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The Quaternary vertebrate fauna of the limestone cave Gruta do Ioiô, northeastern Brazil

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ABSTRACT

The present study reports the Quaternary vertebrate fauna of Gruta do Ioiô, a partially submerged limestone cave located in central Bahia, northeastern Brazil. A semi-arid weather prevails nowadays in the area, which is mostly covered by a xeric low arboreal scrubland known as Caatinga. The identified taxa include: *Rhambdia* (Osteichthyes, Siluriformes), *Caiman* (Crocodyliformes, Caimaninae), *Myocastor* cf. *Myocastor coypus* (Rodentia, Myocastoridae), *Holochilus sciureus* (Rodentia, Sigmodontinae), *Natalus* cf. *Natalus macrourus* (Chiroptera, Natalidae), *Tonatia bidens*, *Trachops cirrhosus* (Chiroptera, Phyllostomidae), and *Eira* cf. *Eira barbara* (Carnivora, Mustelidae). Whereas *Rhambdia* and *Caiman* have scarce fossil records, the recovered mammals have already been reported from Quaternary localities of northeastern Brazil, although only two of them are present in the current local fauna. Taphonomic signatures and the nature of the fossiliferous site indicate that the vertebrates lived inside or nearby the cave, including the swamp by its main entrance. Radiocarbon dating of dental bioapatite yielded calibrated ages between 19,980 and 22,040 BP. This indicates that the accumulation started at least during the late Pleistocene, within the Last Glacial Maximum. In agreement with the mode of life of most taxa recognized here, previous studies indicated that this was a wetter period in the region.

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1. Introduction

Cave deposits are remarkable sources of fossil vertebrates, especially for small forms, which are less commonly preserved in other contexts (Andrews, 1990). These deposits function as natural traps for living animals or burial sites for their remains, protecting the bioclasts from normal processes of disintegration (e.g., scavenging, erosion, weathering, transport; Behrensmeyer and Hook, 1992). Commonly, flooding of underground rivers or the superficial water runoff rework the sediments and mix the fossiliferous horizons, resulting in time averaging of 100 to 10,000 years (Behrensmeyer, 1988; Behrensmeyer and Hook, 1992). The complex nature of sedimentary accumulation processes in caves challenges

a proper contextualization of the fossil material collected in these deposits (Hubbe et al., 2011).

In Brazil, since the pioneering work of the Danish naturalist Peter W. Lund (Lund, 1840), cave deposits provide most of the information on Quaternary faunas (Lund, 1840; Salles et al., 1999, 2014; Santos et al., 2002; Castro and Langer, 2011; Ghilardi et al., 2011; Avilla et al., 2013; Castro et al., 2013). Stratigraphic control has often been poor, and taphonomic and geochronologic studies are scarce (Neves and Piló, 2003; Auler et al., 2006, 2009). The deposits are usually loosely dated as late Quaternary, but recently dated remains indicate a broader range of ages, including Pleistocene records of extant genera and early Holocene records of extinct taxa (Baffa et al., 2000; Neves and Piló, 2003; Auler et al., 2006; Hubbe et al., 2007).

Bahia State, in northeastern Brazil, has remarkable limestone caves, including Toca da Boa Vista, the longest of the Southern Hemisphere, with over 100 km of interfingering passages (SBE, 2014). Paleontological research in these caves revealed rich vertebrate assemblages, and some fossils indicate more humid conditions during the Pleistocene than the semi-arid that prevails nowadays in most of the region (Cartelle and Hartwig, 1996;

Abbreviations: cal, calibrated; GSL, greatest skull length; LPRP, Laboratório de Paleontologia de Ribeirão Preto; USP, Ribeirão Preto, Brazil; UCMP, University of California Museum of Paleontology, Berkeley, California; BP, years before 1950.

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Czaplewski and Cartelle, 1998; Lessa et al., 1998; Auler et al., 2004; Cartelle et al., 2008; Salles et al., 2014). This proposition is also supported by palynological, paleoclimatological, and geomorphological data (see Auler and Smart, 2001 for a revision), showing that the low arboreal scrubs were then mixed with semi-deciduous forests (Auler et al., 2004). In this context, this paper aims to report the Quaternary vertebrate fauna of cave Gruta do Ioiô, located in Bahia, and discuss its taphonomic and environmental aspects.

2. Study area and regional setting

The abundant fossil material reported herein comes from Gruta do Ioiô (12°23'36.3" S, 41°33'11" W; Brazilian cave database identification code = BA_100; see SBE, 2014), a partially submerged limestone cave located in the municipality of Palmeiras, central Bahia, northeastern Brazil (Fig. 1), near the Chapada Diamantina National Park. Gruta do Ioiô is western to the Sincorá ridge, which is more than 1200 m high in some areas (Pedreira, 2002). This ridge acts as an orographic barrier and restricts the annual rainfall compared to nearby regions east of the barrier (Barreto, 2010). The area is covered by a xeric low arboreal scrubland locally known as Caatinga, but the outskirts of the cave show more exuberant vegetation, as the doline associated to the cave accumulates a perennial water source.

Gruta do Ioiô is part of one of the most extensive Brazilian karst systems and is one of the longest Brazilian caves (Fig. 2), with 4 km mapped and abundant speleothems (Rubioli, 1995; Laureano and Cruz, 2002). It is possibly continuous to Gruta do Impossível cave, forming the Ioiô-Impossível cave system. The cave is carved in carbonate rocks of the Salitre Formation (upper unit of Una Group,

Irecê Basin, Neoproterozoic; Inda and Barbosa, 1978), which is mostly composed of calcilutites, calcisiltites, calcarenites, dolomitic limestones, and dolomites deposited in a shallow marine environment (Souza et al., 1993). The entrance of Gruta do Ioiô is placed on the bottom of a doline with a maximum diameter of 200 m and about 60 m deep. The underground passage to the fossil-bearing site is permanently filled with water (1–10 m deep), but with breathable air along the entire way. The water is likely allogenic, and related to the hydraulic gradient created by the Sincorá ridge (Barreto, 2010). The fossil-bearing site is about 250 m in linear distance from the entrance of the cave and it is located in a passage diverging from the main passage (Fig. 2). The deposits are mainly composed of fragmented calcite crusts and limestone clasts of various sizes. The low clay contribution is probably related to the long distance from the entrance, and the consolidated sediments seem to be mostly autochthonous in origin.

3. Results and discussion

3.1. Fauna

OSTEICHTHYES
Siluriformes Cuvier, 1816
Rhamdia Bleeker, 1858

Material

Rhamdia remains (LPRP/USP 0729) are the most abundant fossils recovered from Gruta do Ioiô. Dozens of complete or partial skulls were collected, as well as more than a hundred isolated vertebrae, ribs, pectoral girdle, and fin spines (Fig. 3).

