. chloroticus* (Cope) from southwestern Mexico: Journal of Herpetology 4, 155-164.
- Wisz, M.S., Hijmans, R.J., Li, J., Peterson, A.T., Graham, C.H., Guisan, A., 2008, NCEAS Predicting Species Distributions Working Group: Diversity and Distributions, 14, 763-773.
- Wüster, W., Yrausquin, J. L., Mijares-Urrutia, A., 2001, A new species of Indigo snake from North-Western Venezuela (Serpientes: Colubridae: Drymarchon): The Herpetological Journal, 11, 157-165.
- Xelhuantzi-López, M. S., 1986, Estudio palinológico del perfil estratigráfico de la unidad "El Toro" Grutas de Ioltún, Yucatán: Cuadernos de Trabajo, Departamento de Prehistoria, Instituto Nacional de Antropología e Historia, 31, 1-49.

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