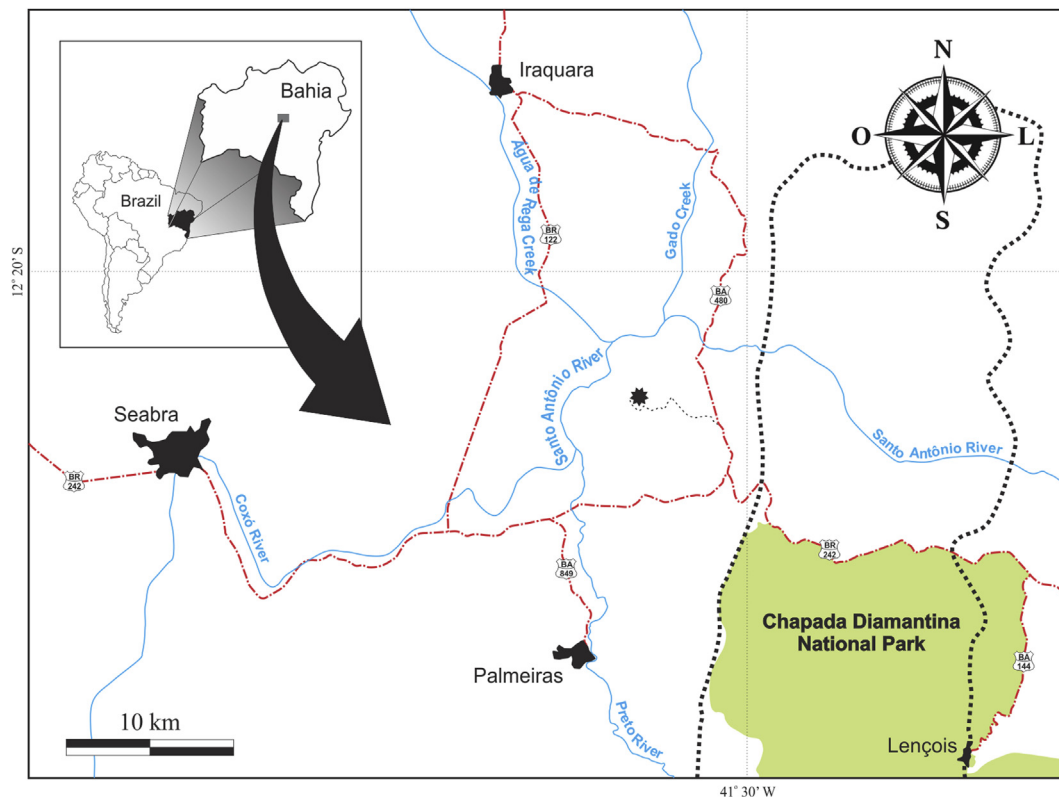


Fig. 1. Location map of Gruta do Ioiô (black star), Bahia, northeastern Brazil. Blue lines = main watercourses; thick black dotted lines = escarpments of Sincorá Ridge; thin black dotted lines = secondary road to Gruta do Ioiô; dotted/dashed red lines = main roads; green shading = Chapada Diamantina National Park. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

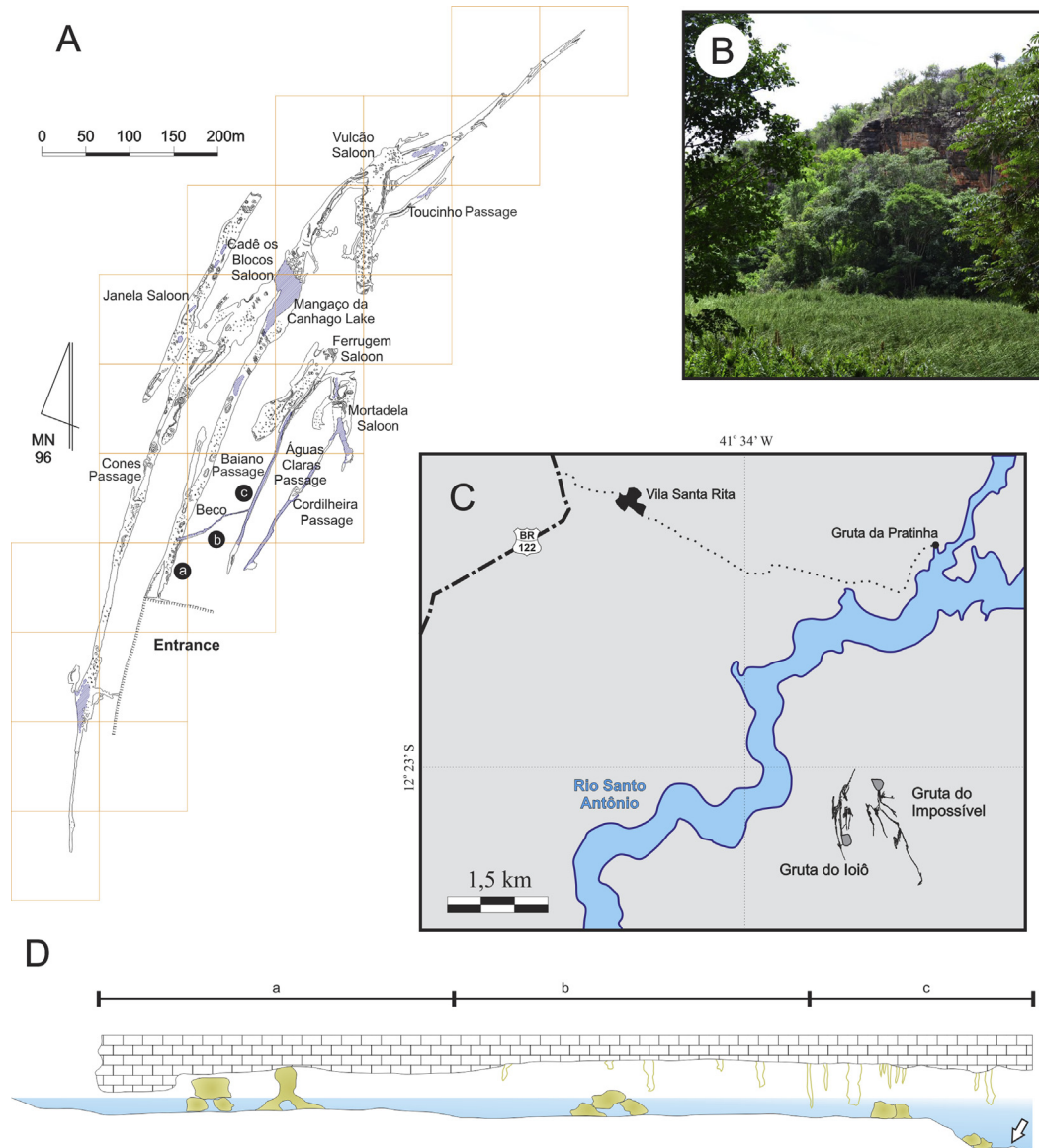


Fig. 2. Gruta do Ioiô. (A) general plan of the cave; (B) photograph depicting part of the doline wall as seen from the swamp at its bottom; (C) detail location map of Ioiô-Impossível cave system; (D) cross section of the passages (a-c as in Fig. 2A) leading to the fossil-bearing site (white arrow). Credits: (A) Grupo Bambuí de Pesquisas Espeleológicas and (D) Frederico Rabello.

Comments

Rhambdia is ubiquitous in rivers, caves, and reservoirs from southern Mexico to northern Argentina (Silfvergrip, 1996; Perdices et al., 2002; Bichuette and Trajano, 2005). More than a hundred binomina were proposed during the last two centuries for taxa of this genus, but a recent revision reduced the number of species to about a dozen (Silfvergrip, 1996). However, this taxonomic arrangement is not fully accepted, particularly concerning the

troglotic taxa, and later works suggest a much higher diversity (see Romero and Paulson, 2001; Weber et al., 2003; Bichuette and Trajano, 2005). The fossil record of the genus is virtually absent, and only fragmentary remains have been reported from the Luján Formation, Pleistocene of Buenos Aires Province, Argentina (Arratia and Cione, 1996). The new fossils from Gruta do Ioiô represent the most important record of the genus for the Pleistocene of Brazil and South America.

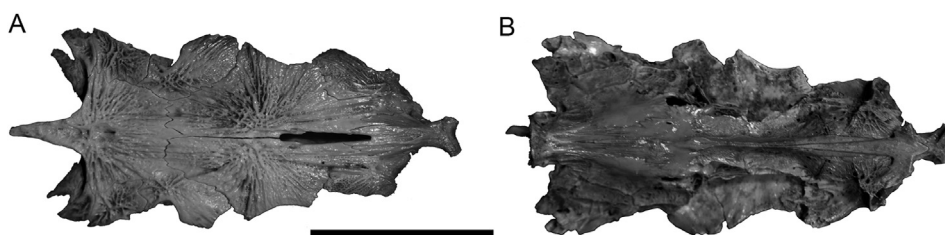


Fig. 3. Neurocranium of *Rhambdia*. LPRP/USP 0729 in dorsal (A) and ventral (B) views. Scale bar = 30 mm.

CROCODYLIFORMES Benton and Clark, 1988
 Caimaninae Brochu, 1999
Caiman Spix, 1825

Material

Crocodile specimens recovered from Gruta do Ioiô comprise at least four individuals (Figs. 4–8). Most of the elements were collected in the consolidated calcareous sediments on the floor of the cave, but the LPRP/USP 0704 skull was wedged between two stalagmites that imbedded part of the cheek and jawbones during precipitation. LPRP/USP 0704 and LPRP/USP 0707 were found in close association, whereas LPRP/USP 0705 and LPRP/USP 0706 were found, respectively, 10 and 5 m apart from the others.

LPRP/USP 0704 is a nearly complete and articulated skull with the lower jaws attached, lacking only the right postorbital bar. The carbonate on the right jugal was mechanically removed, but some of the left bones (premaxilla, maxilla, jugal, and surangular) remain covered (Fig. 4). LPRP/USP 0705 skull is also fairly complete with associated jaws (Fig. 5). The right premaxilla, maxilla, jugal, and quadratojugal are free from the matrix and articulated to the braincase, skull roof, and pterygoid palate. Other elements, especially from the left side of the skull (premaxilla, maxilla, jugal) and lower jaws are semi-articulated and still partially imbedded in the carbonate rock.

LPRP/USP 0706 (Fig. 6) includes semi-articulated skull roof and neurocranium and other disarticulated elements such as the right jugal, premaxillae, and maxillae. In addition, the lower jaws are partially preserved, along with vertebrae, osteoderms, and ribs, all partially imbedded in carbonate. LPRP/USP 0707 (Fig. 7) is a disarticulated skull including premaxillae, maxillae, frontal, parietal, basioccipital, supraoccipital, and left lacrimal, postorbital, jugal, squamosal, pterygoid, and dentary, along with other fragmentary mandibular elements.

In addition to the specimens mentioned above, a partial post-cranium was also recovered and assigned to a different number, LPRP/USP 0708. These remains (Fig. 8) were found in close association to LPRP/USP 0704 and LPRP/USP 0707, but cannot be unambiguously assigned to any of them. Preserved elements include partial neck and trunk vertebral series, disarticulated ribs, both humeri, radii, ulnae, and fragmentary pubes, partial left ischium, metapodial elements, and disarticulated osteoderms.

Comments

Although caimans are nowadays common in water bodies of Bahia, including the area of Gruta do Ioiô (Medem, 1981, 1983; Ross, 1998), crocodile remains are rare in South American Pleistocene

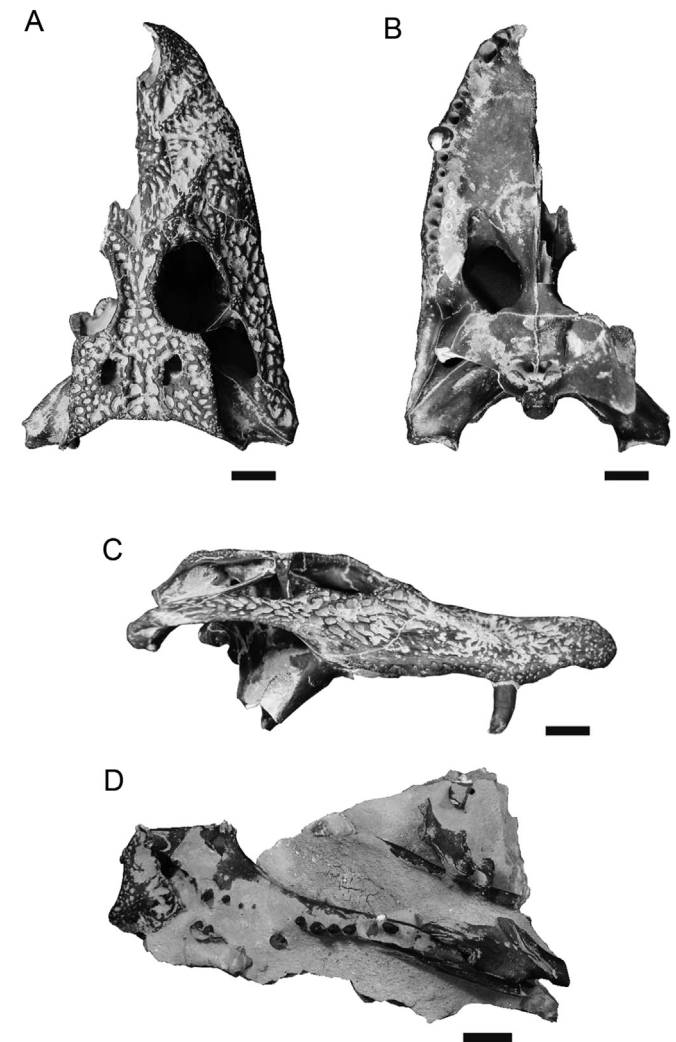


Fig. 5. Partial skull and lower jaws of *Caiman* from Gruta do Ioiô. LPRP/USP 0705, (A–C), partial skull in dorsal, ventral, and lateral views, respectively; (D) left mandible/premaxilla in occlusal/lateral views, respectively. Scale bars = 20 mm.

deposits (see Fortier and Rincón, 2013 for a revision). This is particularly the case in northeastern Brazil, where they are limited to fragmentary remains. This demands a more thorough comparative analysis of the specimens, which is provided below.

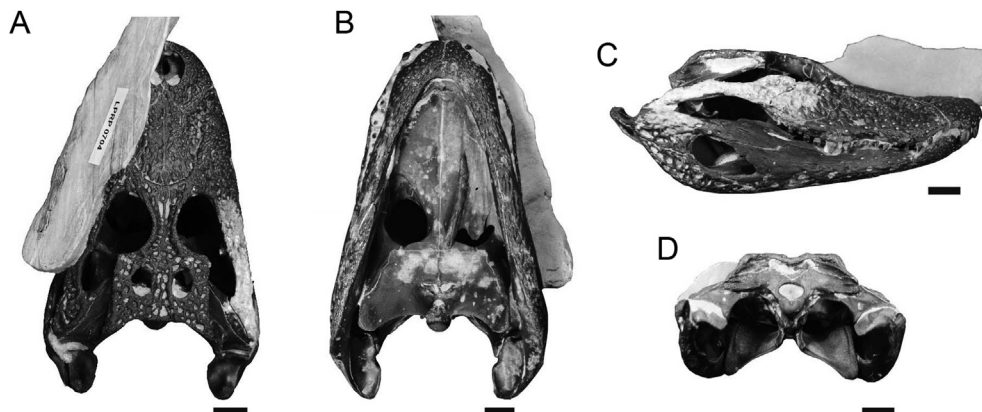


Fig. 4. Nearly complete skull and lower jaws of *Caiman* from Gruta do Ioiô. (A–D) LPRP/USP 0704 in dorsal, ventral, lateral, and occipital views, respectively. Scale bars = 20 mm.

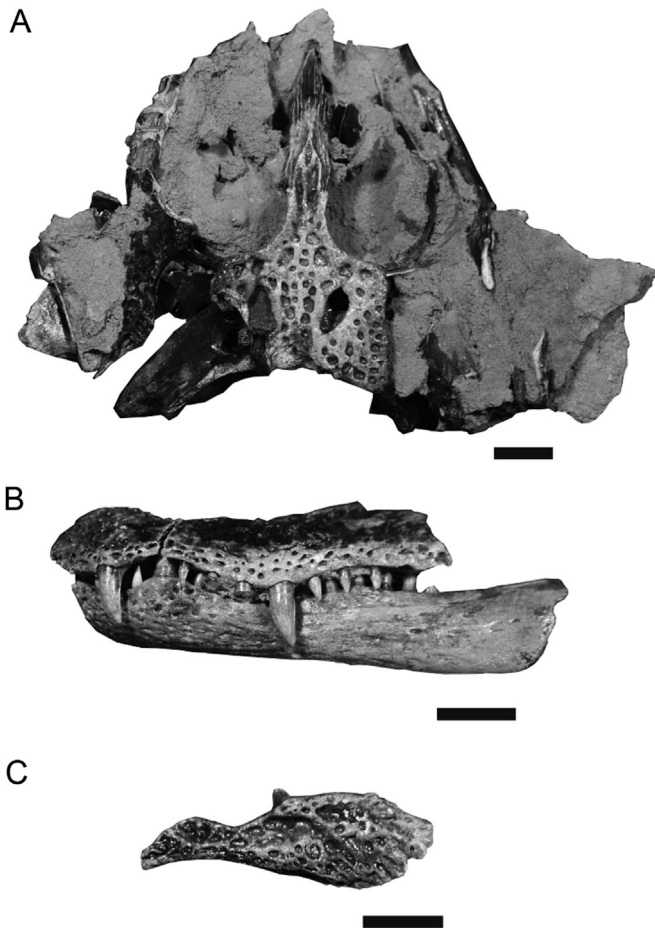


Fig. 6. Skull elements of *Caiman* from Gruta do Ioiô. LPRP/USP 0706, (A) semi-articulated skull roof in dorsal view; (B) partial rostrum and mandible in left lateral view; (C) right jugal in lateral view. Scale bars = 20 mm.

For topotypic reasons, all fossil crocodiles collected in Gruta do Ioiô are inferred to represent the same taxon, the taxonomic affinities of which will be fully explored elsewhere. Its nesting in Caimaninae is supported by all synapomorphies proposed for the clade: splenial excluded from the mandibular symphysis and passing dorsal to the Meckelian groove, angular-surangular suture extending broadly along the ventral margin of the external mandibular fenestra, parietal excluded from the edge of the skull table, and slender ventral exoccipital processes approaching the basioccipital tubera (Brochu, 1999, 2010, 2011; Hastings et al., 2013). The taxon can be referred to Crown-Group caimans based on the presence of the ectopterygoid-ptyergoid flexure and dermal bones of the skull roof overhanging the rim of supratemporal fenestrae (Brochu, 1999). Its placement within Jacarea (*sensu* Brochu, 1999) is suggested by the medially bowed lateral edge of the sub-orbital fenestra (Brochu, 1999, 2010, 2011). In addition, based on the presence of prominent rostral canthi (Brochu, 1999, 2010, 2011; Hastings et al., 2013; Pinheiro et al., 2013), we suggest a close affinity to the unnamed clade comprising the extant *Caiman latirostris* and *Melanosuchus niger*, as well as *Caiman lutescens* from the Miocene of Argentina and *C. cf. lutescens* from the Miocene of Colombia.

The remarkable broad snout of the caiman from Gruta do Ioiô resembles that of *Caiman latirostris*, *C. cf. lutescens* (UCMP 39978), and *Caiman gasparinae*. The former two might share a common ancestor (Pinheiro et al., 2013) or even represent the same taxon

(Gasparini, 1981; Langston and Gasparini, 1997; Bona et al., 2013; *contra* Brochu, 1999, 2010, 2011; Hastings et al., 2013; Pinheiro et al., 2013; see Bona et al., 2013 for a taxonomic revision of *C. lutescens*). In addition, unlike the condition in *Melanosuchus* (Medina, 1976; Brochu, 1999; Bona et al., 2013; Hastings et al., 2013), there is no palatal exposure of the vomer, and unlike the condition in *Caiman crocodilus* and *Caiman yacare* (Brochu, 1999), there is no occlusion pit between the 7th and 8th maxillary teeth. Also, a peculiar trait suggests a closer affinity of the Gruta do Ioiô caiman to the Colombian *C. cf. lutescens* (UCMP 39978; Langston, 1965). In both forms, the nasal bone enters the external nares via a stout spina, below the medial contact of the premaxillae, posterior to the external nares. The same feature is seen in some specimens of extant *Melanosuchus*, *C. yacare*, and *C. crocodilus*, but it is unknown to *C. latirostris* (Langston, 1965), even though the premaxillae contact one another posterior to the external nares in some specimens of that taxon (Bona and Desojo, 2011; Bona and Carabajal, 2013).

MAMMALIA

RODENTIA Bowdich, 1821

MYOCASTORIDAE Ameghino, 1904

Myocastor cf. Myocastor coypus Molina, 1782

Material

Partial skull, preserved from the anterior end to the frontoparietal suture, including the left zygomatic arch, right M2 and M3 (LPRP/USP 0709; Fig. 9A–B); partial skull preserving the anterior portion of the zygomatic arches and all teeth, both M3 recently erupted (LPRP/USP 0710; Fig. 9C); maxillae with both incisors and

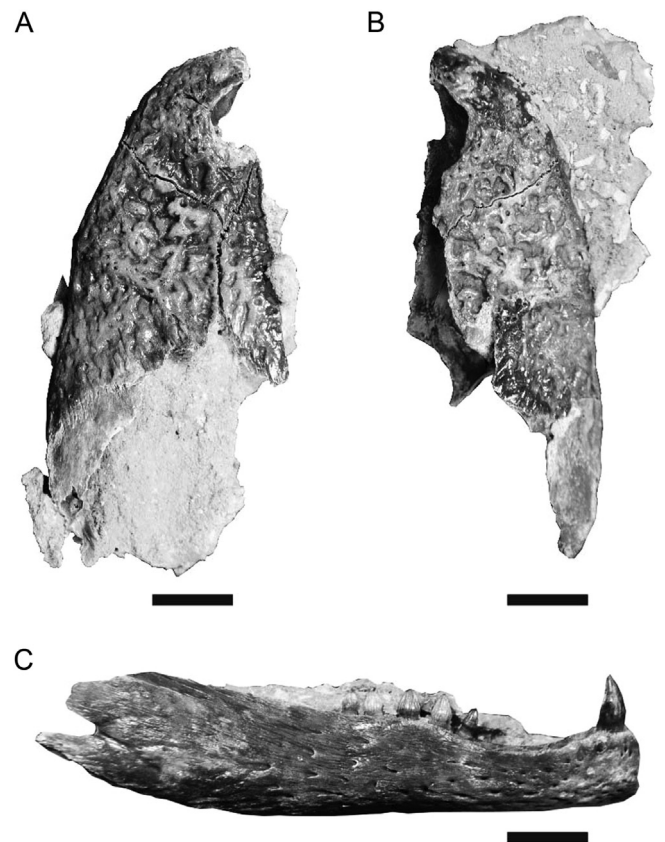


Fig. 7. Disarticulated skull elements of *Caiman* from Gruta do Ioiô. LPRP/USP 0707, (A) left partial portion of the skull in dorsal view; (B) right partial portion of the skull in dorsal view; (C) partial right mandible in lateral view. Scale bars = 20 mm.

base of right DP4–M2, partial left M2 and complete M3 (LPRP/USP 0711); incisor, six cheek teeth, and two unguis phalanxes (LPRP/USP 0712); two mandibular rami, the right one preserving the condyle and the cheek teeth (tooth row 35.1 mm long) and the left ramus bearing the symphysis and all the cheek teeth (LPRP/USP 0713; Fig. 9D); somewhat worn right mandibular ramus with no teeth (LPRP/USP 0714); partial humerus and partial right os innominatum (LPRP/USP 0715); partial ulna and radius (LPRP/USP 0716); partial radius lacking epiphyses (LPRP/USP 0717); partial sacrum, one thoracic, and seven caudal vertebrae (LPRP/USP 0718). Dental measurements are given in Table 1.

Table 1
Occlusal dental measurements (mm) of *Myocastor* cf. *M. coypus* from Gruta do Ioiô.

Tooth	Length	Width
I	–	6.0
DP4	6.4–6.6	6.2
M1	7.0	6.2–6.8
M2	8.0–8.4	6.6–8.2
M3	3.5 ^a –8.9	4.5 ^a –7.5
dp4	7.1	7.2
m1	6.7	5.7
m2	9.0	7.1
m3	10.2–11.4	7.2

^a Recently erupted.

Comments

Myocastor is known from the late Miocene of Argentina (Mesopotamian; Candela and Noriega, 2004) to the recent. In the Pleistocene, it has been recognized in Argentina (Tonni and Fidalgo, 1978), Uruguay (Ubilla, 2004), Bolivia (Frailey et al., 1980), and Brazil (Rodrigues and Ferigolo, 2004; Kerber et al., 2011; Pereira et al., 2012), reaching as far north as Bahia (Cartelle and Lessa, 1989). This indicates a much wider distribution in the past, as *M. coypus* is currently restricted to wet environments of Argentina, Bolivia, Chile, Paraguay, Uruguay, and southern Brazil (Lessa et al., 2008).

SIGMODONTINAE Wagner, 1843
Holochilus sciureus Wagner, 1842

Material

Partial skull with incisors, right M2 and left M1–M3 (LPRP/USP 0719); skull partially covered by sediment with visible incisors and left M1–M3 (LPRP/USP 0720); partial skull with all teeth (LPRP/USP 0721; Fig. 9E–H); two left femora (LPRP/USP 0722). Measurements (mm): interorbital width 4.1–4.3; zygomatic width 18.5–19.0; estimated GSL 31–35; M1 (length/width) 2.2–2.5/1.5–2.1; M2 (length/width) 1.8–2.0/1.5–2.1; M3 (length/width) 1.7–1.8/1.4–1.7; length of the upper molar series 6.3–6.6.

Comments

Holochilus (the marsh rat) has semi-aquatic habits and is widely distributed in grasslands, savannas, and wetlands of South America nowadays (Barreto and García-Rangel, 2005). Although present in the north and west parts of Bahia (Bonvicino et al., 2008), it has never been recorded in the area of Gruta do Ioiô (Pereira and Geise, 2009). Fossils of *Holochilus* were recovered in the Pleistocene of Venezuela (*H. sciureus*), Bolivia (*Holochilus primigenus*), and Argentina (*Holochilus brasiliensis* and *Holochilus chacarius*) (see Pardiñas and Teta, 2011). In Brazil, the genus has been recognized in Lagoa Santa (Winge, 1888), Serra da Bodoquena (Salles et al., 2006), and Toca da Boa Vista (Parisi Dutra, 2012), from cave deposits generally dated as late Pleistocene–Holocene. *Holochilus sciureus*

differs from the other species of the genus by its smaller size and dental morphology (Barreto and García-Rangel, 2005; Pardiñas and Teta, 2011; Pardiñas et al., 2013), allowing the identification of the material presented here. The comparison with extant *H. sciureus* from Venezuela (Barreto and García-Rangel, 2005) revealed that the individuals from Gruta do Ioiô were slightly smaller.

CHIROPTERA Blumenbach, 1779
NATALIDAE Gray, 1866
Natalus cf. *Natalus macrourus* (Gervais, 1856)

Material

Almost complete skull with right P3–M3, and left M1–M3 (LPRP/USP 0723; Fig. 10A–C); partial skull with left M1 (LPRP/USP 0724); partial skull with left P3, M1–M3 (LPRP/USP 0725). Measurements (mm): GSL 15.9–16.3; zygomatic width 8.7; postorbital width 3.1–3.3; length of maxillary tooth row 6.4–6.9.

Comments

The taxonomy of the genus *Natalus* has been recently revised. Tejedor (2011) proposed that populations occurring south of the Amazon River in Brazil, Bolivia, and Paraguay represent a single species: *N. macrourus* (Brazilian funnel-eared bat; Garbino and Tejedor, 2012), the cranial anatomy and measurements of which (Taddei and Uieda, 2001; Tejedor, 2011; Rocha et al., 2013) agree with that of the specimens from Gruta do Ioiô. *N. macrourus* has been recorded in all Brazilian biomes, frequently associated with humid caves that contain open bodies of water. In Bahia, it is found in the south and along a central belt, including the Chapada Diamantina area (Taddei and Uieda, 2001; Sbragia and Cardoso, 2008; Tejedor, 2011). Fossils of *N. macrourus* were reported in the Quaternary of Minas Gerais (Winge, 1893), Goiás (Fracasso and Salles, 2005), and Bahia (Czaplewski and Cartelle, 1998).

PHYLLOSTOMIDAE Gray, 1825
Tonatia bidens (Spix, 1823)

Material

almost complete skull (lacking mastoid area and anterior tip of rostrum) with right P4 and M3, and left P4–M3 (LPRP/USP 0726; Fig. 10D–F). Measurements (mm): estimated GSL 28.0; zygomatic width 14.0; postorbital width 6.2; estimated length of maxillary tooth row 8.6.

Comments

Molecular phylogenies restricted the diversity of *Tonatia* to two species: *T. bidens* and *Tonatia saurophila* (Lee et al., 2002; Porter et al., 2003). Cranial traits distinguish both species, and the morphology and measurements of LPRP/USP 0726 agrees with *T. bidens* (Williams et al., 1995). This species is currently distributed in various biomes from northeastern Brazil to Paraguay and north Argentina, and Rio São Francisco, Bahia, is its type locality (Williams et al., 1995). Although present in a cave in southern Bahia (Faria et al., 2006), it was never recorded in Chapada Diamantina National Park (Sbragia and Cardoso, 2008). Fossils of *T. bidens* were recovered in the Quaternary of Minas Gerais (Winge, 1893), Bahia (Czaplewski and Cartelle, 1998), and Piauí (Guerin et al., 1999).

Trachops cirrhosus (Spix, 1823)

Material

Almost complete skull with the base covered by sediments, preserving the P2 and part of M2 on the right side (LPRP/USP 0727; Fig. 10G–H). Measurements (mm): GSL 27.4; estimated zygomatic width 15.0; postorbital width 4.8.

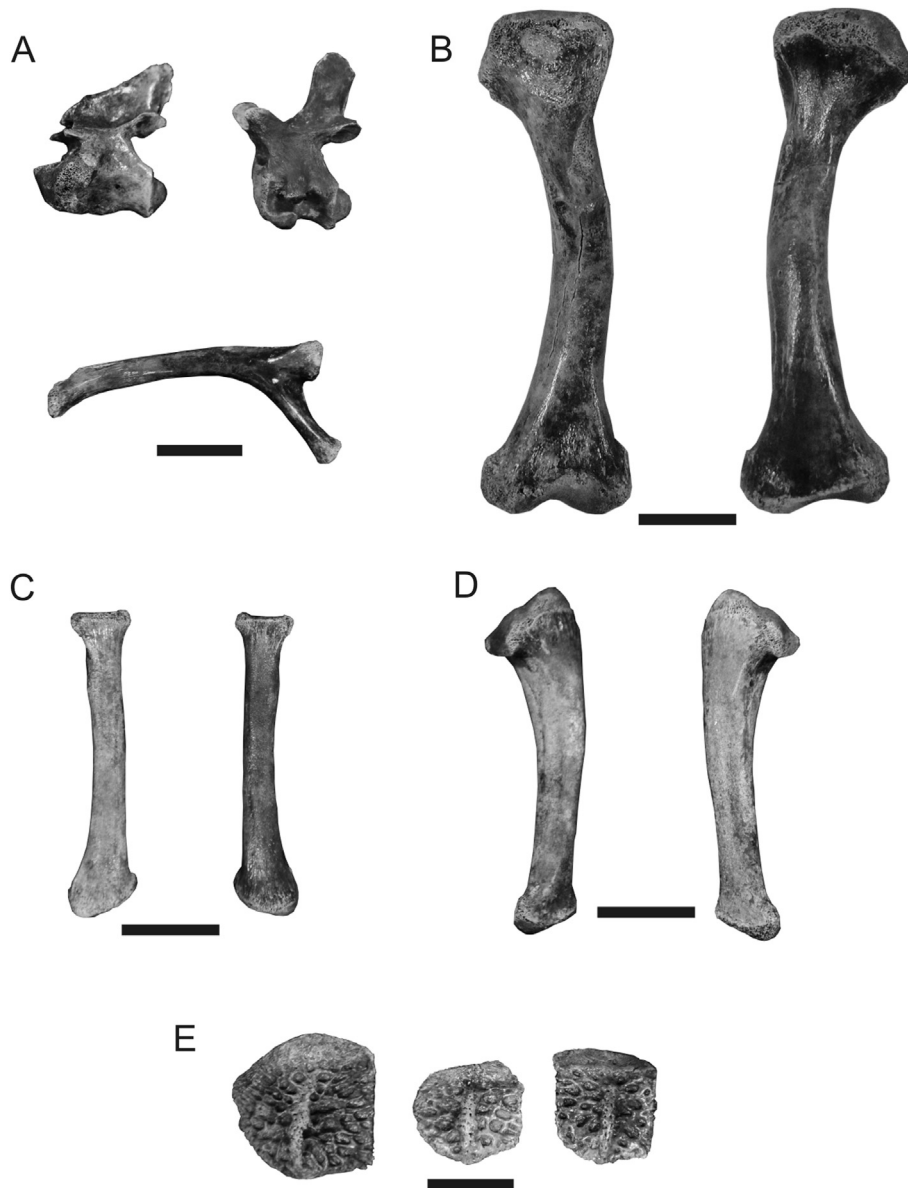


Fig. 8. Postcranial elements of *Caiman* from Gruta do Ioiô. LPRP/USP 0708, (A) axis, cervical vertebra, and cervical rib in right lateral, right lateral, and medial views, respectively; (B) left humerus in anterior and posterior views; (C) left and right radius in posterior view; (D) left and right ulna in lateral view; (E) disarticulated cervical and dorsal osteoderms in dorsal view. Scale bars = 20 mm.

Comments

The monotypic genus *Trachops* (fringe-lipped bat) has an elongated skull, with a well-developed sagittal crest, large rounded braincase, small I2, and straight zygomatic arches (Cramer et al., 2001). The taxon is currently distributed from southern Mexico to southern Brazil, including areas of Ecuador, Colombia, and Bolivia, usually at lower elevations (Simmons, 2005). It is strongly associated with tropical forests, also occurring in dry deciduous forests near moist habitats. Colonies are small and tend to roost in caves (Miller et al., 2008). *T. cirrhosus* is common in all Brazilian biomes, including Caatinga close to rocky outcrops (Willig, 1983; Marinho-Filho and Sazima, 1998). It forages over streams, ponds, or other wet areas (Einsenberg, 1989), preying mainly on insects and small vertebrates (Tuttle et al., 1982; Rodrigues et al., 2004). Fossils of *T. cirrhosus* are only known for the late Quaternary of Tobago (Eshelman and Morgan, 1985) and for the late Pleistocene of Venezuela (Czaplewski et al., 2005).

CARNIVORA Bowdich, 1821

MUSTELIDAE Fischer von Waldheim, 1817

Eira cf. *Eira barbara* Linnaeus, 1758

Material

Partial skull with superficial incrustation, lacking from the maxillae to the anterior extremity (LPRP/USP 0728; Fig. 11). Measurements (mm): interorbital constriction 27.0; maximum width of the skull 48.5; width of occipital condyles 23.5; maximum length of preserved portion 95.9; estimated GSL 104.

Comments

At present, *E. barbara* (tayra) occurs in tropical and subtropical forests from Mexico to southern Brazil, but not in the Caatinga area of northeast Brazil, where Gruta do Ioiô is located (see map in Presley, 2000), and is the most common medium-sized predator throughout much of its range (Emmons and Freer, 1990). In Brazil,

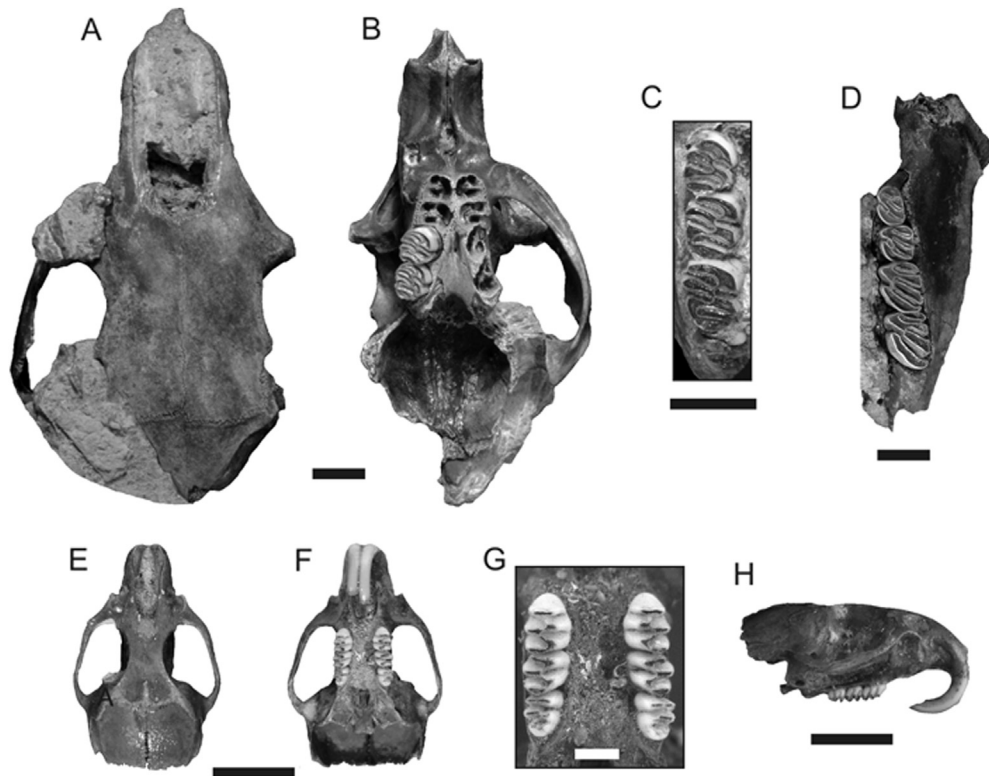


Fig. 9. Rodents from Gruta do Ioiô, *Myocastor* cf. *Myocastor coypus* (A–D) and *Holochilus sciureus* (E–H). (A–B), partial skull LPRP/USP 0709 in dorsal and ventral views, respectively; (C) right upper tooth row of LPRP/USP 0710; (D) left mandibular ramus of LPRP/USP 0713; (E–F), partial skull LPRP/USP 0721 in dorsal and ventral views, detail of upper dentition, and lateral view, respectively. All scale bars = 10 mm, except for (G), which scale bar = 2 mm.

fossils of *Eira* were previously recovered in Bahia (a skull and a mandible; Lessa et al., 1998), Minas Gerais (Lund, 1843), and Ceará (Gomide, 1989). With partially webbed feet, tayras have been reported swimming across ponds and rivers (see Presley, 2000; Bezerra et al., 2009).

Other than the taxa mentioned above, an avian tibiotarsus (provisionally attributed to a charadriiform or passeriform) and three partial frog humeri have been recovered from the deposits. Toads, in particular, are very abundant in the present fauna of the entrance of the cave. The faunal list of Gruta do Ioiô, composed of eight genera

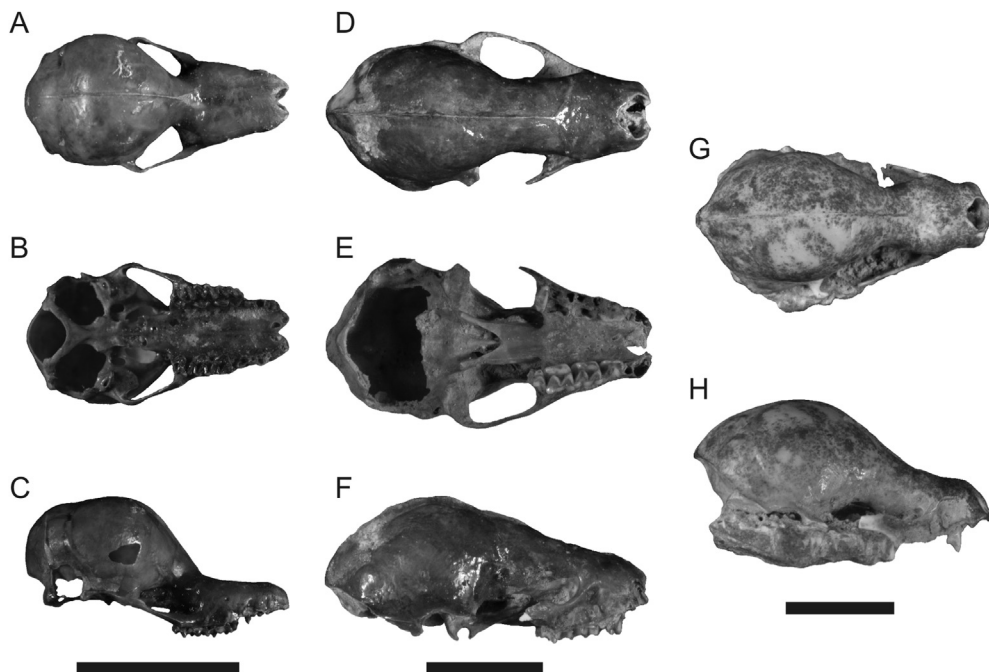


Fig. 10. Bats from Gruta do Ioiô, *Natalus* cf. *N. macrourus* (A–C), *Tonatia bidens* (D–F), and *Trachops cirrhosus* (G–H). (A–C) LPRP/USP 0723 in dorsal, ventral, and lateral views; (D–F) LPRP/USP 0726 in dorsal, ventral, and lateral views; (G–H) LPRP/USP 0727 in dorsal and lateral views. Scale bars = 10 mm.

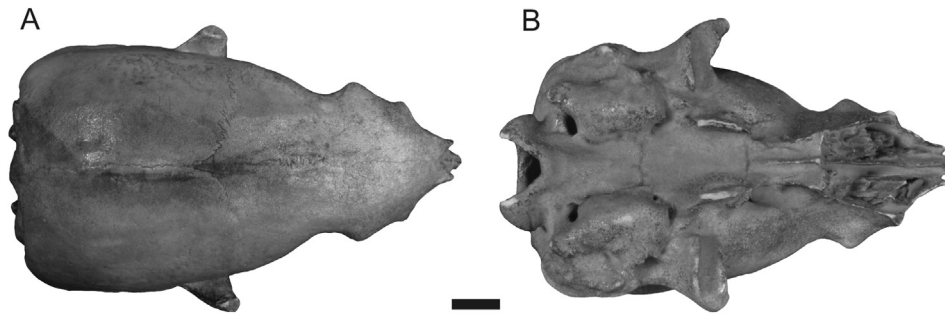


Fig. 11. Partial skull of *Eira* cf. *Eira barbara* from Gruta do Ioiô. (A–B) LPRP/USP 0728 in dorsal and ventral views, respectively. Scale bar = 10 mm.

(Table 2), is lower in diversity relative to other Brazilian caves (e.g., Auler et al., 2006; Castro and Langer, 2011). The caimans are surely the uncommon element in the fauna of Gruta do Ioiô, due to the scarcity of crocodiles in South American Quaternary deposits (Fortier and Rincón, 2013). The record of the catfish *Rhamdia* is also relevant, as only fragmentary remains of this taxon were previously reported. On the other hand, all mammal taxa but for *T. cirrhosus* were already recorded in Quaternary localities of northeastern Brazil, including the caves of Bahia (Cartelle and Lessa, 1989; Czaplewski and Cartelle, 1998; Lessa et al., 1998; Parisi Dutra, 2012). Except for *N. macrourus* and *T. cirrhosus* (Cramer et al., 2001; Sbragia and Cardoso, 2008), these are absent in the present local fauna. Also, none of the bats identified here are present in the faunal list of a recent paper on bat humeral remains from Ioiô-Impossível cave system (Salles et al., 2014). *Holochilus*, *Tonatia*, and *Eira* are found in other areas of Bahia (Presley, 2000; Faria et al., 2006; Bonvicino et al., 2008), but *Myocastor* is restricted to southern Brazil (Lessa et al., 2008). These shifts in the

taxon distribution suggest the occurrence of climatic changes in the area of Gruta do Ioiô during the Quaternary, as discussed below.

3.2. Taphonomic aspects

Taphonomic analyses revealed that bone accumulations of most Brazilian caves are reworked by floods, which destroy the stratigraphic stacking and mix the horizons (Auler et al., 2006, 2009; Ghilardi et al., 2011). The floods may be caused by the raise of the phreatic level and/or by the entrance of rain runoffs (Auler and Smart, 2001). In deposits where high-energy runoffs strongly control the accumulation, the sediments are poorly sorted, with the presence of large clasts, and most fossil elements are fragmented due to transport and reworking (Lino et al., 1979; Barros Barreto et al., 1982; Castro and Langer, 2011).

In the case of Gruta do Ioiô, taphonomic signatures and the nature of the fossiliferous site (subaquatic and distant from the cave entrance) suggest that external influence was minimal in the accumulation process. Large clasts are absent and the specimens are disarticulated, but rarely fragmented. This indicates a low-energy internal hydraulic dynamic, probably associated to variations in the water table level. Several skulls are preserved, demonstrating the presence of elements that tend to resist transportation (Voorhies, 1969). These data indicate that the fossil assemblage of Gruta do Ioiô is autochthonous, i.e., composed of taxa that lived inside or nearby the cave, including the swamp that (at least currently) surrounds its entrance. Thus, the animals probably entered the cave by their own means ('autopod mechanism' of Vrba, 1976) and died subsequently, or died by/in the pond and their carcasses floated into the cave, possibly along with water influx during strong rain events. The taphonomic analyses presented by Salles et al. (2014) indicate that other modes of accumulation also occur in the cave complex.

3.3. Age

Tested samples from Gruta do Ioiô were devoid of collagen, the most common source for radiocarbon dating, as the proteins probably decomposed rapidly under the hot and humid conditions of the site. Bioapatite, on the other hand, does not usually undergo microbiological decomposition. Cherkinsky et al. (2013), also dealing with fossils from northeastern Brazil, proposed a technique to separate diagenetic carbonates without destroying the bioapatite, and their results greatly agreed with other methods. Consequently, following the same protocol (see also Cherkinsky, 2009), the dental bioapatite of two samples from Gruta do Ioiô were radiocarbon dated in the Center for Applied Isotope Studies (CAIS) at the University of Georgia.

A *Caiman* tooth yielded a $18,260 \pm 50$ BP age, whereas a *Myocastor* incisor was dated as $16,900 \pm 50$ BP. Calibrated ages adopting IntCal09 (Reimer et al., 2009) are respectively 21,520–22,040 and

Table 2

Taxonomically identified specimens from Gruta do Ioiô.

LPRP/USP	Taxon	Material
0729	<i>Rhamdia</i>	Several skulls and postcranial elements
0704	<i>Caiman</i>	Nearly complete skull and jaw
0705	<i>Caiman</i>	Nearly complete skull and jaws
0706	<i>Caiman</i>	Partial skull, jaws, vertebrae, osteoderms, ribs
0707	<i>Caiman</i>	Partial skull and mandibular elements
0708	<i>Caiman</i>	Postcranial elements
0709	<i>Myocastor</i> cf. <i>M. coypus</i>	Partial skull with M2 and M3
0710	<i>Myocastor</i> cf. <i>M. coypus</i>	Partial skull with all teeth
0711	<i>Myocastor</i> cf. <i>M. coypus</i>	Maxillae with incisors and cheek teeth
0712	<i>Myocastor</i> cf. <i>M. coypus</i>	Incisor, cheek teeth, and ungual phalanxes
0713	<i>Myocastor</i> cf. <i>M. coypus</i>	Partial mandibular rami with cheek teeth
0714	<i>Myocastor</i> cf. <i>M. coypus</i>	Right mandibular ramus with no teeth
0715	<i>Myocastor</i> cf. <i>M. coypus</i>	Partial humerus and os innominatum
0716	<i>Myocastor</i> cf. <i>M. coypus</i>	Partial ulna and radius
0717	<i>Myocastor</i> cf. <i>M. coypus</i>	Partial radius lacking epiphyses
0718	<i>Myocastor</i> cf. <i>M. coypus</i>	Partial sacrum and vertebrae
0719	<i>Holochilus sciureus</i>	Partial skull with incisors and cheek teeth
0720	<i>Holochilus sciureus</i>	Partial skull with incisors and left M1–M3
0721	<i>Holochilus sciureus</i>	Partial skull with all teeth
0722	<i>Holochilus sciureus</i>	Two left femora
0723	<i>Natalus</i> cf. <i>N. macrourus</i>	Nearly complete skull with right P3–M3 and left M1–M3
0724	<i>Natalus</i> cf. <i>N. macrourus</i>	Partial skull with left M1
0725	<i>Natalus</i> cf. <i>N. macrourus</i>	Partial skull with left P3, M1–M3
0726	<i>Tonatia bidens</i>	Nearly complete skull with right P4 and M3, and left P4–M3
0727	<i>Trachops cirrhosus</i>	Nearly complete skull with right P2 and M2
0728	<i>Eira</i> cf. <i>E. barbara</i>	Partial skull lacking the anterior extremity

19,980–20,250 cal BP. Both materials have a late Pleistocene age (Lujanian *sensu* Cione and Tonni, 2005), within the Last Glacial Maximum (ca. 24,000–15,000 cal BP). Conversely, AMS radiocarbon dating of a *Nothrotherium* specimen collected in the same cave system indicated a Holocene age (8700 ± 50 BP; Salles et al., 2014). As illustrated by the broad range of dates reported for mammalian faunas of northeastern Brazil (Auler et al., 2006), time averaging is extremely common in cave deposits. Thus, the older age found here is taken as a minimal age for the beginning of the accumulation in Gruta do Ioiô.

3.4. Environmental aspects

Previous studies indicate that the environmental conditions of northeastern Brazil during the late Pleistocene, including the Last Glacial Maximum, greatly diverged from the present semi-arid Caatinga (Auler et al., 2004; Wang et al., 2004). The presence of an extinct bear (*Arctotherium brasiliense*; Cartelle, 1998) and a large monkey (*Caipora bambuorum*; Cartelle and Hartwig, 1996) suggest a cooler and wetter environment, based on the distribution of their living relatives. The fossil chiroptero-fauna from other deposits in Bahia (including a radiocarbon dated material of 24,000 cal BP) also support this pattern, as many taxa currently occupy moister habitats or humid caves (Czaplewski and Cartelle, 1998).

Geomorphological and paleoclimatological data indicate wetter conditions throughout much of the Pleistocene, specifically the late Pleistocene, in the presently semi-arid northeastern Brazil (Auler and Smart, 2001; Wang et al., 2004). Dever et al. (1987) inferred a wetter period between 26,000 and 20,000 cal BP based on the isotopic composition of carbonate soil concretions. Based on the flux of terrigenous material found in ocean cores from offshore northeastern Brazil, Arz et al. (1998) inferred episodes of increased precipitation/runoff during the Last Glacial Maximum. Wang et al. (2004) presented a 210-ky record of wet periods in northeastern Brazil based on speleothems and travertine deposits. Their analyses indicated that those periods, possibly generated by a southward displacement of the Intertropical Convergence Zone, were episodically punctuated within extended intervals of dry conditions. During these wetter periods, the Caatinga was replaced or mixed with a semi-deciduous forest, which is more compatible with some of the fossil elements recovered in the region, and may have connected the Amazon and the Atlantic rainforests (Auler et al., 2004; Wang et al., 2004).

The modes of life/distribution of taxa can be employed as qualitative palaeoenvironmental proxies (Auler et al., 2004), and this is the case of Gruta do Ioiô. The presence of *Myocastor* indicates the existence of perennial wet environments (Pereira et al., 2012), and its absence in the present Caatinga fauna indicates the establishment of dryer/warmer conditions. Because of their semi-aquatic habit, *Holochilus* and the caimans are also associated with mesic environments. Interestingly, remains of *Holochilus* have been found in stomach contents of caimans (Barreto and García-Rangel, 2005). The presence of *Eira*, which currently does not occupy the Caatinga biome, also indicates a humid forested environment. The bats (*N. macrourus*, *T. bidens*, and *T. cirrhosus*) and the abundant fish remains are uninformative in reconstructing the past conditions of the area, as the bat species are common in caves and eurytopic in modern biomes, while *Rhamdia*, both epigeal and hypogean species, exist in the area nowadays.

4. Conclusions

The crocodile and fish elements are the more unusual components in the fauna of Gruta do Ioiô, as most of the mammals were already reported for other Quaternary localities in northeastern

Brazil. The taphonomic signatures and the nature of the fossiliferous site indicate that the recovered taxa lived inside or by the cave, what might explain the comparatively low diversity of the deposit. Various taxa (*Myocastor*, *Holochilus*, *Tonatia*, *Trachops*, and *Eira*) are absent in the present local fauna, suggesting different environmental conditions in the past. Their modes of life are consistent with wetter settings, as implied by previous faunistic, geomorphological, and paleoclimatological data. The dental biopapatite of two samples yielded ages within the Last Glacial Maximum (ca. 24,000–15,000 cal BP), a presumably more humid period in the region.

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